Spatial ecology of white-clawed crayfish Austropotamobius pallipes and signal crayfish Pacifastacus leniusculus in upland rivers, Northern England

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This thesis is submitted in candidature for the degree of Doctor of Philosophy

Declaration

The material contained in this thesis has not previously been submitted for a degree at the University of Durham or any other university.

SPATIAL ECOLOGY OF WHITE-CLAWED CRAYFISH *AUSTROPOTAMOBIUS PALLIPES* AND SIGNAL CRAYFISH *PACIFASTACUS LENIUSCULUS* IN UPLAND RIVERS, NORTHERN ENGLAND.

Damian H. Bubb

The American signal crayfish *Pacifastacus leniusculus*, an invasive species widely introduced throughout Europe, is a major threat to native European crayfish species and is causing increasing concern because of its wide impact on aquatic ecosystems. This thesis investigates the within catchment expansion of signal crayfish populations in two upland rivers and the spatial ecology and movement of the introduced signal crayfish and the indigenous white-clawed crayfish *Austropotamobius pallipes*.

Populations of signal crayfish are established and expanding on the upland rivers Wharfe and Ure. On the Wharfe the signal crayfish population is well established and now occupies about 30 km of river and is currently expanding at a rate in excess of 2 km $year^{-1}$. On the Ure the signal crayfish population is younger and currently occupies 1.6 km and is currently expanding at about 0.5 km $year^{-1}$. The range expansion is biased towards downstream in both rivers, by a ratio of about 3:1 (downstream:upstream).

The movements and dispersal of white-clawed and signal crayfish was studied utilising a combination of radiotelemetry and internal and external Passive Integrated Transponder (PIT) tags.

Radiotagged adult signal crayfish were capable of substantial active movements (maximum movement 790m in 79 days). The level of movement of adults suggests they may have the potential to be responsible for the observed rates of population expansion. Although the movements of radiotagged adult signal crayfish within main river channel were equally distributed upstream and downstream, in-stream barriers both natural and artificial were found to limit the upstream movements of PIT tagged crayfish and this may contribute to the observed downstream bias of signal crayfish population expansion. The movements and dispersal of PIT tagged white-clawed crayfish within a small upland high gradient stream were strongly biased towards downstream.

Maximum movement of radiotagged adult signal crayfish occurred during midsummer. Temperature appeared to be a major factor influencing the timing and extent of movements between tracking periods although there was a large variation between individuals. All significant downstream movements made by crayfish were active movements and not the result of passive movement during periods of high discharge. There were no sex or size differences in the dispersal and movement of radiotagged and PIT tagged signal crayfish whilst in PIT tagged white-clawed crayfish size, sex, injuries and duration of tracking influenced extent of movement.

The expansion of the signal crayfish population in the River Wharfe appears to lead to the progressive loss of white-clawed crayfish populations where they come into direct contact. Limited differences in the microhabitat utilised by the two species were found where the species were syntopic, suggesting the potential exists for direct competition between the two species. In addition signal crayfish showed greater movement and dispersal than white-clawed crayfish. This may contribute to the ability of signal crayfish to colonise rivers rapidly and may also offer a competitive advantage over white-clawed crayfish thus contributing to the observed replacement.

The results are discussed in the context of the conservation and management of crayfish and the ecology of invasive species.

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CONTENTS

INTRODUCTION

This thesis investigates the spatial ecology and movement of the non-indigenous signal crayfish *Pacifastacus leniusculus* (Dana) and the indigenous white-clawed crayfish *Austropotamobius pallipes* (Lereboullet) and the within-catchment expansion of signal crayfish populations.

Freshwater crayfish because of their large size and high potential population densities are important trophic components of freshwater ecosystems (Lodge & Hill 1994, Momot 1995, Nyström 2002). Their loss or introduction to new habitats may have a significant impact on the aquatic environment (Matthews & Reynolds 1992, Nyström & Strand 1996). Due to human-mediated translocations the signal crayfish now has one of the widest geographical ranges of any crayfish species (Lewis 2002). Originating in North America, it is now found across Europe where there is increasing concern regarding its impact on the native crayfish fauna and the wider freshwater ecosystem.

Crayfish are large mobile invertebrates capable of making substantial active movements (Bohl 1999, Schütze et al. 1999, Gherardi & Barbaresi 2000). Knowledge of the spatial behaviour of crayfish is likely to be important in understanding the colonisation and expansion of populations and informing management strategies, for both the control of non-indigenous species and conservation of native species.

Previous studies of movement and colonisation by crayfish have been predominantly concerned with populations in lakes and lowland rivers (Abrahamsson 1981, Guan & Wiles 1997a, Kirjavainen & Westman 1999). Crayfish are also an important component of upland river ecosystems and their spatial behaviour under the more variable and rapidly changing conditions in upland rivers and streams is mostly unreported. This thesis therefore concentrates on the spatial behaviour of crayfish in upland rivers and streams. Fieldwork was conducted in the Rivers Wharfe and Ure, two upland rivers with relatively unmodified river channels in the north east of England. These rivers have historically contained extensive, abundant and widely distributed populations of white-clawed crayfish but both have expanding introduced signal crayfish populations.

Chapter 1 provides a general introduction to the impact and introduction of non-indigenous species with particular emphasis on the introduction of crayfish. It also

provides background information on the life cycle and ecology of signal and white-clawed crayfish to provide the context in which to interpret the following chapters.

In order to manage and protect indigenous crayfish species, it is imperative to have good knowledge of the distribution, abundance and expansion of crayfish populations. Whilst the distribution of introduced crayfish has been described on a national basis and in some cases on a more local scale, the within catchment expansion and rates of colonisation have received little attention. In Chapter 2 the expansion and distribution of the signal crayfish population in the Rivers Wharfe and Ure is documented and the distribution of white-clawed crayfish in the River Wharfe is described. Comparisons are made between the rates of upstream and downstream spread, and between populations of differing ages.

Chapter 3 reviews and summarises the current state of knowledge of the spatial behaviour of crayfish to provide the contextual understanding and background necessary for interpretation of the results and discussion presented in Chapters 4, 5 and 6. The study of the behaviour of free-living nocturnal animals in aquatic ecosystems presents numerous methodological difficulties. In Chapter 3 methods used for studying space use in crayfish are discussed and two novel techniques based on Passive Integrated Transponder (PIT) tag technology are developed. Passive Integrated Transponder technology has been quite widely used for studying spatial ecology in fishes but has received little use in aquatic invertebrate studies. The two methods developed in this study add to the range of previously available techniques and were used to address questions relating to spatial behaviour of crayfish investigated in Chapters 4 and 5.

In many groups of animals there is a strong sex and age bias in the animals that undertake the largest movements and disperse. The movement ability of different sexes and age classes and their comparative role in dispersal of signal crayfish populations is not well understood. In Chapter 4 the influence of size and sex on the movement and dispersal of signal crayfish was investigated. The use of externally attached large (23-mm) PIT tags (as developed in Chapter 3) enabled high numbers of repeat locations on a large number of individuals over a wide range of ages to be obtained.

Headwater streams appear to provide an important habitat for remaining populations of white-clawed crayfish, yet studies of the spatial behaviour of white-clawed crayfish in upland streams are limited. In addition most studies on the spatial behaviour of white-clawed crayfish have been limited to summer months when water temperatures are highest and crayfish most active. The use of internal PIT tags (as developed in Chapter 3) enabled the movement patterns of individual white-clawed crayfish to be investigated over an extended (>1 year) period of time. The pattern, extent and the influence of size and sex on movements within the population is investigated and discussed.

A thorough understanding of the spatial and temporal patterns of movement in signal crayfish is relevant to understanding their colonisation ability. Chapter 6 utilises radiotelemetry to investigate the movement patterns of adult signal crayfish. The seasonal pattern of movement, the relationship with environmental conditions and the influence of density on movement is studied. Signal crayfish are considered to be highly invasive species whilst white-clawed crayfish are generally considered to be non-invasive. The presence of syntopic white-clawed and signal crayfish in the River Wharfe and the use of radiotelemetry allowed the direct comparison of their spatial behaviour and habitat use. Differences in the spatial behaviour of the two species and the influence that this may have on interspecific competition are discussed in Chapter 6.

Overall the thesis provides detailed information on the expansion of signal crayfish populations and the spatial ecology of signal and white-clawed crayfish in upland rivers. Chapter 7 provides an overview of this study, the thesis is summarised and comparisons of the individual studies are made and interpreted more broadly. The importance of this research in the field of crayfish ecology and conservation and how it integrates more broadly are discussed and suggestions for further work are made.

CHAPTER 1. INTRODUCED SPECIES, LIFE-CYCLE AND ECOLOGY OF CRAYFISH

This chapter provides a general introduction to the impact and introduction of non-indigenous species with particular emphasis on the introduction of crayfish. It also provides background information on the lifecycle and ecology of signal and white-clawed crayfish.

1.1 Introduced species

The introduction of non-indigenous species has been recognised as second only to land use change as the most significant threat to global biodiversity (Walker & Steffen 1997, Lodge et al. 2000a, Sala et al. 2000). It has been argued that it may soon surpass habitat loss and fragmentation as the primary threat to biodiversity (Crooks & Soulé 1999). Humans have transported and moved organisms outside their natural range by a wide variety of means, both accidentally and deliberately. Most organisms die in transport or soon after release (Kolar & Lodge 2001). However those species that persist, become established and undergo population expansion can have major consequences, often resulting in significant loss in the economic value, biological diversity and function of invaded ecosystems. The economic impact of non-indigenous species is huge. In the United States alone economic losses from non-indigenous species are estimated at over $125 billion per year (Pimentel et al. 2000). The effects on native biodiversity and ecosystem function can be equally large (Sala et al. 2000). Species have been transported from their native ranges to new previously unoccupied areas for as long as humans have travelled over and between land-masses (Diamond 1998). However, the rate at which species have been introduced has increased dramatically in the last century (Wellcome 1988), apparently linked to increased human movement and transportation of products and goods.

Freshwater ecosystems are among the most invaded ecosystems in the world, especially in temperate regions, where invasions of non-indigenous organisms is still occurring at a high rate (Moyle 1999). The purposeful introduction of aquatic organisms, especially fish is common. The Food and Agriculture Organisation (FAO) Fisheries department maintains a database on introductions of aquatic species (http://www.fao.org/waicent/faoinfo/fishery/statist/fisoft/dias/mainpage.htm). This documents over 3000 international introductions of non-indigenous species into fresh waters across the globe, and is likely to only represent a small fraction of the true number of introductions as

many will be unrecorded. The impact of introduced aquatic species can be diverse and wide-ranging, including the displacement of native species (Moyle 1999), homogenisation of assemblages (Moyle & Randall 1998), erosion of genetic diversity (Beverage et al. 1994), impacts on native vegetation and structural and functional changes to food webs (Simon & Townsend 2003). Aquatic organisms have been introduced for a variety of reasons. Whilst fish and large invertebrates (including crayfish) have sometimes been accidentally introduced outside their normal range, purposeful introductions have been far more common (Lever 1994, Bartley & Subasinghe 1996). Reasons for these introductions include biocontrol, aquaculture, supplementing fisheries, use of bait and the release of pet and aquarium animals (Kolar & Lodge 2002, Ormerod 2003).

Invasion by non-indigenous species is a process consisting of several transitions, each with an independent probability of failure. Each sequential transition must be made by a species moving outside its natural range. To begin the invasion process a species must be entrained by a transport pathway. It must then survive transportation and introduction. After introduction the species must then establish a self-sustaining population in the invaded ecosystem. The final stage of a species invasion is usually the spread or dispersal of the invading species into the surrounding environment (Kolar & Lodge 2001). A species that invades but does not spread is unlikely to become as serious a problem as a species that rapidly expands its range (Kolar & Lodge 2002). Whilst some introduced species rapidly expand their range, others remain localised, dispersing only short distances from the site of introduction (Mooney & Drake 1989). The progressively smaller proportion of non-indigenous species which remain after each transition is the basis of Williamson's 'tens rule' (Williamson 1996). This suggests that 10% of non-indigenous species imported into a region appear in the wild, only 10% of these establish and 10% of the established species are invasive, thus 0.1% of imported species are invasive. The rule appears to fit for angiosperms and pines in the United Kingdom, and for some other groups in other parts of the world. However it does not appear to fit all animal groups (Williamson 1996) but does serve to illustrate that only a small proportion of introduced species will become established.

The prediction of which species are probable invaders has been of long-standing but increasing interest to ecologists (Elton 1958). Whether characteristics exist that predispose a species to become a successful invader has received increasing attention.

Initial attempts to describe such characteristics were of limited success (Drake et al. 1989, Williamson 1996). It has been suggested that this was partially due to searching for characteristics that apply generally to all taxonomic groups and all ecosystems. Recent work focussing on individual taxonomic groups and ecosystems (for review see Kolar & Lodge 2001) has been more successful. In addition there is increasing recognition that different characteristics may be important in different transitions in the invasion process (Kolar & Lodge 2001, 2002).

As a group, crayfish exemplify the impact which introductions can have and the threat to biodiversity that the translocations pose. The current distribution of crayfish across the world has been altered substantially through their movement by humans between and within continents. Of particular importance has been the movement of North American species to every continent with the exception of Australasia (Holdich 1999). The majority of introductions have involved red swamp crayfish *Procambarus clarkii* and signal crayfish *Pacifastacus leniusculus,* both of which originate from North America, and now have the widest geographical range of any crayfish species. Taylor (2002) estimates that between 30 and 50% of the world's crayfish are threatened with population decline or extinction. The factors causing these declines are varied and include habitat loss and degradation, pollution and over-harvesting (Taylor 2002). However, Taylor (2002) considers the greatest threat, and the one causing the most irreversible damage to crayfish biodiversity, is from the introduction of non-native crayfish and associated diseases and parasites. The introduction of non-native crayfish has had dramatic effects on the crayfish fauna of both North America and Europe (Lodge et al. 2000a,b). Endemic crayfish from both regions have suffered severe declines as a result of the introduction and movement of crayfish outside their natural range. In North America direct competition and displacement by introduced species has led to the loss of populations. In Europe the effects of disease carried by introduced crayfish has been most significant, with direct competition and displacement of secondary importance.

1.2 Crayfish distribution

1.2.1 Native crayfish in Britain and Europe

The native crayfish fauna of Europe (west of the Ural Mountains) is relatively impoverished, consisting of a single family, the Astacidae. Members of the family occur across continental Europe almost continually from the Urals west to the Iberian

Peninsula including Scandinavia and the British Isles (Hobbs 1988, Holdich 2002, Taylor 2002). The taxonomy of crayfish in Europe has been much debated, with five revisions of the taxonomic status of European crayfish in the last half century (Albrecht 1983, Hobbs 1988, Starobogatov 1995). The diversity of opinions ranges from five species, assigned to one genus (Albrecht 1983) to 19 species assigned to five genera (Starobogatov 1995). The main disagreements concern *Astacus leptodactylus* and *Austropotamobius pallipes* that appear to be species complexes. *A. leptodactylus* is a very plastic species from the morphological, ecological and physiological point of view (Holdich 2002) with little agreement as to its taxonomic status. The understanding of the *Austropotamobius pallipes* species complex has been improved by the application of various genetic techniques. The most recent review by Grandjean et al. (2002) suggested a new classification, based on morphologic, new genetic and distributional data. They identified two species *A. pallipes* and *A. italicus* with three subspecies *A. i. carinthiacus, A. i. carsicus* and *A. i. italicus*. The distribution of the proposed species is shown in Figure 1.1.

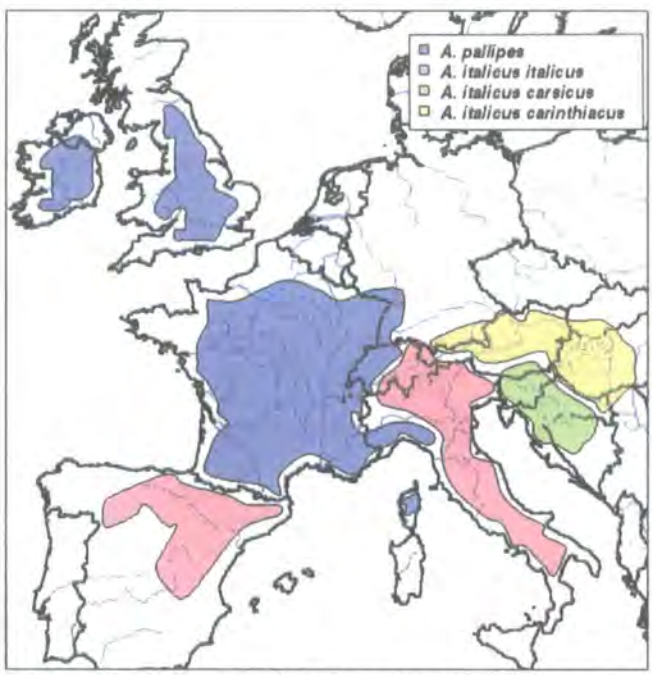


Figure 1.1 Geographic distribution of proposed species and subspecies within *Austropotamobius* genus (from Grandjean et al. 2002).

Since the late 1800s there has been a widespread decline across Europe of native crayfish, due to a combination of introduced crayfish species, the introduced crayfish plague fungus, *Aphanomyces astaci* carried by North American crayfish and habitat destruction and degradation (Henttonen & Huner 1999, Holdich et al. 1999, Skurdal et

al. 1999, Vogt 1999,). All species are now listed as 'vulnerable' on the 2003 IUCN red list of threatened species (http://www.redlist.org).

The British Isles has only one native species of crayfish, the white-clawed crayfish, *Austropotamobius pallipes* (Figure 1.2a). In the British Isles the white-clawed crayfish has a widespread, though patchy distribution across England, Wales and Ireland. It mainly inhabits clean, relatively hard, mineral-rich waters with a pH between 7 and 9 and calcium concentrations above 5 mg L^{-1} (Jay & Holdich 1981, Holdich et al. 1999). It is absent from areas where waters are acidic due to the underlying geology, such as Cornwall and large areas of Wales (Holdich et al. 1995). It is also absent from Scotland despite the presence of apparently suitable areas (Holdich et al. 1995) although an introduced population has existed at Loch Crispol in Northern Scotland since the 1940s (Maitland 1996). Populations of white-clawed crayfish occur in a wide range of habitats including lakes, reservoirs, water filled quarries, as well as rivers and streams.

The origins of white-clawed crayfish in the British Isles are unclear and a number of possibilities exist. Although white-clawed crayfish may naturally exist in Great Britain, having colonised from glacial relict populations or across land bridges that linked Britain to continental Europe, it appears increasing likely that their presence is due to historical introductions made by humans. Mitochondrial DNA analysis has shown relatively little divergence between English and Welsh populations, and a high level of similarity with populations from northern France (Grandjean et al. 1997a,b). Recent research using rapid amplification of polymorphic DNA (RAPD) markers have shown a higher level of diversity throughout all populations, but demonstrated a lack of genetic diversity between British and northern French populations (Souty-Grosset et al. 1999). They suggest that white-clawed crayfish in Great Britain exhibits relatively recent divergence from the mainland European stock and that this supports a hypothesis of origin through recent anthropogenic movements. The studies were based on analysis of a limited number of individuals and populations; it remains possible that white-clawed crayfish in the British Isles has diverse origins.

1.2.2 Non indigenous crayfish in Britain and Europe

The decline in Europe of native crayfish species from the 1800s onwards was one of the factors leading to attempts to replace and supplement native stocks with more productive and plague-resistant introduced species. Most introductions have been

intentionally made for aquaculture purposes, with additional introductions apparently made unintentionally through the release of unused bait or unwanted aquarium pets (Lodge et al. 2000a). Whilst introductions may have initially been made into contained ponds and lakes, crayfish are very difficult to contain and escapes have frequently occurred leading to the development of wild populations. There are currently five species of non-native crayfish known to be established with reproducing wild populations in Europe, yabby *Cherax destructor,* spinycheek crayfish *Orconectes limosus,* calico crayfish *Orconectes immunis,* signal crayfish *Pacifastacus leniusculus* and red-claw crayfish *Procambarus clarkii.* Of these, two species *Cherax destructor* and *Orconectes immunis* have very limited distributions in Spain and Germany respectively. The other species *Orconectes limosus, Pacifastacus leniusculus, Procambarus clarkii* are widespread across Europe.

In comparison with much of Europe the introduction of non-indigenous crayfish into the British Isles did not occur until relatively recently. However, since the 1970s a number of introductions of non-indigenous crayfish into Britain, primarily signal crayfish, have been made. Introductions have been made into England, Scotland and Wales whilst Ireland has remained free of non-indigenous crayfish species. Signal crayfish (Figure 1.2b) are widespread in England and there are large numbers of wild riverine populations (Holdich et al. 1995, Sibley et al. 2002). The introduction of signal crayfish into Britain followed publicity in the 1970s that claimed that crayfish farming was a lucrative business. Numerous introductions were made into England and Wales (Lowery & Holdich 1988, Holdich & Reeve 1991, Holdich et al. 1999). Most introductions were into enclosed fish farms or lakes. However, some were directly into the wild and many of the apparently enclosed populations subsequently escaped into the wild. Though not all introductions were successful, those that became established have led to the widespread distribution of signal crayfish, especially in southern England.

1.2.3 Crayfish plague

The impact of the introduction of North American crayfish species into Europe have been especially severe due to the effects of the crayfish plague fungus that has caused the loss of many populations of native European crayfish. This disease is caused by the oomycete *Aphanomyces astaci* Schikora and is commonly known as crayfish plague. It is believed to be endemic to North America; crayfish from this area are largely immune to the disease. Although North American crayfish are resistant to the fungus, they act as

hosts and transmission of crayfish plague from American to European species occurs. Crayfish plague is very virulent and lethal to all European species. It can cause 100% mortality within infected populations and the whole catchment is at risk of infection. Different genotypes of the crayfish plague fungus have repeatedly been introduced into Europe with their natural American host species (Vogt 1999). As well as by their primary host (American crayfish species), zoospores can be transmitted to other waters by a number of means including damp mud and fish (Holdich et al. 1995). Zoospores can re-encyst several times if they do not find an appropriate host, however they only remain infective for a limited time and to persist the plague fungus requires crayfish. This results in the disease dying out if all infected crayfish die and has allowed the successful restocking of areas that were infected with crayfish plague.

The first instance of crayfish plague in Europe is believed to have occurred in the Po valley of Italy in the early 1860s (Alderman & Polelase 1988). Subsequently in the late nineteenth and early twentieth centuries crayfish plague spread and infected areas of northern Italy, France, Germany, the Netherlands, Belgium, Romania, Russia, Finland and Sweden. Today almost all countries in Europe have been infected, including Britain and Ireland. Crayfish plague was relatively late in affecting Britain, although since the 1980s numerous rivers and lakes have been infected causing widespread mortalities. There is no clear pattern to the outbreaks although the majority have been found in areas where there are signal crayfish farms (Alderman & Polelase 1988, Holdich *et al.* 1995). It is unclear if all populations of introduced North American crayfish are carriers of crayfish plague. In most instances where introduced North American crayfish come into contact with native European crayfish the native crayfish are eliminated by crayfish plague. However in some limited instances North American crayfish have formed syntopic populations with European species without any apparent transmission of crayfish plague (Söderbäck 1991, Holdich et al. 1995, Holdich & Domaniewski 1995).

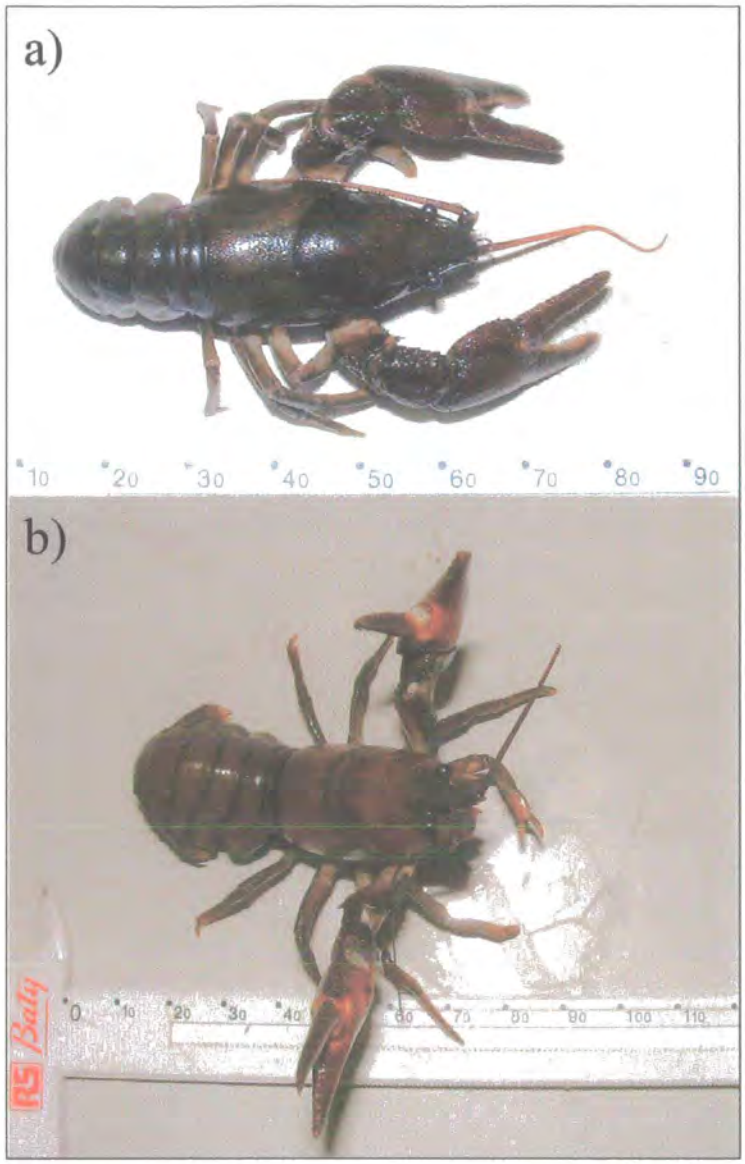


Figure 1.2 a) Adult male white-clawed crayfish *Austropotamobius pallipes* and b) adult female signal crayfish *Pacifastacus leniusculus* in threat posture with chelae raised. Scale on vernier callipers shows measurement in millimetres. The two species can be easily distinguished as adults by body shape, colour and markings. As juveniles the two species can be reliably distinguished by examination of rostrum and body. White-clawed crayfish have prominent spines on the shoulder of the carapace, just behind cervical grove these are lacking on signal crayfish. The rostrum of white-clawed crayfish has smooth sides, converging towards base of small triangular apex whilst in signal crayfish the sides of the rostrum are more or less parallel, the apex is prominent with sides sloping down to prominent shoulders (for more details see *A guide to identifying freshwater crayfish in Britain and Ireland, Anon, National Rivers Authority*).

1.3 Crayfish biology, ecology and life history

Freshwater crayfish, Astacida, belong to the crustacean taxon, the Decapoda. They have a body plan typical of higher crustaceans (Malacostraca) and characteristically possess

five pairs of walking legs; one pair being robust claws or chelae. Development is direct and all the larval stages are embryonised, although the first instar lacks uropods. As adults they vary considerably in size from species a few centimetres in length to the giant *Astacopsis gouldi* of Tasmania that can weigh up to 4.5 kg and is the largest freshwater invertebrate worldwide (Lowery 1988). All crayfish primarily inhabit freshwater environments, however some species can live out of water for long periods, and others inhabit partially saline environments. Within crayfish there is great ecological diversity represented. Crayfish occur as obligate cavernicoles, primary burrowers, stream, pond, lake, swamp and estuarine dwellers. Many of the burrowing species have become virtually terrestrial; they are able to survive out of water for long periods within burrows as long as the air within burrows is sufficiently humid to keep their gill chambers moist (Holdich & Reeve 1988). Both white-clawed and signal crayfish are primarily limited to freshwater environments.

1.3.1 Life cycle of white-clawed and signal crayfish

The growth of white-clawed crayfish progresses, like that of all crustaceans, through a series of moults, during which animals increase in size. Hatching of eggs occurs in late spring and early summer in Britain, the timing depending on the temperature (Lowery 1988). Following hatching, the young are carried by the female for about three moults. During this time they are protected under the tail of the female and are reliant on their yolk mass for food. After about three moults (several weeks to a month after hatching), the juveniles become independent and during their first summer they undergo seven or eight moults. Growth does not occur during the winter, when the temperature declines, but continues in the spring when temperatures increase. The number of moults in subsequent years decreases as the size of animals increase (Pratten 1980). Adult males generally moult twice each year, although the largest males may only moult once. Females that bear eggs moult only once, in autumn (Brown & Bowler 1977). Maturity is reached when carapace length is about 22 mm (Holdich 1991). This is usually between their third and fourth year in southern England (Pratten 1980), but may occur later in more northerly populations (Brewis & Bowler 1982). At maturity the chelae of males increase in size in relation to the carapace, and the tails of females become wider.

The timing of mating varies between years and areas in Britain but generally does not start until mid to late October, although it may be later in northern England (Brown & Bowler 1977). The differences are possibly the result of differences in temperature and

growing seasons between sites and years. During mating the male deposits a spermatophore on the ventral surface of the female. The eggs are laid shortly after and are fertilised externally by sperm released from the spermatophore. The eggs form an egg mass and become attached to the pleopods by an adhesive secretion (Lowery 1988). The number of eggs carried by females varies, with between 20 and 150 commonly being recorded (Brewis & Bowler 1985, Holdich 1991). The variation is partially due to egg loss that occurs during incubation but also to different numbers of eggs being produced by different individuals; generally larger females produce more eggs (Rhodes & Holdich 1982, Brewis & Bowler 1985).

Table 1.1 Comparative life histories of *Pacifastacus leniusculus* and *Austropotamobius pallipes* held at the same ambient temperature (from Holdich et al. 1995)

Month	*P. leniusculus*	*A. pallipes*
09	Mating, Egg laying	↓
10	↓	Mating, Egg laying
11	↓	↓
12	↓	↓
Year 1	↓	↓
01	Overwintering berried females	Overwintering berried females
02	↓	↓
03	↓	↓
04	↓	↓
05	Hatching	↓
06	↓	Hatching
07	↓	↓
08	8+ moults*	5-7 moults*
09	↓	↓
10	↓	↓
11	↓	↓
12	Overwintering juveniles	Overwintering juveniles
	↓	↓
Year 2	Summerlings (46 mm TL)	Summerlings (24 mm TL)
	↓	↓
Year 3	Sexual maturity (80 mm TL)	↓
	↓	↓
Year 4	120-125 mm TL	Sexual maturity (50-60mm TL)

TL – total length. Juveniles released several weeks to a month after hatching.

The breeding biology of signal crayfish is similar to that of white-clawed crayfish, although the timing is somewhat different. Breeding in signal crayfish commences earlier, it has been recorded in late September (Holdich et al. 1995, Guan & Wiles 1999). The earlier mating results in earlier hatching with the release of juveniles occurring in April and May. The number of eggs carried by signal crayfish also differs. An average of 150 eggs are carried by signal crayfish females compared with an average of 20 carried by female white-clawed crayfish (Lowery 1988). The growth rate of signal crayfish is also greater. Individuals attain maturity faster and mature individuals grow to a greater size compared to white-clawed crayfish (Lowery 1988). Both signal crayfish and white-clawed crayfish believed to be relatively long lived although the aging of crayfish is problematic especially when older crayfish are considered as all hard parts bearing seasonally induced growth rings are not retained through moult. A recent approach based on lipofuscin, a neuronal age pigment has been used successfully to estimate ages of adult crayfish. The analysis extended the known longevity of signal crayfish to approximately 16 years (Belchier et al. 1998) a similar longevity of white-clawed crayfish might be expected although this requires investigation.

1.3.2 Ecology

Freshwater crayfish, because of their size and population density are important trophic components of freshwater ecosystems. In most of Europe they are the largest mobile freshwater invertebrates, and where they occur they commonly dominate the biomass of benthic organisms (Momot 1995, Nyström 2002). Crayfish do not fit easily into the classic trophic level concept. They are ecologically important at three different levels, simultaneously acting as herbivores, detritivores and predators. They may also be important prey for many organisms (Hogger 1988). The loss of crayfish populations or their introduction to new habitats may have a significant impact on the aquatic ecosystem (Matthews & Reynolds 1992, Nyström & Strand 1996).

Crayfish are omnivores, simultaneously consuming a wide variety of material (Hogger 1988, Guan & Wiles 1998). Whilst detritus, macrophytes and algae may constitute a large proportion of the diet, the growth of crayfish appears to be proportional to the relative protein content of their diet (Momot 1995, Parkyn et al. 2001). The importance

of protein for rapid growth partly explains the higher proportion of animal food found in the diets of juvenile crayfish. The presence of food limitation on crayfish populations has received relatively little investigation. There are indications that food availability and competition for food is a limiting factor in some populations (Lodge & Hill 1994). In most environments when crayfish are first introduced, the growth rates of individuals are usually high. As the population increases, the individual growth rate usually declines. This may be the result of food limitation, but it is difficult to distinguish between food limitation and other factors that change simultaneously with increased population density, such as competition for refuges.

Cannibalism by crayfish appears to be widespread (Holdich et al. 1995, Momot 1995, Guan & Wiles 1998). In laboratory populations losses of crayfish by cannibalism can be high. Juveniles and smaller age classes are particularly affected, but all crayfish when undergoing moult are vulnerable. In laboratory tanks, the availability of adequate shelter can influence the prevalence of cannibalism. The remains of crayfish are often found in the stomachs of wild crayfish (Guan & Wiles 1998) suggesting cannibalism may be important in the natural environment, and crayfish have been observed consuming conspecifics (Holdich et al. 1995). However the extent of cannibalism and its role in population regulation requires investigation.

Crayfish have been shown to have substantial negative effects on aquatic macrophytes (Matthews & Reynolds 1992, Creed 1994, Lodge et al. 1994, for review see Nyström 1999). The reduction of macrophyte biomass is not only due to direct consumption but also non-consumptive cutting of stems (Lodge et al. 1994). Aquatic macrophytes are an important component of freshwater ecosystems, influencing abiotic factors (e.g. water oxygenation, flow) and biotic interactions within the ecosystem. Reductions in macrophyte biomass caused by crayfish are likely to have negative effects on invertebrate diversity and abundance (Nyström et al. 1996) and to modify the functioning of the aquatic ecosystem. As well as indirect effects on invertebrates, through the consumption and reduction of macrophytes, crayfish may directly impact on invertebrates. Freshwater macroinvertebrates are an important food source for crayfish (Momot 1995, Guan & Wiles 1998). Many studies have shown a strong negative impact of crayfish on populations of aquatic snails (for review Nyström 1999). The effects of crayfish appear greatest on less mobile invertebrates such as snails. Studies have shown that in environments with high crayfish density there may be a change in species

composition of macroinvertebrates towards active and sediment-burrowing taxa that are not dependent on macrophytes (Abrahamsson 1965, Matthews & Reynolds 1992, Nyström 1999).

The effects of crayfish on vertebrates are less well documented. Crayfish can potentially have negative effects on fish and amphibians through direct predation and predation of eggs and larvae, but also through competition for food and shelter and by destroying breeding sites (i.e. macrophyte reduction). Guan & Wiles (1997a) found a negative relationship between fish density and crayfish density for signal crayfish and benthic fishes. Laboratory experiments suggested that the reduction in fish density might have been caused by direct predation but also by displacement from shelters. The eviction of fish from shelters by crayfish may increase their susceptibility to predation by crayfish, and other species especially birds, mammals and fish (Rahel & Stein 1988). Similarly, the reduction of cover (macrophytes) by crayfish may indirectly affect fish assemblages and abundance through increasing their vulnerability to predation. Although the ability of crayfish to capture swimming fish may be limited they may directly affect fish populations through the consumption of their eggs and larvae. Laboratory experiments have shown crayfish to be capable of consuming eggs (Miller et al. 1992), however field studies have not demonstrated a significant impact (Savino & Miller 1991). The spread of crayfish into new habitats can have negative effects on amphibian populations (Gamradt & Kats 1996, Nyström 1999) principally through decreased egg and larval survivorship (Kats & Ferrer 2003).

There is an association between substratum type and crayfish abundance for most temperate crayfish species. Refuges are a critical resource for crayfish survival (Gherardi 2002). Their availability is considered by Hobbs (1976) to be the 'principle resource bottleneck' in crayfish populations. Crayfish density increases with increasing particle size of sediment (Foster 1995). Crayfish are most abundant in areas of refuge-providing substrate (Lodge & Hill 1994, Capelli & Magnuson 1983). Whilst substrate may be an important factor, crayfish have the ability to modify the habitat by burrowing and so not rely on 'natural' refuges. Burrowing has been reported for both white-clawed and signal crayfish (Huxley 1880, Guan 1994), although it appears more widespread in signal crayfish. The density of burrows reported from signal crayfish populations can be as high as 5 m^{-2} (Guan 1994) representing significant habitat modification and provision of shelters. Nevertheless successful burrowing is only possible in certain substrata. In

the River Great Ouse signal crayfish burrows were concentrated in podzolic soils and none was found in banks that were predominantly gravel and sand (Guan 1994). The importance of refuges and complex substrata appears to be related to the avoidance of predation and adverse environmental conditions (Hill & Lodge 1999). Crayfish have a wide range of predators, including birds, mammals, aquatic invertebrates and predatory fish (review in Hogger 1988). Although the potential predators may be numerous most have not been shown to have a significant direct impact on crayfish abundance (Hogger 1988). However the nocturnal activity pattern of many temperate crayfish and a strong association between crayfish and refuges may be interpreted, at least partially, as anti-predator responses.

CHAPTER 2. DEVELOPMENT, EXPANSION AND DISTRIBUTION OF CRAYFISH POPULATIONS IN THE RIVERS WHARFE AND URE

This chapter describes the expansion and distribution of the signal crayfish *Pacifastacus leniusculus* population in the Rivers Wharfe and Ure and the distribution of white-clawed *Austropotamobius pallipes* crayfish in the River Wharfe.

2.1 Introduction

Of the non-indigenous crayfish species that have been introduced into northern Europe, the most widespread species is the signal crayfish *Pacifastacus leniusculus* (Dana). Endemic to western North America, the signal crayfish has been introduced into over 20 countries in Europe since the 1960s (Lewis 2002, Holdich 2002). It frequently carries crayfish plague to which it is resistant but which is lethal to European crayfish. The effects of crayfish plague combined with the competitive advantage of signal crayfish have been partially responsible for the decline of European native crayfish species (Henttonen & Huner 1999, Holdich et al. 1999). The continued spread of signal crayfish within and between catchments is causing further losses of indigenous European crayfish stocks (Holdich et al. 1995) and has the potential for substantial disruption of the river ecosystem (Guan & Wiles 1997a, Nyström 1999, Nyström 2002, Statzner et al. 2003).

In order to manage and protect indigenous crayfish species, it is imperative to have good knowledge of crayfish distribution and abundance. The distribution of introduced crayfish in Europe has been described on a national basis and in some cases at a more local scale, by presence/absence between catchments or within grid squares (Holdich 2002). There is, however, little information on the within catchment expansion of non-indigenous crayfish species. In England and Wales, catchments have been classified on the basis of the presence of either native crayfish, introduced crayfish or both native and introduced species (Sibley et al. 2002). The majority of catchments in England and Wales that have native populations also now contain non-indigenous populations. Within catchment expansion is likely to become of increasing importance as populations of non-indigenous crayfish become established and expand. Knowledge of the rates of expansion of non-indigenous crayfish populations is of key importance in assessing the timescale of the threat that they pose to both native populations and the wider aquatic ecosystem.

The Rivers Wharfe and Ure have both historically been considered important white-clawed crayfish rivers with extensive and abundant populations reported, but now they also have populations of the introduced signal crayfish. The expansion of signal crayfish populations in the Wharfe and Ure was studied. The populations are of contrasting age. The population studied in the River Wharfe is an extensive established population whilst the River Ure population is a relatively young population with a limited distribution.

In addition to expansion in the main stem of rivers, the expansion and colonisation of tributaries by signal crayfish is likely to be important. White-clawed crayfish were known to occur within the Captain Beck sub-catchment that joins the main River Wharfe near Grassington. The expansion of signal crayfish into the tributary and the extent of the white-clawed crayfish population were investigated.

2.2 Site history and characteristics

The rivers Wharfe and Ure are major tributaries of the Yorkshire Ouse which discharges into the Humber estuary on the east coast of England (Figure 2.1). The Wharfe and Ure both rise as a series of streams at an altitude of over 600 m in the Pennine Hills (Yorkshire Dales) where they have adjacent catchments. The upper catchments of both rivers are predominantly rural with sheep and cattle pasture comprising the main land use. The geology of both upper catchments is mainly carboniferous limestone, with areas of shales, sandstones and millstone grit present, and as a result the rivers are rich in dissolved calcium carbonate. The upper Ure catchment drains an area of 510 km^2 at Kilgram Bridge (15 km upstream from the source of signal crayfish introduction), with a mean annual flow of 15.07 $m^3 s^{-1}$. The upper Wharfe catchment drains an area of 427 km^2 at Addingham (22 km downstream from the source of the signal crayfish introduction) with a mean annual flow of 14.82 $m^3 s^{-1}$ (Environment Agency unpublished information).

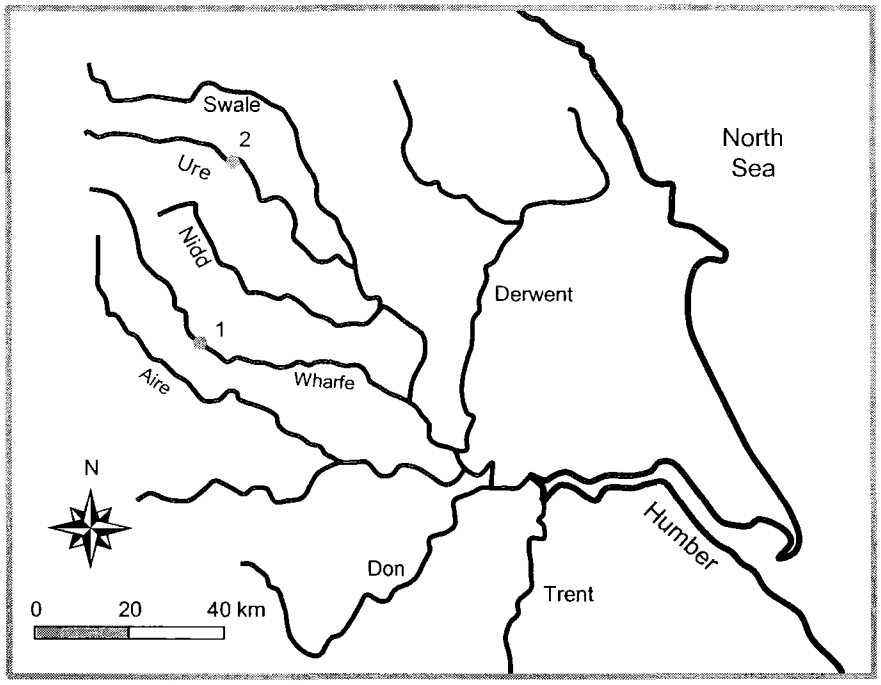


Figure 2.1 Principal rivers of the Humber Basin, North East England. 1 – Addingham gauging station (Upper Wharfe), 2- Kilgram Bridge gauging station (Upper Ure).

The flows of the upper River Ure and Wharfe are dominated by surface water flow. They are considered 'flashy' with both rivers responding rapidly to rainfall. The upper Ure has a largely natural flow regime although some minor abstraction occurs. The flow of the upper Wharfe is altered by abstraction at Lobwood (National Grid Reference: SE 075 520) and by releases from Grimwith Reservoir (NGR: SE 060 645) to the River Dibb.

River Wharfe

Signal crayfish were first introduced into trout fishing lakes at Kilnsey (NGR: SD 974 677) adjacent to the River Wharfe in 1983. The motivation behind the introduction is believed to be have been a combination of supplying the restaurant trade and control of aquatic vegetation in the fishing ponds. The trout ponds are close to White Beck (<20 m), and the outlet discharges directly into it. White Beck is a small tributary of the River Wharfe and joins the River Wharfe approximately 1 km downstream from where the trout ponds discharge. Signal crayfish became established in the fishing ponds and moved relatively unhindered through the outflow and via White Beck into the Wharfe.

Signal crayfish had become established in White Beck by 1987 (Peay 1997) and were caught in traps in the River Wharfe at the confluence with White Beck in 1990. By 1995

a mixture of signal and white-clawed crayfish was recorded at Grassington (4.1km downstream (DS) of the confluence of White Beck with the Wharfe) with only white-clawed crayfish at Burnsall (8.9 km DS) and at sites further downstream. In an extensive survey of the distribution of signal crayfish in the River Wharfe downstream of White Beck, Peay (1997) recorded only signal crayfish from White Beck downstream to Grassington. From Linton Stepping Stones (5.1 km DS) to Burnsall Bridge a mixture of signal and white-clawed crayfish was recorded. From the Dibb confluence (10.5 km DS) downstream only white-clawed crayfish were recorded.

Captain Beck Sub-catchment

Captain Beck joins the main River Wharfe close to Grassington. The sub-catchment has historically been known to contain white-clawed crayfish and sporadic records of white-clawed crayfish have been made by environmental consultants ABCS. Yearly surveys by environmental consultants ABCS have been conducted across the catchment since 1995. In early surveys by ABCS white-clawed crayfish were recorded in Eller Beck and in Linton Beck in the area around Linton village; more recent surveys only recorded white-clawed crayfish from Eller Beck.

River Ure

Signal crayfish were introduced into a trout fishing lake (NGR: SE 258 776) adjacent to the River Ure in the late 1980s. They were introduced primarily for the purposes of aquatic weed control, with crayfish stock believed to have originated from Kilnsey trout ponds. Water flows from the lake via an underground pipe to a small fish farm before it discharges directly into the River Ure on the left bank (facing downstream).

The outlet from the fishing lake was originally a single pipe, approximately 20 cm in diametre. In 2001, to try and prevent further escapes of crayfish from the lake, an up-flow bell chamber was installed at the lake outlet (for details see Peay 2001). After travelling underground for approximately 0.5 km the water rises to the surface from the underground pipe via a vertical pipe that feeds directly into the first stew pond of a fish farm. Water continues to flow from this pond into a section of open stream (< 1 m wide). This stream then fills a set of ponds approximately 50 m downstream that discharge directly into the River Ure via two steep outlet channels spaced 25 m apart on the left bank (facing downstream) of the river. The section of stream lies in a marshy area and receives one additional surface inflow.

Signal crayfish were first recorded in the River Ure in 1997, close to where the fish farm discharges. A preliminary survey, involving hand-searching within likely refuges and capturing disturbed crayfish, was undertaken by the Environment Agency in 1997 (Rogers 1998). Spot-checks were made at locations upstream and downstream of the fish farm outlets. Signal crayfish were not found at locations greater than 100 m from the outlets. In 1998 a more intensive survey was conducted using both hand-searching and traps. Crayfish were only captured on the left side (when facing downstream) of the river, up to 50 m downstream and 25 m upstream from the downstream and upstream discharge pipes respectively, a total range of 100 m (Rogers 1998). Attempts to remove signal crayfish from the river channel in 2000 by intensive trapping were ineffective despite significant numbers of crayfish present in the river (Peay 2001).

During 1999 and 2000, large numbers (>1500) of signal crayfish were removed from the stream within the fish farm (Rogers & Loveridge 2000). This, combined with habitat changes in the stream, and changes to the outlet from the lake has reduced the number of crayfish in the stream. However signal crayfish still remained numerous throughout the fish farm system in 2001-03, and continued to move into the River Ure (D. Bubb pers. obs.).

2.3 Methods

All surveying for crayfish within the Ure and Wharfe was conducted by handsearching. Sites were selected that would provide abundant refuges for crayfish and which could be effectively and safely searched by surveyors. All sites that were searched consisted of relatively unembedded cobble and boulder substrate which provided potential refuges in areas of low turbidity and were less than 0.6m deep. Survey work was carried out during periods of low water. Trained surveyors, experienced at searching for and catching crayfish, supervised by D.Bubb, carried out all surveys. During searching, any crayfish seen were caught if possible. If crayfish were observed but could not be captured a visual estimate was made of their size. Captured crayfish were identified, sexed, the carapace length measured and any missing or regenerating chelae recorded. The carapace length of crayfish, from the rostral apex to the posterior median edge of the cephalothorax, was measured to the nearest 0.1 mm using vernier callipers.

All distances relating to recorded crayfish distributions refer to distances along the midline of the river, measured within ArcGIS (ESRI) using Ordnance Survey landline 1:10,000 and OS Strategi 1:25,000 map information. Distances from the source of introduction refer to distances upstream and downstream along the Ure and Wharfe. The source of introduction on the River Ure was taken as the midpoint between the two outflows from the fish farm and on the River Wharfe the source of the introduction was taken as the confluence of White Beck with the Wharfe.

River Wharfe

Thirty four sites distributed along the upper River Wharfe were surveyed for crayfish. A combination of timed effort handsearching and fixed area searches was used to survey sites. In fixed area searches between 25 and 50 quadrats (0.49 m^2) were searched. Quadrats were placed in suitable habitat and used to demark the area, within which all refuges were searched and crayfish captured (for further details see Appendix 1). Surveys were undertaken in 2001-2003 between May and September in all years. Detailed surveys at the apparent upstream and downstream extent of the signal crayfish population were conducted in 2003. The locations and details of sampling sites and search effort are shown in Figure 2.2 and Table 2.1.

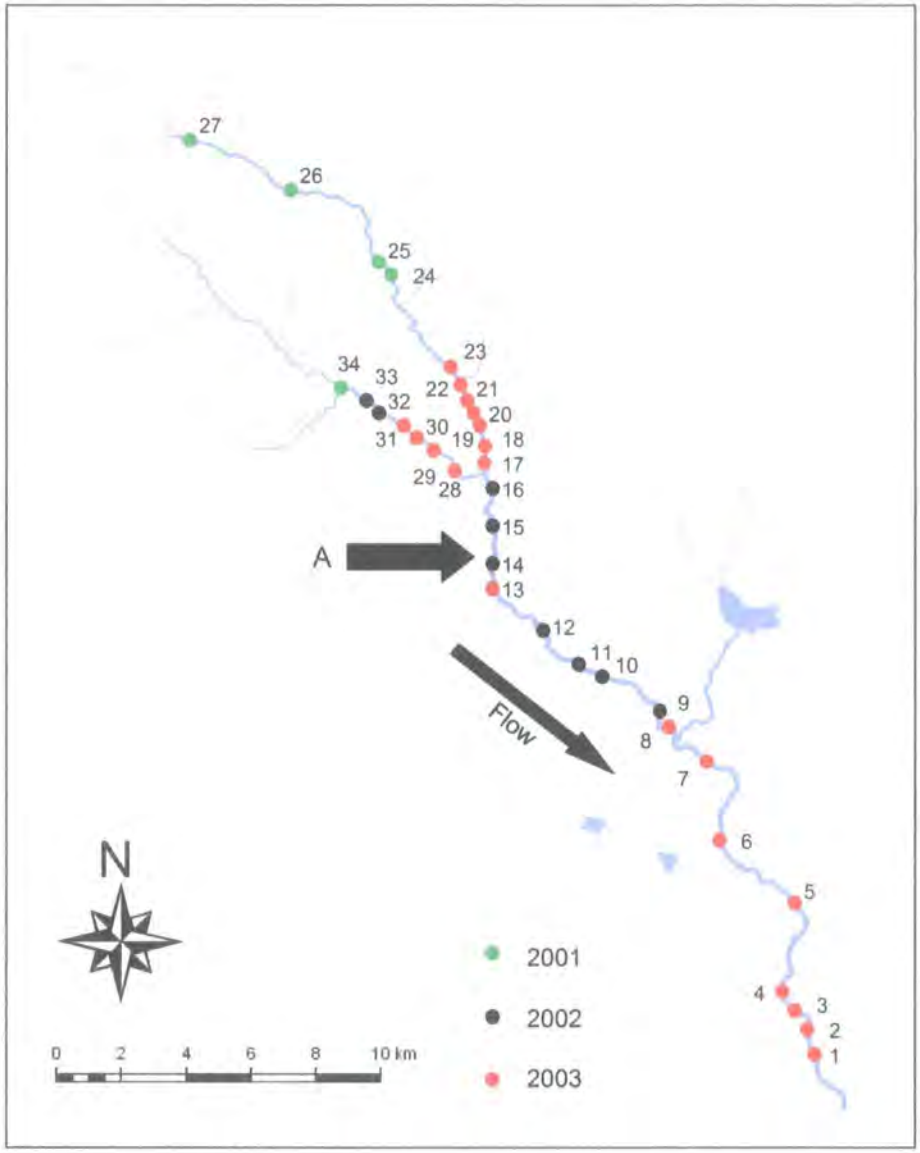


Figure 2.2 Locations of sites and year surveyed for crayfish, River Wharfe, 2001-2003. Arrow A denotes site of introduction of signal crayfish. For details of site locations see table 2.1.

River Ure

Surveying was carried out on the River Ure in the area surrounding the source of the introduction of signal crayfish into the river. Surveys were carried out in late August and early September in 2001, 2002 and 2003. At each selected site 0.5 person-hour searches were conducted. The distribution of sites searched is shown in Figure 2.3. A total of 30 sites were searched in 2001, 26 in 2002 and 24 in 2003 (Table 2.2). Eighteen of the selected sites were searched in all years. Sites upstream and downstream of those surveyed in 2001 were included in the surveys during 2002 and 2003 due to the observed expansion of the population.

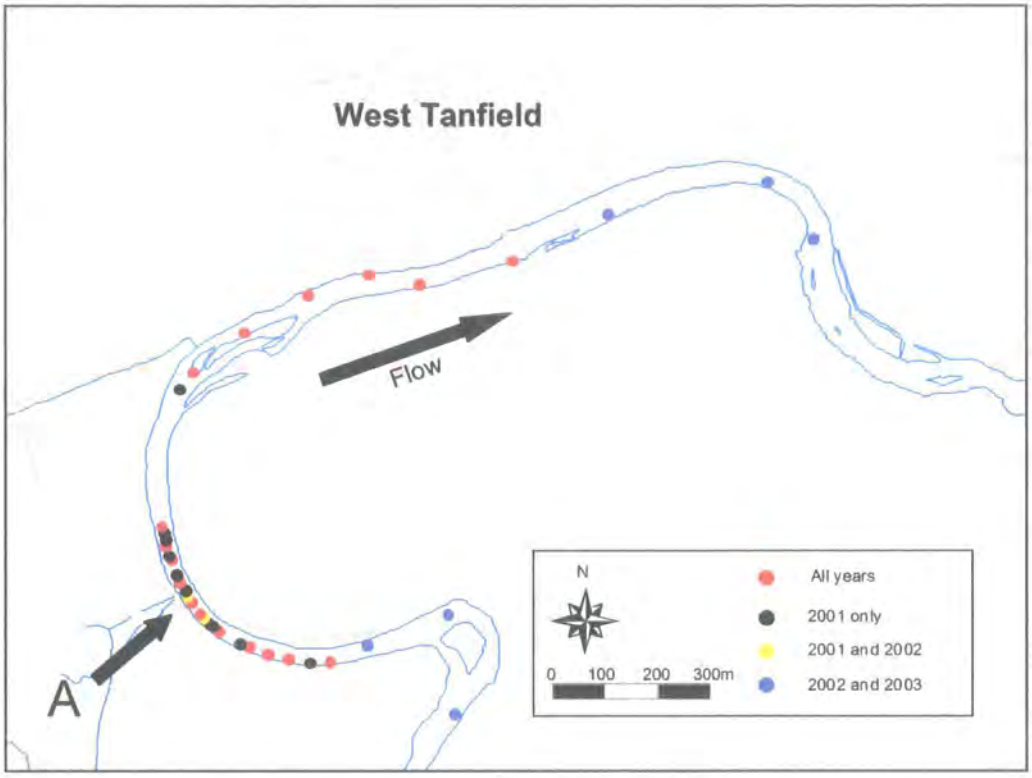


Figure 2.3 Positions of standardised effort handsearches for signal crayfish in the River Ure, 2001 – 2003. Arrow A denotes source of signal crayfish into the river. This map is reproduced with Ordnance Survey Landline data obtained with permission from Edina Digimap.

Captain Beck Catchment

A combination of handsearching, trapping and night view was used during surveys of Captain Beck catchment. Trapping was conducted using Swedish Trappy™ crayfish traps baited with fresh liver. Traps were set during late afternoon or evening and emptied the following morning. Traps were placed in areas of suitable habitat which provided stable refuges as assessed by an experience fieldworker. During night view surveyors slowly waded up the stream with torches. The stream bed was searched for visible crayfish, the numbers and species of crayfish observed was recorded. Nine sites were surveyed as part of this project. In addition a further 14 sites surveyed by ABCS environmental consultants during 2003 are included within the Results (section 2.4). Details of the sites surveyed and sampling effort are shown in Figure 2.4 and Table 2.3.

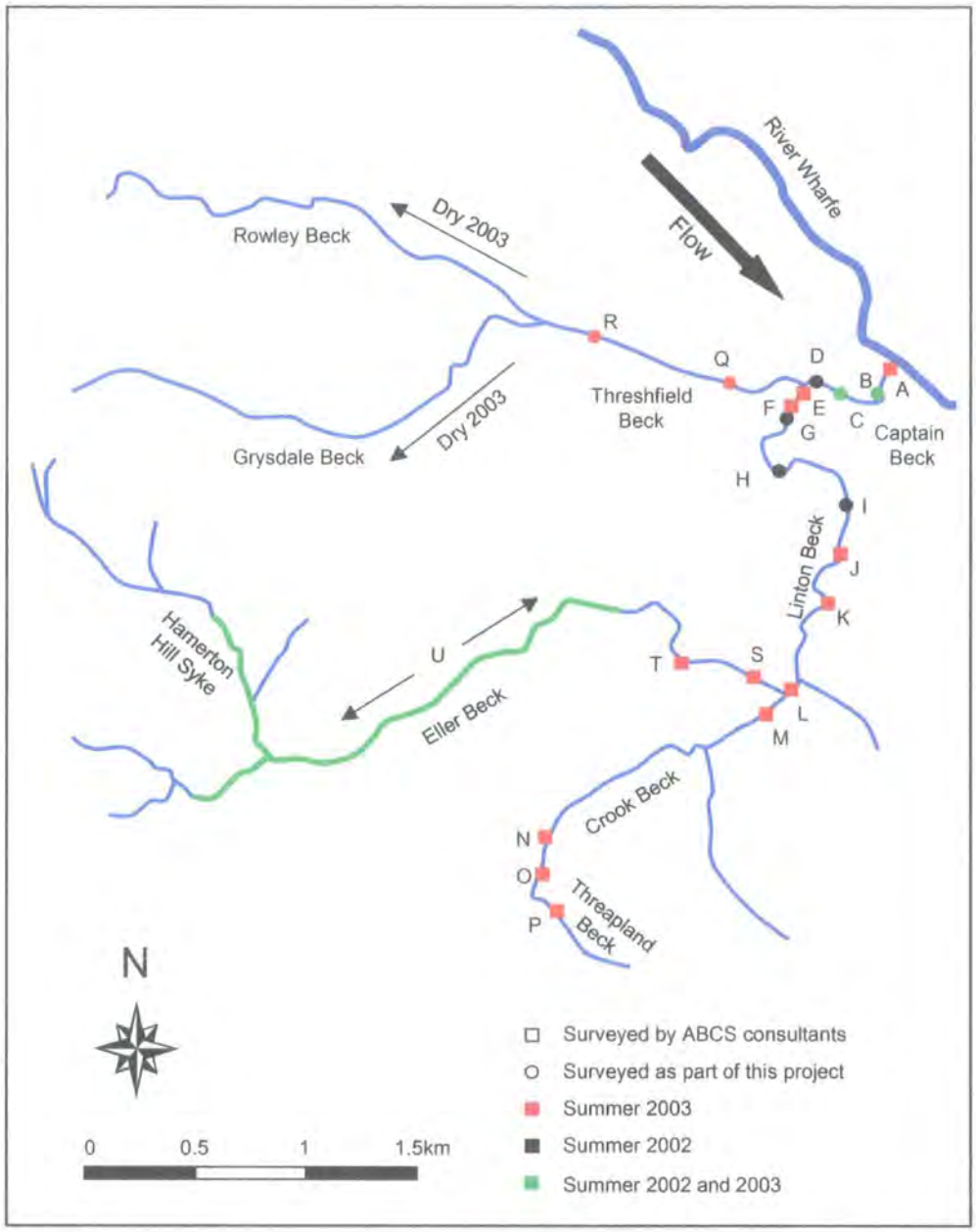


Figure 2.4 Locations of sites and year surveyed for crayfish, Captain Beck sub-catchment, 2002-2003. Letters refer to site details given in table 2.3.

2.4 Results

River Wharfe

Crayfish were recorded at 24 of the 34 sites surveyed (Table 2.1, Figure 2.5). In 2003 signal crayfish were recorded a maximum of 23.3 km downstream from the source of the introduction into the Wharfe and 6.1 km and 4.6 km upstream in the Skirfare and Wharfe respectively (Figure 2.6). If it is assumed that signal crayfish first reached the Wharfe in 1990 (unpublished information National Rivers Authority) and there have been no other introductions this represents an average rate of downstream expansion of the population of 1.8 km year^{-1}, and upstream expansion of 0.47 km year^{-1}and 0.35 km

year^{-1} in the Skirfare and Wharfe respectively. After reaching Burnsall (8.9 km downstream) in 1997 (Peay 1997) they have spread a further 14.4 km downstream (Figure 2.7) at an average rate of 2.06 km year $^{-1}$.

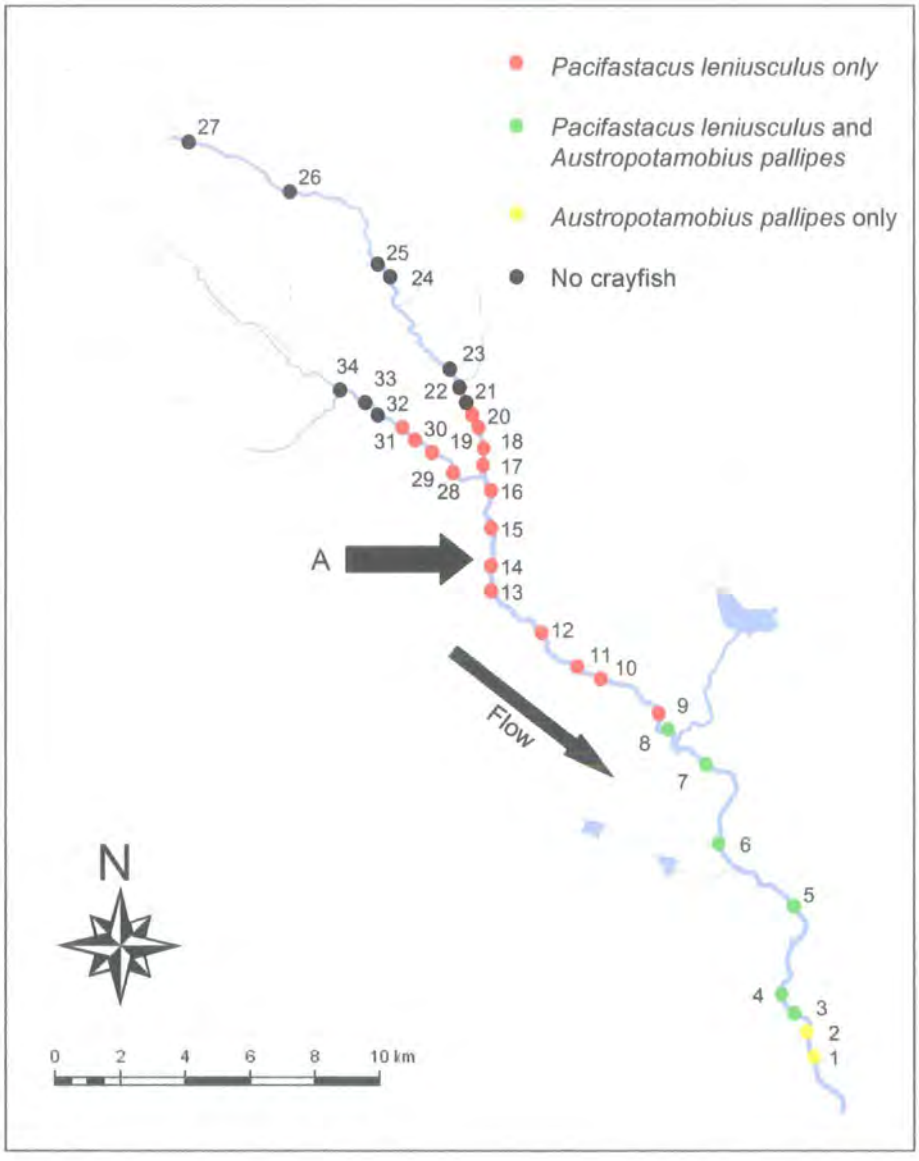


Figure 2.5 Distribution of crayfish recorded during surveys of River Wharfe 2001-2003. Arrow A denotes site of introduction of signal crayfish. For details of site locations see table 2.1.

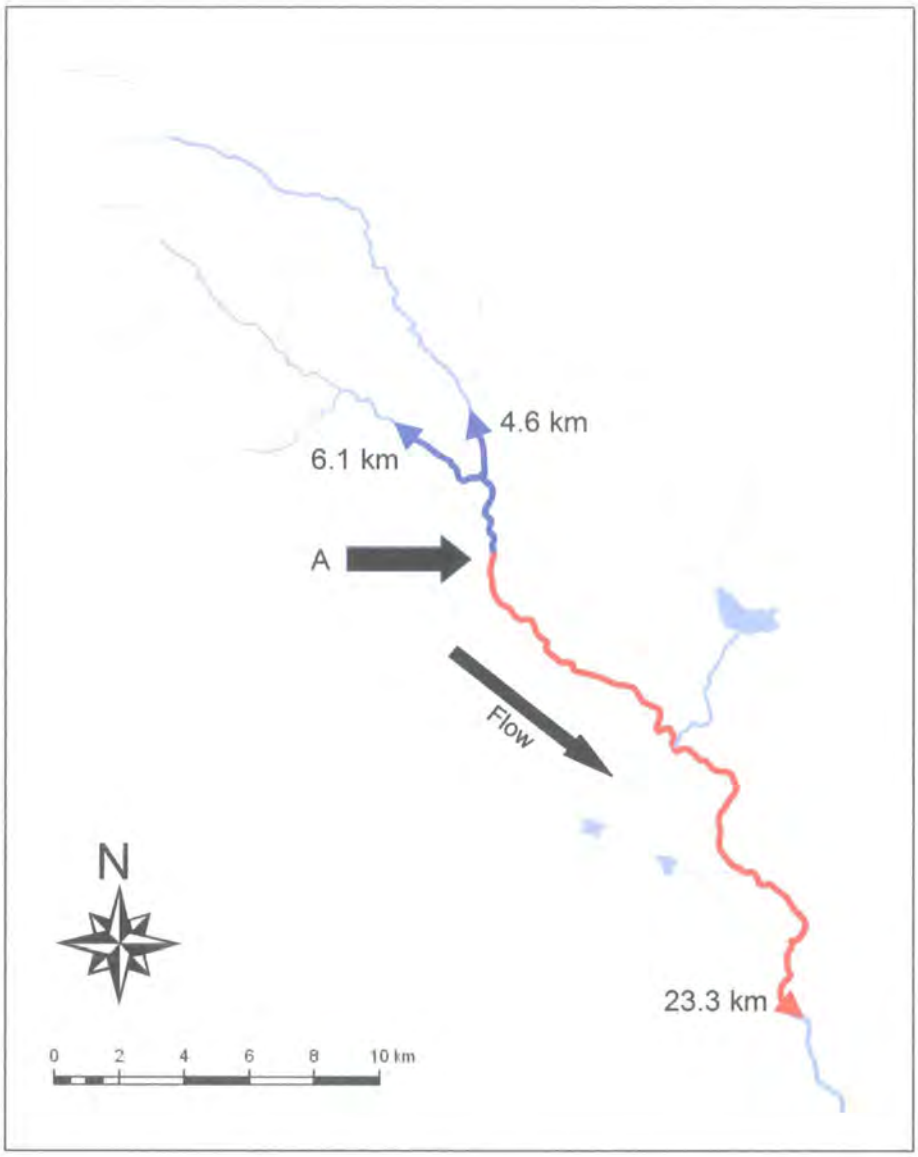


Figure 2.6 Signal crayfish distribution upstream (blue arrow) and downstream (red arrow) in River Wharfe, Summer 2003. Arrow A shows the source of signal crayfish in the Wharfe at the confluence of White Beck with the River Wharfe.

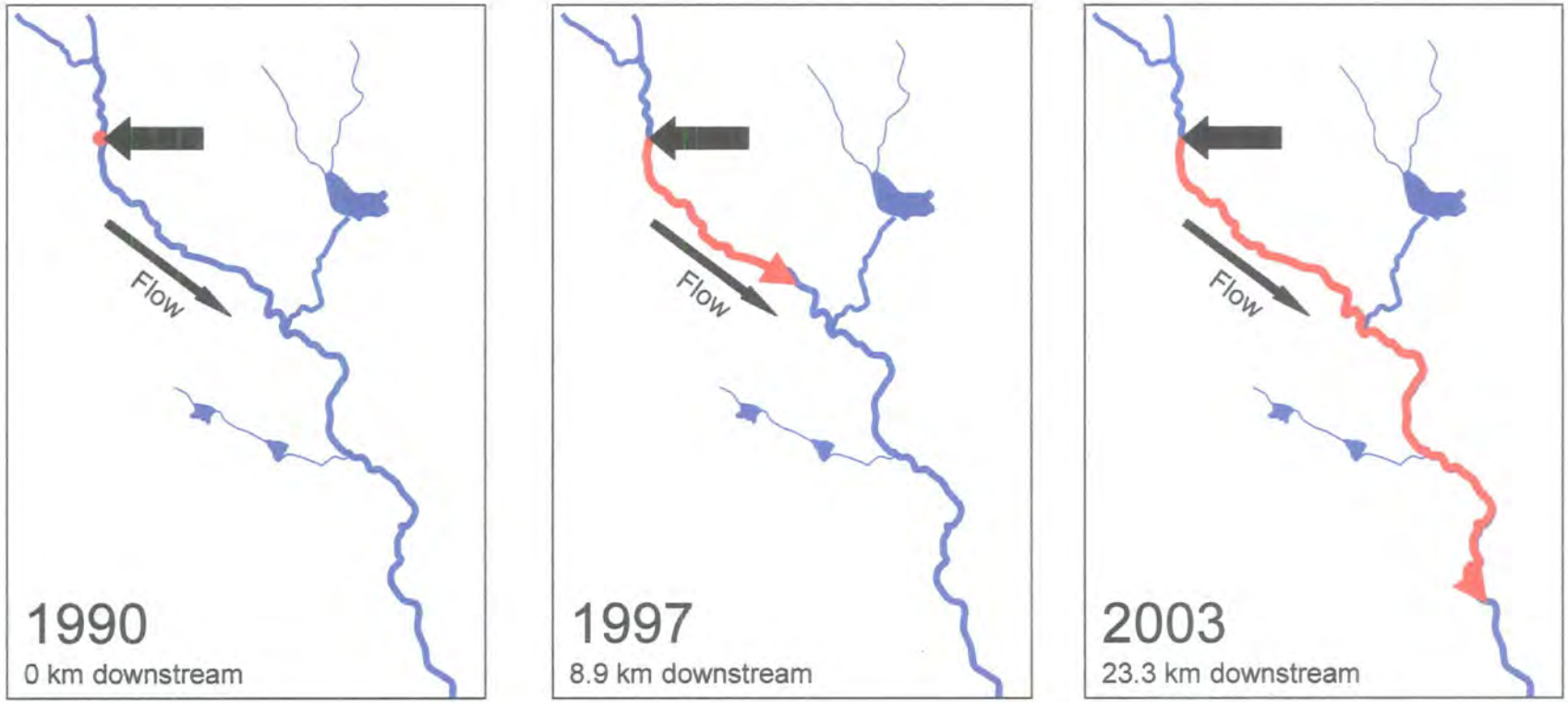


Figure 2.7. Downstream expansion of the signal crayfish population in the River Wharfe. Arrow denotes source of introduction into the Wharfe.

A mixed zone of white-clawed crayfish and signal crayfish was recorded over the lower 14.4 km of the signal crayfish population. White-clawed crayfish were present downstream of the mixed zone. No white-clawed crayfish were recorded upstream of the confluence of White Beck with the Wharfe in either the Skirfare or Wharfe. The change from signal-only population to white-clawed only-population appeared to approximate to a linear transition (Figure 2.8, $R^2 = 0.96$).

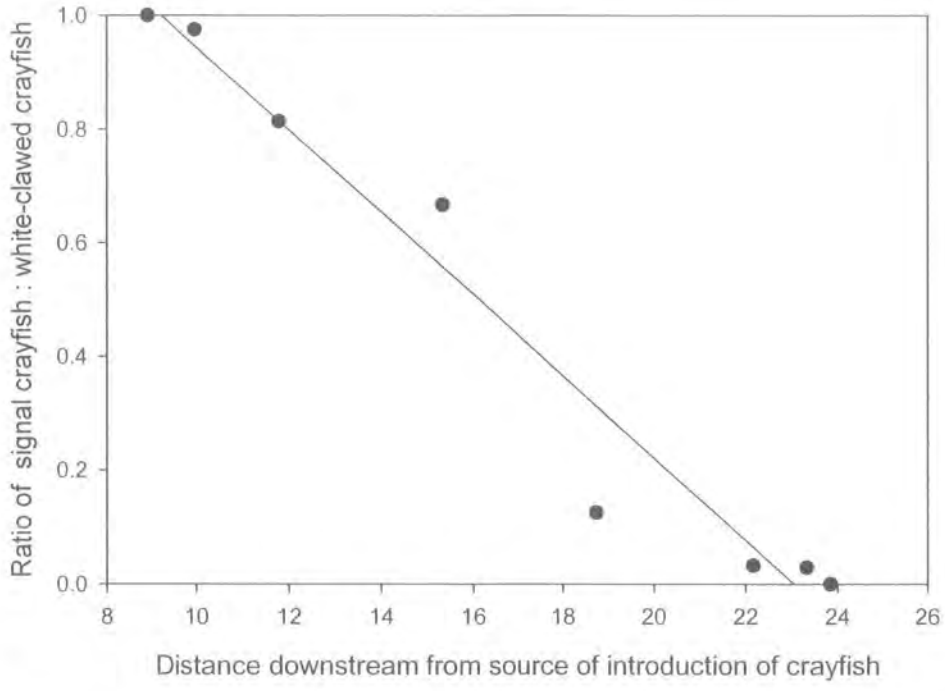


Figure 2.8 Change in the ratio of signal crayfish to white-clawed crayfish with increasing distance downstream in the River Wharfe, Summer 2003. Data from Table 2.1.

Captain Beck Sub-catchment

An extensive population of white-clawed crayfish was found to exist in Eller Beck. White-clawed crayfish occupied virtually the entire length of Eller Beck. They occurred upstream in Eller Beck almost as far as there is permanent flowing water. Signal crayfish were recorded over the lower 750 m of Captain Beck sub-catchment. Only a single white-clawed crayfish was recorded within the Captain Beck sub-catchment outwith Eller Beck. The rate of expansion by signal crayfish upstream into Captain Beck catchment is relatively slow. Assuming signal crayfish reached the confluence of Captain Beck with the River Wharfe at Grassington in 1995, they have expanded upstream in Captain Beck at less than 100 m $year^{-1}$.

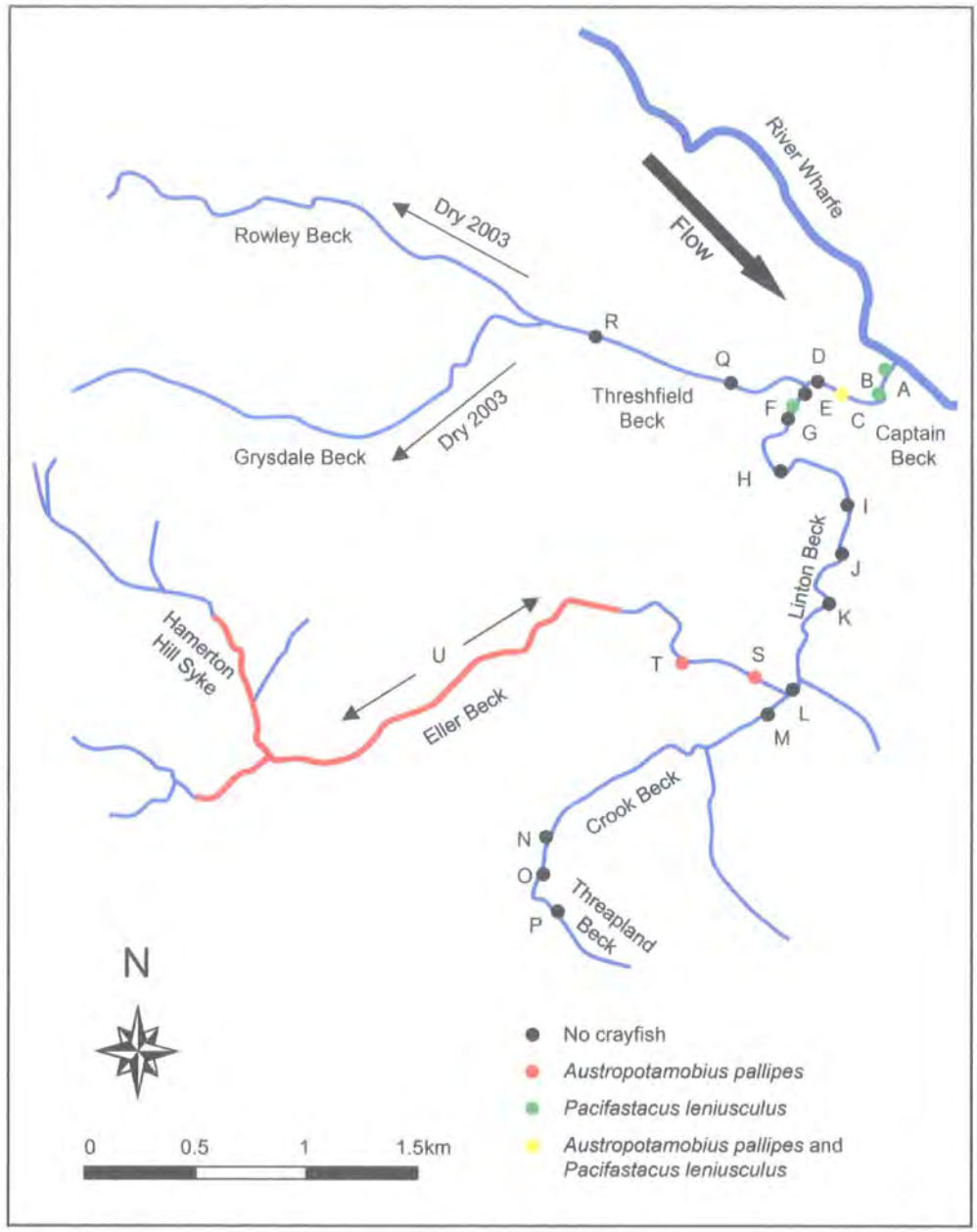


Figure 2.9 Distribution of crayfish within Captain Beck sub-catchment recorded during surveys 2002-2003.

River Ure

All crayfish captured were signal crayfish, no evidence of white-clawed crayfish presence in the area of the Ure surveyed was obtained. In 2003, signal crayfish were recorded a maximum of 400 m upstream and 1281 m downstream of the source. Assuming signal crayfish first reached the Ure in 1996 this represents an average rate of downstream expansion of the population of 183 m yr^{-1} and upstream expansion of 57 m yr^{-1}. The rate of population expansion was not constant between 1996 and 2003. Between 1996 and 2001 the signal crayfish occupied 574 m linear distance, representing

an increase in range of 115 m yr^{-1} whilst between 2001 and 2003 the recorded range increased to 1681 m, an increase in range of 554 m yr^{-1} between 2001 and 2003 (Figure 2.10). The rate of upstream expansion of the population was slower than the downstream expansion in both periods; 1996-2001 upstream 37 m yr^{-1} downstream 78 m $year^{-1}$; 2001-2003 upstream 108 m $year^{-1}$, downstream 446 m yr^{-1}.

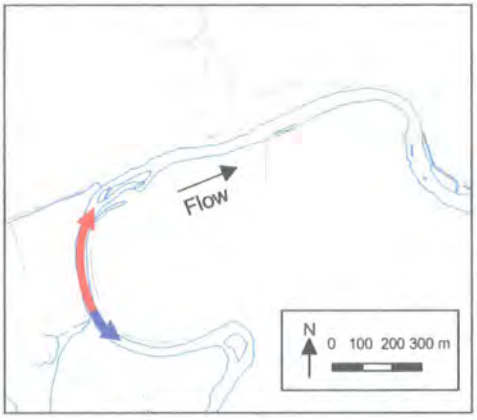
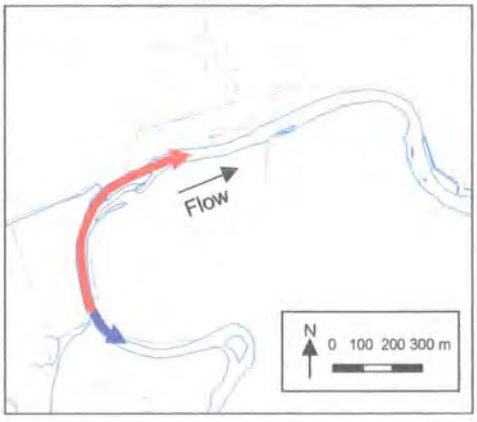


Figure 2.10. Maximum recorded upstream and downstream distributions of signal crayfish, River Ure, 2001-2003. Red arrow – downstream, Blue arrow - upstream

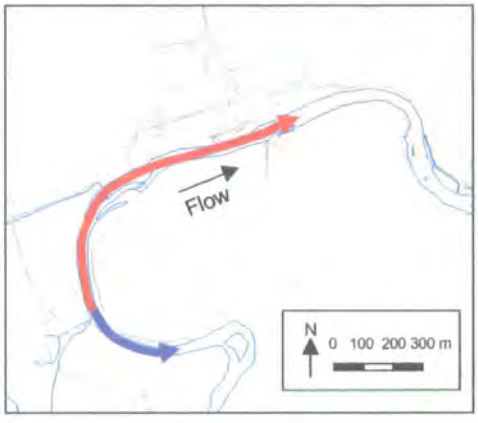
2001

Upstream 184 m: downstream 390 m



2002

Upstream 184 m: downstream 824 m



2003

Upstream 400 m: downstream 1281 m

In all years there was a general decline in the numbers of crayfish recorded during each timed search with distance from the source of introduction, in both upstream and downstream directions (Figure 2.11). At the 18 sites surveyed in 2001 and 2003 there was a significant increase (Wilcoxon Signed Ranks Test, $T = 17$, $P < 0.05$) in abundance of crayfish between these years. However there was no significant difference in abundance between 2001 and 2002 or 2002 and 2003 (Wilcoxon Signed Ranks Test, both $P > 0.05$).

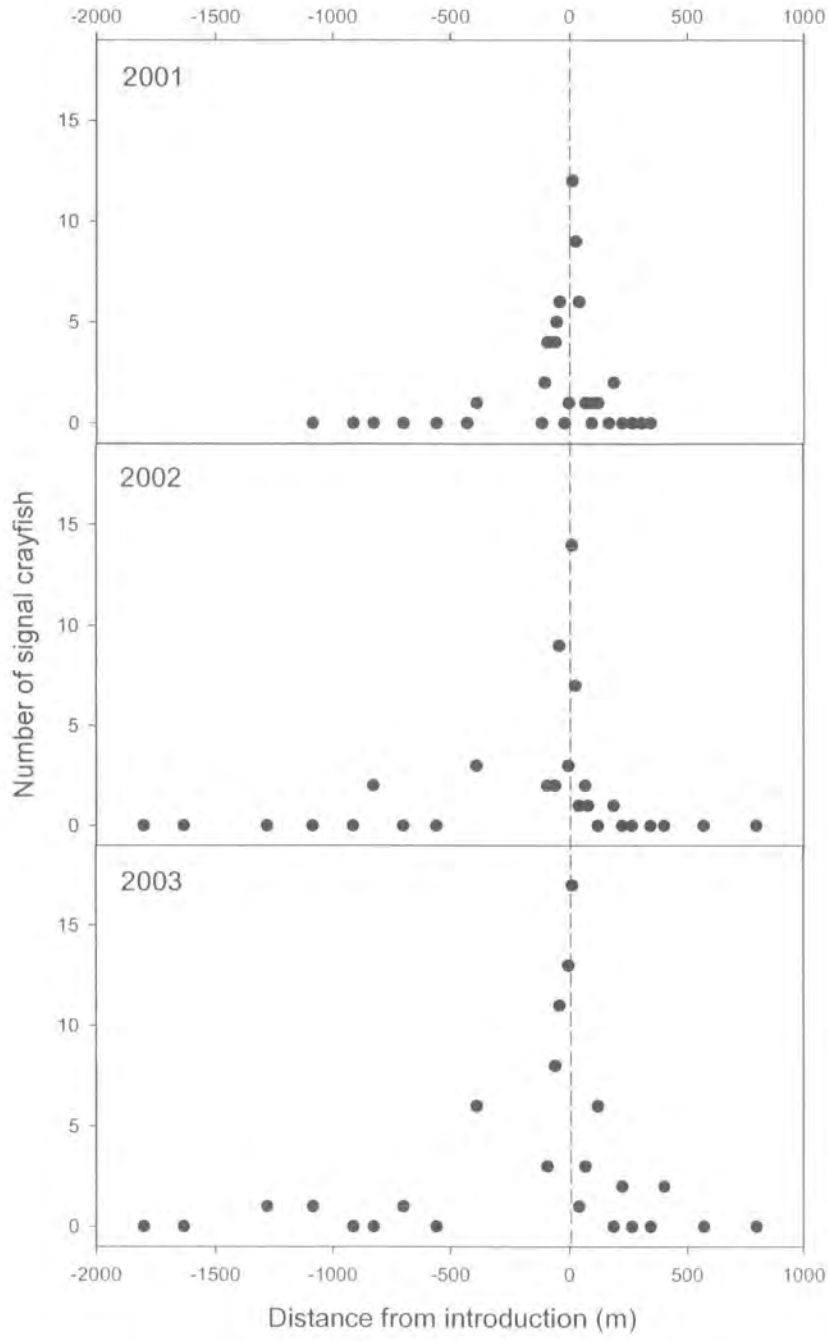


Figure 2.11 Number of signal crayfish recorded in 2001, 2002 and 2003 during standardised effort (0.5 person-h^{-1}) searches of the Ure, with increasing distance upstream (+ve) and downstream (-ve) from the source of introduction

Table 2.1. Details of survey sites and numbers of crayfish recorded during distributional surveys on the River Wharfe, 2001-2003.
Distance – Distance along midline of river from source of introduction (Confluence of White Beck) +ve values refer to upstream, -ve values downstream. Species – AP white-clawed crayfish *Austropotamobius pallipes*, PL signal crayfish *Pacifastacus leniusculus*.

Site	Grid ref.	Distance	Location	Dates	Quadrat counts (crayfish m^{-2}) (area searched)	Handsearch (crayfish person-hr^{-1}) (search time)
1	SE 080508	-24.90	U.S. Addingham Weir	8/6/03		51 AP (1 hr)
2	SE 081513	-23.85	D.S. Lobwood 2	4/6/03		46 AP (1 hr)
3	SE 077518	-23.33	D.S. Lobwood 1	5/6/03	6.8 AP + 0.2 PL (9.8 m^2)	
4	SE 071526	-22.16	Bolton Bridge	8/6/03		31 AP + 1 PL (1 hr)
5	SE 076555	-18.74	Lund Island	8/7/03		17 AP + 1 PL (1 hr)
6	SE 053573	-15.34	Barden Bridge	8/7/03		15 AP + 30 PL (1hr)
7	SE 047601	-11.78	Appletreewick	30/6/03		8 AP + 35 PL (1 hr)
8	SE 036609	-9.96	D.S. Burnsall	8/6/03		1 AP + 39 PL (1 hr)
9	SE 033616	-8.92	Burnsall	22/9/02	7.9 PL (12.2 m^2)	
10	SE 012628	-5.64	Lythe House	20/9/02	19.75 PL (12.2 m^2)	
11	SE 007632	-5.01	Stepping stones	21/9/02		53 PL (1 hr)
12	SD 997639	-4.14	Grassington	30/7-19/8/02	7.98 PL (39.2 m^2)	
13	SD 980663	-0.72	D.S. Mill Scar Falls	18-21/8/03		~67.8 PL (6+ hr)
14	SD 979668	0	White Beck Confluence	3/9/02	12.11 PL (14.7m^2)	
15	SD 977680	1.30	US Conistone	16/9/02	9.84 PL (12.2m^2)	
16	SD 977693	2.62	DS Confluence	21/9/02	8.10 PL (14.7 m^2)	
17	SD 977694	2.83	US Confluence	14/7/03		32 PL (1 hr)
18	SD 976701	3.44	Low Close Lathe	14/7/03		2 PL (1 hr)
19	SD 975704	3.70	Low Monk Leys	14/7/03		7 PL (1 hr)
20	SD 973709	4.55	D.S. Stepping Stones	14/7/03		4 PL (1 hr)
21	SD 972715	5.04	Knipe Close	14/7/03		0 (1 hr)
22	SD 968721	5.73	Kettlewell	17/7/03		0 (1 hr)
23	SD 968724	6.14	Kettlewell	17/7/03		0 (1 hr)
24	SD 938772	12.75	Buckden	8/01		0 (1 hr)
25	SD 938776	13.63	Buckden	8/01		0 (1 hr)
26	SD 927783	14.45	Hubberholme	8/01		0 (1 hr)
27	SD 903792	17.42	Yockenthwaite	8/01		0 (1 hr)
28	SD 971692	3.52	US Skirfare Bridge	15/7/03		12 PL (1 hr)
29	SD 966696	4.19	Sleets Gill Wood	15/7/03		1 PL (1 hr)
30	SD 959702	5.02	Old Rams Barn	15/7/03		1 PL (1 hr)
31	SD 953708	6.07	U.S. Hawkswick Foot Bridge	15/7/03		1 PL (1 hr)
32	SD 947709	7.14	Dibb Barn Flats	15/7/03		0 (1 hr)
33	SD 943712	8.10	Dibb Barn Flats	15/7/03		0 (1 hr)
34	SD 934719	8.33	D.S. Arncliffe	8/01		0 (1 hr)

Table 2.2. Location of survey sites and number of signal crayfish *Pacifastacus leniusculus* recorded during standard effort (0.5 person-h) handsearches, River Ure, 2001-2003. Distance from source of introduction, +ve values refer to upstream, -ve values downstream. - indicates not surveyed

National Grid Reference	Distance from source of introduction (m)	2001	2002	2003
SE 26846 77834	796	-	0	0
SE 26834 78025	570	-	0	0
SE 26728 77986	400	-	0	2
SE 26609 77935	341	0	0	0
SE 26569 77933	301	0	-	-
SE 26528 77941	262	0	0	0
SE 26489 77950	221	0	0	2
SE 26456 77963	184	2	1	0
SE 26437 77970	163	0	-	-
SE 26397 77993	118	1	0	6
SE 26386 78003	103	1	-	-
SE 26377 78009	91	0	-	-
SE 26366 78020	77	1	1	-
SE 26360 78027	66	1	2	3
SE 26343 78049	39	6	1	1
SE 26335 78061	25	9	7	-
SE 26331 78073	12	2	14	17
SE 26321 78086	-4	1	3	13
SE 26314 78101	-21	0	-	-
SE 26305 78130	-41	6	9	11
SE 26299 78130	-54	5	-	-
SE 26299 78138	-60	4	2	8
SE 26293 78156	-79	4	-	-
SE 26293 78169	-92	4	2	3
SE 26291 78181	-104	2	-	-
SE 26287 78193	-116	0	-	-
SE 26320 78456	-390	1	3	6
SE 26346 78489	-430	0	-	-
SE 26447 78565	-559	0	0	0
SE 26567 78636	-699	0	0	1
SE 26684 78676	-824	0	2	0
SE 2678078656	-912	0	0	0
SE 26957 78702	-1086	0	0	1
SE 27143 78792	-1281	-	0	1
SE 27445 78854	-1586	-	0	0
SE 27534 78745	-1801	-	0	0

Site	Stream	National Grid Reference	Survey Method	Year	Surveyors	Crayfish
A	Captain Beck	SE 000633	2 Traps, 0.25 person hrs Handsearch, Nightview	2003	ABCS	1 PL
B	Captain Beck	SD 999633	1person hrs. Handsearch	2002	Durham Uni.	None
B	Captain Beck	SD 999633	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	4 PL
C	Captain Beck	SD 997633	1person hrs Handsearch	2002	Durham Uni.	1AP + 1PL
C	Captain Beck	SD 997633	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	None
D	Captain Beck	SD 996633	1person hrs Handsearch	2002	Durham Uni.	None
E	Linton Beck	SD 996633	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	None
F	Linton Beck	SD 995632	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	2 PL
G	Linton Beck	SD 995631	1person hrs. Handsearch	2002	Durham Uni.	None
H	Linton Beck	SD 994630	1person hrs. Handsearch	2002	Durham Uni.	None
I	Linton Beck	SD 997628	0.5 person hrs. Nightsearch	2002	Durham Uni.	None
J	Linton Beck	SD 997625	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	None
K	Linton Beck	SD 997623	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	None
L	Crook Beck	SD 995618	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	None
M	Crook Beck	SD 994618	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	None
N	Crook Beck	SD 984613	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	None
O	Crook Beck	SD 982611	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	None
P	Threapland Beck	SD 981608	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	None
Q	Threshfield Beck	SD 992633	0.66 person hrs. Handsearch	2003	YDNP	None
R	Threshfield Beck	SD 987635	0.66 person hrs. Handsearch	2003	YDNP	None
S	Eller Beck	SD 993620	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	4 AP
T	Eller Beck	SD 989620	2 Traps, 0.25 person hrs. Handsearch, Nightview	2003	ABCS	7 AP
U	Eller Beck	SD 987622 to SD 967623 / SD 966614	Trapping / Nightview see Chapter 5 for details.	2002/2003	Durham Uni.	Continuous AP

Table 2.3. Location of survey sites and number of crayfish recorded during surveys of Captain Beck catchment, 2002 and 2003. Crayfish – AP *Austropotamobius pallipes*, PL *Pacifastacus leniusculus*. YDNP – Yorkshire Dales National Park Authority, ABCS – Environmental Consultants.

2.4 Discussion

Populations of signal crayfish are established and expanding on both the Rvers Wharfe and Ure. The rates of expansion differ markedly between the two rivers. The rate of population range expansion since introduction of the Ure population is approximately one tenth of that recorded from the Wharfe. This appears to reflect the different ages of the two populations. Initial population range expansion in the first few years as recorded on the Ure, and during the early establishment of signal crayfish in the Wharfe appears to occur slowly with gradual increase in the rate of spread occurring as the population becomes established and its abundance increases.

The current rate of population range expansion in the Wharfe (>2 km yr^{-1}) appears to be high although comparisons with other rivers are difficult due to the lack of published information. Rates of expansion of 1 km yr^{-1} have been reported from the River Wreake, Leicestershire (Holdich et al. 1995) and 1.1 km yr^{-1} from the River Great Ouse, Buckinghamshire (Guan & Wiles 1999).

There was a bias towards downstream colonization in the two upland rivers studied (upstream: downstream ratio of distance colonised from source of introduction; River Wharfe 1:3.8, River Ure 1:3.2). This contrasts with records from lowland rivers. Guan & Wiles (1999) reported that the expansion of a signal crayfish population in the River Great Ouse in eastern England was only weakly biased in a downstream direction (4.3 km upstream: 5.8 km downstream from the source of introduction). A similar pattern of weak bias towards downstream colonisation was reported in the River Bain, eastern England (3.5 km upstream: 4.5 km downstream from the source of introduction; Holdich et al. 1995). The gradient of the Great Ouse in the locality of the crayfish survey is less than half that of the Ure and Wharfe (Great Ouse 1:850, Ure 1:430, Wharfe 1:270). The higher gradient of upland rivers is associated with an increased number of riffles and falls, which, whilst not forming an absolute barrier to signal crayfish, may have a reduced permeability to movements contributing to the observed reduced upstream expansion. Higher gradient is also associated with higher mean water velocity (Wetzel 2001). This may potentially also contribute to the downstream bias in colonization. The importance of passive downstream movements by crayfish leading to the colonisation of new areas is unknown. The patterns of movements of signal crayfish and the relation of individual movements to the observed population expansion are examined in Chapters 4 and 6.

In the Wharfe an extensive mixed population of white-clawed and signal crayfish was recorded. However the expansion of the signal crayfish population is associated with the progressive loss of river populations of white-clawed crayfish. The development of a mixed population of white-clawed and signal crayfish as observed on the Wharfe is a relatively rare event. Although signal crayfish now exist in many waters previously occupied by white-clawed crayfish, in most cases the white-clawed crayfish have been eliminated by crayfish plague, *Aphanomyces astaci,* for which signal crayfish have acted as a vector, with little or no direct contact between the two species. In the limited number of cases in which signal crayfish have formed mixed populations with white-clawed crayfish, without any apparent transmission of crayfish plague to white-clawed crayfish, the loss of white-clawed crayfish has occurred over several years (Holdich et al. 1995). The local extinction of white-clawed crayfish in the Wharfe appears to occur 6-7 years after the first colonisation by signal crayfish. This rate of extinction of white-claws is similar to that described in other mixed populations (Holdich et al. 1995; Holdich & Domaniewski 1995) although the published information on lotic mixed signal and white-clawed crayfish populations is not very detailed (Holdich et al. 1995). In continental Europe, two mixed populations of apparently plague-free signal crayfish with noble crayfish *Astacus astacus* have been documented. In a Swedish lake signal crayfish rapidly displaced noble crayfish over a five-year period (Söderbäck 1991), whilst in contrast, the same two species have cohabited in a Finnish lake for over 20 years (Westman et al. 1993).

Further expansion of the signal crayfish populations in the Wharfe and Ure is expected. This will almost certainly lead to the continued loss of populations of white-clawed crayfish from the River Wharfe. Populations of white-clawed crayfish are present downstream along the River Wharfe as far as Boston Spa, just above the tidal limit (Holdich & Rogers 1995). Assuming continued expansion of signal crayfish at similar rates to present, signal crayfish might be expected to colonise the entire river downstream in about 36 years. This assumes that the downstream expansion of the signal crayfish population will occur at a similar rate in the more lowland lower reaches of the Wharfe as occurred in the upland Wharfe as has been documented here. It seems unlikely that weirs and natural obstructions will have any significant impact on the downstream rates of expansion.

In contrast to the Wharfe, where white-clawed crayfish populations are downstream of the signal crayfish population in the Ure the majority of white-clawed populations are upstream from the signal crayfish populations. Extensive white-clawed populations are present several kilometres upstream of the signal population in the Ure and are widely distributed along the upper Ure and its tributaries (Environment Agency, unpublished information). The upstream expansion of the signal crayfish population in the Ure seems likely to lead to some direct contact between white-clawed and signal crayfish, with the probable loss of the white-clawed crayfish populations. The extent that signal crayfish will continue to colonise upstream is unclear. Several weirs and substantial natural waterfalls (e.g Aysgarth Falls; NGR SE 018 889) occur upstream of the signal crayfish population and below abundant white-clawed crayfish populations. It is possible that these may prevent or slow the upstream expansion of signal crayfish. A detailed understanding of the role of flow and obstructions on the movement and colonisation ability of signal crayfish is required for predictions to be made regarding the upstream colonisation and fate of white-clawed crayfish in the Ure. The greatest immediate threat to populations of white-clawed crayfish in the upper Ure from signal crayfish appears to be from new foci and introductions upstream of the present signal population.

The population of white-clawed crayfish in Eller Beck is the most extensive known stream population of white-clawed crayfish within the upper Wharfe catchment. The lower reaches of Eller Beck were formerly (early 1990s) heavily polluted by highly alkaline leachate from the adjacent limestone quarry. Improvements in the drainage and pumping of leachate back into the quarry has improved the conditions and this has apparently allowed the population of white-clawed crayfish to expand downstream and they now appear to be present along the length of Eller Beck. The colonisation of the lower reaches of the Captains Beck catchment by signal crayfish is a potential threat to this population. The colonisation of the catchment by signal crayfish appears to be occurring only slowly (<100 m yr^{-1}), and if it continues at this current rate does not pose an immediate threat with over 2 km between signal and white-clawed populations. However the current rate of expansion may have been limited by pollution events and signal crayfish may have the potential to expand at a greater rate than this estimate. In the late 1990s there was a suspected sheep dip pollution incident in Linton Beck. This is believed to have led to the loss of the white-clawed crayfish population in the lower reaches of Linton Beck, and it is also likely that it killed any signal crayfish which had

moved into the lower reaches of the catchment. The gradient and characteristics of Captain Beck may have also influenced the rate at which signal crayfish have colonised. The lowest 100 m of Captain Beck from the confluence with the Wharfe is a series of falls. This may have reduced the initial permeability of the stream to colonisation by signal crayfish. The gradient of Linton and Eller Beck is much less steep than the initial stretch of Captains Beck adjoining the river Wharfe. This may result in an increased rate of colonisation now that signal crayfish are present and apparently breeding in the lower reaches of Linton Beck above the falls.

CHAPTER 3. REVIEW OF THE SPATIAL BEHAVIOUR OF CRAYFISH, TECHNIQUES USED FOR ITS STUDY AND DEVELOPMENT OF NOVEL PIT TELEMETRY METHODS

This chapter reviews and summarises the current state of knowledge on spatial behaviour of crayfish and provides a broad introduction to the spatial behaviour of crayfish considered in Chapters 4, 5 and 6. Additionally methods used for studying space use in crayfish are discussed and two novel techniques are developed i) internal implantation and remote detection of 12 mm passive integrated transponder (PIT) tags and ii) external attachment and remote detection of 23 mm PIT tags. These techniques are utilised in Chapters 4 and 5 for studying the movements of signal crayfish *Pacifastacus leniusculus* and white-clawed crayfish *Austropotamobius pallipes*.

3.1 Spatial behaviour of crayfish

In an ecological context, information about animal movements and activity is important in contributing to an understanding of habitat requirements, patterns of resource utilisation and the potential for interspecific interaction (Sutherland 1996). Crayfish are large, mobile invertebrates capable of making substantial active movements. An understanding of the spatial behaviour of crayfish is likely to be important in informing any management strategies, for both control of introduced species and conservation of native species. It is also likely to provide information of relevance to understanding colonisation and expansion of populations.

3.1.1 Diel and seasonal activity

Most crayfish species are considered to be predominately nocturnal; remaining in refuges during the day and making active movements and foraging during the night. Much of the information regarding their diel activity cycle rests on observation without any quantitative data. Peay (1997) found the emergence of signal crayfish and white-clawed crayfish occurred 2-3 hours after sunset in the River Wharfe. Abrahamsson (1981) described signal crayfish to be predominately active at night with peak in activity in evening after sunset. Robinson (1997) found white-clawed crayfish to be significantly more active during the dusk than dawn, morning or afternoon based upon local activity data obtained from radiotracking adults during summer. Using trapping data over 24 hours Brown (1979) showed that if trap catches are used as an indication of activity, white-clawed crayfish were predominately active during darkness, a similar pattern was

reported by Barbaresi & Gherardi (2001) in a laboratory population of white-clawed crayfish. Hazlett et al. (1979) recorded at least three times the number of *Orconectes immunis* observed active at night than during the day. The nocturnal behaviour of crayfish is usually considered to be adaptive to minimise the risks of being preyed on by species that are visual hunters (Flint 1977), although the effect of predators on the timing of activity has never been investigated and other factors such as food availability may influence the activity patterns observed.

Seasonal changes in environmental conditions may result in alternating periods of favourable and unfavourable conditions for activity and life cycles (Gherardi 2002). As ectotherms, crayfish are generally more active at higher temperatures and seasonal changes in water temperature appear to be reflected in seasonal changes in activity. Below 10°C, growth in white-clawed crayfish is minimal (Brewis & Bowler 1982). Water temperature appears to be a major factor influencing the activity of crayfish (Flint & Goldman 1975, Abrahamsson 1981, Lozán 2000, Barbaresi & Gherardi 2001) although other factors such as moulting state, breeding, flow conditions and starvation may also influence the activity (Troschel et al. 1995, Schütze et al. 1999). In general crayfish are most active during warmer summer months and, at least at higher latitudes, during the colder winter months are relatively inactive (Brewis & Bowler 1982, Troschel et al. 1995, Barbaresi & Gherardi 2001)

3.1.2 Foraging

There is relatively little published information on the foraging and feeding behaviour of crayfish in the wild. This is likely to be partially a result of their nocturnal habits. Several researchers have attempted to describe and study the foraging of crayfish (Robinson 1997, Gherardi et al. 2001). Robinson (1997) utilised luminescent radioisotope tags attached to crayfish to follow the movements of foraging white-clawed crayfish. Foraging crayfish exhibited relatively localised movements confined to a small area of the streambed (< 3 m^2). Crayfish repeatedly made circular foraging journeys returning to the same initial location, were orientated in an upstream direction whilst foraging and moved rapidly downstream to return to their original location. Studying the foraging behaviour of white-clawed crayfish in a small Apennine stream in Italy, Gherardi et al. (2001) reported that foraging excursions were relatively short (<1 hr) and crayfish moved slowly, covering a small area.

3.1.3 Movements

In addition to short range foraging movements crayfish also regularly make larger movements. It is these larger movements that are likely to be of primary importance in dispersal processes and expansion of populations. Several researchers have studied and described the movements of various crayfish species in a variety of habitats (Black 1963, Momot 1966, Momot & Gowing 1972, Hazlett et al. 1974, Brown 1979, Abrahamsson 1981, Guan & Wiles 1997b, Huolila et al. 1997, Robinson 1997, Gherardi et al. 1998, Bohl 1999, Kirjavainen & Westman 1999, Schütze et al. 1999, Gherardi & Barbaresi 2000, Gherardi et al. 2000b, McCreesh 2000, Robinson et al. 2000, Armitage 2001, Gherardi et al. 2002, Light 2003). Summaries of the main findings of these studies are shown in Table 3.1. These studies, whilst varying in their scope, demonstrate that crayfish are capable of significant active movements. In most studies there was a high degree of individual variability in the distance moved, but maximum movements made by individual crayfish were often of several hundred metres or more.

Although difficult to compare due to different methodologies, several studies appear to describe a similar pattern of movement (Hazlett et al. 1974, Gherardi et al. 1998, Gheradi et al. 2000b, Gherardi & Barbaresi 2000, Robinson et al. 2000). Crayfish often appear to remain in a restricted area for a period of time followed by rapid, relatively large movements to a new area where they remain for a further period of time. During the stationary phase they may make short foraging movements in the area surrounding the burrow (Robinson et al. 2000, Gherardi et al. 2001) but appear to return to the same refuge. During this period Robinson et al. (2000) suggested that *A. pallipes* could be described as maintaining an 'ephemeral home range'. There is no evidence of crayfish returning to a previously occupied refuge after making a movement to a new refuge. In displacement experiments Robinson et al. (2000) found no evidence of crayfish returning to the previously occupied refuge. Gherardi et al. (1998) suggested that white-clawed crayfish demonstrated slow return to home site following experimental displacement, however the predicted return of three months suggests that any homing response is weak.

Several studies have reported a relationship between crayfish body size and extent of movement (Hazlett et al. 1974, Robinson et al 2000, Light 2003). Although the pattern

is not universal, it appears that in some cases larger crayfish may tend to move larger distances. Several other studies have found no relationship between size and movement (Guan & Wiles 1997b, McCreesh 2000), although this may be partially due to the limited size range of crayfish marked or tagged.

In many groups of animals, dispersal is strongly sex biased (Hemker et al. 1984, Logan et al. 1986, Caudill 2003). In crayfish, increased movement of one or both sexes during the mating season has been recorded by several authors (Momot & Gowing 1972, Hazlett et al. 1974, Gherardi et al. 1998, Bohl 1999). Guan & Wiles (1997b) found no sex differences in the distance moved by tagged signal crayfish over several months including the breeding season. The differences in the distances moved by males and females outside the breeding season reported by Light (2003) and Robinson et al. (2000) were fairly small and only applied to movements in a specific direction. During the period when carrying eggs and young, female crayfish have been reported to be less active (Brown & Brewis 1979, Abrahamsson 1981). Whether this is also reflected in reduced distances moved during these periods is not known.

The motivation behind large movements has not been investigated, although factors such as food, finding mates and searching for suitable refuges may all be influential. It does appear that disturbance in the form of electrofishing, tagging or introduction into unfamiliar environment can on occasion stimulate long distance movements (Schütze et al. 1999, Robinson et al 2000).

Table 3.1 Summary of key papers investigating the movements of crayfish.

Species	Methodology	Main Findings	Reference	Study Area
Austropotamobius pallipes	Mark-recapture	No evidence of home range. Large movements of 100 m + recorded	Brown 1979	Manmade aqueduct Northumbria
Austropotamobius pallipes	Mark-recapture	Nomadic movements intercalated by stationary phases. Very weak tendency to return to home pool. Equal upstream and downstream movements	Gherardi, Barbaresi & Villanelli 1998	Fosso di Farfereta Stream, Italy
Austropotamobius pallipes	Radio-telemetry and mark-recapture	Post-release 'fright response' for two days. No evidence of homing. No directional bias. 2/5 crayfish killed by flood. Positive correlation between downstream movements and size. No sex differences. Mean daily movement 4.6 m (males) 1.5 m (females). Nomadic movement intercalated by stationary phases	Robinson 1997, Robinson 2000	Dalton Beck, NE England
Austropotamobius pallipes	Radio-telemetry	No significant difference in us/ds movements. No size or sex differences. Most crayfish remained < 200 m from release location. Single crayfish made large downstream movement 1.4 km in 10 days.	McCreesh 2000	River Rye and River Goul, Ireland
Austropotamobius pallipes	Radiotelemetry	Downstream distances moved were greater. Movements of several hundred metres recorded but most crayfish remained close to release location.	Armitage 2002	River Wansbeck, NE England
Pacifastacus leniusculus	Mark-recapture	Widespread dispersal with movements up to 700 m	Abrahamsson 1981	Lake Natoma USA
Pacifastacus leniusculus	Tag-recapture	No size or sex differences in distance moved. Most recaptures within 200 m of release. No difference between size of upstream and downstream movements.	Guan & Wiles 1997b	River Great Ouse, SE England
Pacifastacus leniusculus	Mark-recapture	Most crayfish remained close to release location (< 100 m) a few travelled large distances up to 580 m	Kirjavainen & Westman 1999	Lake Karisjarvi, Finland
Pacifastacus leniusculus	Mark-recapture	Crayfish moved up to 277 m, at rates up to 120 m/day. Larger crayfish moved greater distances and were more likely to move downstream	Light 2003	Sagehen Creek, California
Astacus astacus	Mark-recapture	Average distance moved 250 m but movements of up to 2 km in 1.5 months.	Abrahamsson 1981	River Iskan, Sweden

Species	Methodology	Main Findings	Reference	Study Area
Astacus astacus	Group mark-recapture	Migrations up to 2.5 km in 1 year	Huolila et al 1997	River Kalajanjoki, Finland
Astacus astacus	Radio-telemetry	Following introduction high levels of movement (> 1 km) were observed. Tendency to move downstream	Schutze, Stein & Born 1999	River Sempt, Germany
Astacus astacus	Radio-telemetry	Remained static when river in flood. Introduced crayfish moved large distances whilst resident crayfish moved smaller distances. Large movements > 1 km tended to be downstream.	Bohl 1999	Rotterbach Creek, Bavaria
Orconectes virilis	Trapping	Migration of females to deeper water	Momot & Gowing 1972	Marl Lakes, Michigan
Orconectes virilis	Mark-recapture	Sequence of numerous days of scarce mobility followed by one or more days of longer displacements (50-200 m)	Hazlett, Rittschof & Rubenstein 1974	Michigan Stream, USA
Orconectes nais	Mark-recapture	Upstream migration linked with recolonisation following floods	Momot 1966	Glasses Creek, Oklahoma
Procambarus penni and *Procambarus bivittatus*	Mark-recapture	Some evidence of home range/remaining in same approximate area of stream	Black 1963	Talisheek Creek, Louisiana, USA
Procambarus clarkii	Radio-telemetry	Two patterns of activity: a wandering phase in which breeding males show large/extemsive movement (up to 17 km in 4 days) and a stationary phase during which crayfish move little	Gherardi & Barbaresi 2000	Rice Fields, Guadalquivir, Spain
Procambarus clarkii	Mark-recapture	Two patterns of movement: stationary phase interposed with nomadic phases of movement	Gherardi, Barbaresi & Salvi 2000b	Irrigation Ditch System, Tuscany
Procambarus clarkii	Radio-telemetry	No evidence of homing. Locomotory speed correlated with size.	Gherardi, Tricarico & Ilheu 2002	Temporary stream, Portugal

3.2 Methods for studying the spatial behaviour of crayfish

Marking and releasing organisms in the wild and their subsequent recapture or relocation has been used for many years to study movements, rates of growth, mortality and abundance of animals (McFarlane et al. 1990). All marks have limitations, which determine their ultimate feasibility. Timescale is an important consideration, some methods are particularly suitable for short-term studies whilst others are more suited to long-term studies. There is often a tradeoff between the precision of the information gathered, the duration of the study, the numbers of animals from which relevant information can be gathered, disturbance by the method and budget (Lucas & Baras 2001). A variety of techniques have been developed and utilised for investigating crayfish spatial behaviour and movement, many of the techniques are more widely used for fisheries research and have been adapted for use tagging crayfish and other crustaceans. Tags are generally considered a subgroup of marks, marks encompass all methods used for distinguishing between groups and individuals whilst tags can be considered physical objects attached to organism to enable their identification. Studies of the spatial ecology and movement of crayfish (section 3.1.) have principally used two methods, mark-recapture and radiotelemetry.

Mark-recapture

In most recent ecological studies of crayfish movement, external marks have been applied to the carapace by branding (e.g. Abrahamsson 1965, Brewis & Bowler 1982, Robinson et al. 2000, McCreesh 2000) or by the clipping and punching of holes in the telson and uropods (Momot 1966, Guan 1997). By applying a combination of marks in different areas these methods allow a large number of crayfish to be coded and individually recognised on recapture. Guan (1997) described a system of hole punching for crayfish by which over 10,000 individuals could be coded. These marks tend to become less distinct, with tissue regeneration occurring on ecdysis, and marks are completely lost after 2 or 3 moults (Abrahamsson 1965, Guan 1997). Guan (1997) showed that in laboratory experiments, clipping and punching holes in the telson and uropods resulted in a significant reduction in growth. He also suggests that branding is likely to have similar or greater effects on growth although this has yet to be tested. The suggestion has also been made that branding of small crayfish may interfere with moulting (Peay 1997). Painting of the exoskeleton or attachment of numbered tags has been used (Peay 1997, Gherardi et al. 1998) but these marks will only persist, at most until the animal moults and are thus most suitable for short-term studies.

Several tags such as streamer and anchor tags have been developed which attempt to overcome the problems of loss of exoskeleton by anchoring external tags through the exoskeleton into muscle. These have proved successful in some large crustaceans (e.g. *Jasus verreauxi* - Montgomery & Brett 1996). In other situations they have been associated with problems including failed moulting, infection, tag loss, lowered survival and attraction of predators (Hurley et al. 1990, Benzie et al. 1995, Linnane & Mercer 1998).

With the problems associated with external marks and tags, one solution is to implant a tag into the animals' body that is not lost during moulting. Several internal tags have been developed including elastomer visual implant (EVI), alphanumeric visual implants (AVI) and coded microwire tags.

EVI and AVI tags are reliant on implanting material beneath transparent or translucent tissue. EVI consists of a florescent elastomer material that is injected as liquid and solidifies into a biocompatible solid. A limited number of individual tags can be obtained by using combinations of colours and different marking locations, although it is more suited to batch marking. AVI are small rectangles (smallest available 1.0 mm x 1.5 mm) of biocompatible polyester which are inserted beneath transparent tissue. They allow the unique identification of individuals through a three character alphanumeric combination, and are available in various colours that further extends the number of individual combinations. Both EVI and AVI have been tested as a method for identifying crayfish (Isely & Stockett 2001, Jerry et al. 2001). Initial trials suggest that both tags offer the potential to mark crayfish including juveniles. Jerry et al. (2001) reported that tagging with EVI and AVI lead to 13% and 11% mortality in juvenile *Cherax destructor*, whilst Isely & Stockett (2001) recorded 100% survival in AVI tagged juvenile *Procambarus clarkii*. Tags were retained through moult although both studies reported tag loss of about 20% (Isely & Stockett 2001, Jerry et al. 2001).

Microwire or coded wire tags (CWT) were one of the earliest internal tags to be developed (Jefferts et al. 1963) and are the most widely utilized tag in fin fish stock enhancement, assessment and research applications. They are small (smallest commercially available 0.5 mm x 0.25 mm) stainless steel magnetised wire tags which are marked with rows of laser-etched numbers denoting specific batch or individual

codes which are injected by hypodermic needle into suitable tissue. Upon recapture the animal can be examined for presence of CWT with a magnetic detector. The individual identification through reading the code is usually reliant on the removal of the tag and examination of the CWT under a low-powered microscope. CWT have been used successfully in a range of marine crustaceans (e.g. *Callinectes sapidus* Van Montfrans et al. 1986, Fitz & Wiegart 1991, *Homarus americanus* Uglem & Grimsent 1995, Cowan 1999) and recently in crayfish (*Procambarus clarkii* Isely & Eversole 1998). The removal of the tag usually results in death of the individual however it is possible to inject the tag at the base of the leg allowing the leg to be removed without killing the tagged individual.

The tagging and marking methods outlined above are reliant on the recapture of crayfish. Recovery of substantial numbers of marked crayfish often requires considerable fishing effort. In most mark-recapture studies the percentage of marked crayfish that are recaptured is low, usually less than 20 % (17%, Guan & Wiles 1997b; 15% Light 2003; 10% Robinson et al. 2000; 1% McCreesh 2000). Furthermore intensive sampling can lead to disruption of the ecosystem through turnover of substrate (handsearching) and/or modification of animal behaviour (trapping).

Radiotelemetry

Several studies have shown radiotelemetry to be a highly effective technique for investigating the spatial behaviour of crayfish (Chapter 6, Bohl 1999, Schütze et al. 1999, Gherardi & Barbaresi 2000, Robinson et al. 2000). It provides fine temporal and spatial scale information on the movements of crayfish and is not reliant on the recapture of animals. As tags transmit actively it is possible to search large areas for animals, this is likely to lead to less bias in sampling effort than mark-recapture studies where sampling effort is usually concentrated in the area surrounding release of organisms and may under-record long distance movements. Due to the relatively large size and weight of transmitters, radiotelemetry has so far been limited to relatively large adult individuals (CL > 30mm). The size of radio transmitters is a trade off between size, operating life and detection range. The smallest radio transmitters currently available weigh less than 0.4 g in air and measure 10 x 5 x 5 mm. Using these transmitters the size range of crayfish tagged could be extended to approximately 25 mm but the life of these transmitters would restrict tracking crayfish to 15-20 days. Radiotelemetry studies using larger transmitters (Bohl 1999, Schütze et al. 1999,

Robinson et al. 2000) have tracked the movements of animals for longer but still restricted periods (<3 months) due to a combination of limited battery life and loss of external transmitters at moulting. A major factor affecting the use of radiotransmitters is the high cost of tags and detection equipment; the numbers of crayfish tagged in radiotelemetry studies is usually low (18 crayfish, Robinson et al. 2000; 14 crayfish, McCreesh 2000; 5 crayfish Gherardi & Barbaresi 2000; 14 crayfish Gherardi et al. 2002; 22 crayfish Bohl 1999; 13 crayfish Schütze et al. 1999) partially as a result of the limited budget of research programs.

Passive Integrated Transponders (PIT) tags

Passive integrated transponder (PIT) tags are sealed electronic modules that when energised from an external antenna, return information programmed into them, typically a unique identification number. The tag consists of an integrated circuit chip, capacitor, and antenna coil encapsulated in a glass cylinder; its operation requires an external energy source. An electromagnetic field is produced by the reading unit inducing current in the antenna coil, which energises the integrated circuit and causes the tag to transmit its electromagnetic identification code to the receiver (Roussel et al. 2000). Each PIT tag has a 10 digit alphanumeric code, this provides several billion possible combinations and allows each tag to have a unique code. There are two basic PIT systems; full-duplex systems (FDX) and half-duplex (HDX) systems. Full-duplex systems operate with the reader emitting a continuous electromagnetic field, the reader is able to receive signals emitted from tags at the same time as producing the electromagnetic field. Half-duplex systems operate with a pulsed reader field and a transponder that emits an identification code in the "quiet" time intervals between the field pulses. PIT tags contain no power source and can theoretically remain functional indefinitely. They are physiologically neutral, and because of their small size (the smallest commercially available are 10.3 mm long x 2.1 mm in diametre) they can be surgically implanted into relatively small animals including large invertebrates.

In the past decade the use of PIT tags for studying the spatial behaviour of fish species has become widespread (e.g. Prentice et al. 1990a,b,c, Castro-Santos et al. 1996, Lucas & Baras 2000, 2001). They have also been utilised for long-term marking of a range of small animals including reptiles (Reading 1997) amphibians (Holenweg & Reyer 2000, Jehle & Hodl 1998), mammals (Harper & Batzli 1996) birds (Jamison et al. 2000,

Carver et al. 1999) and echinoderms (Hagen 1996) and their use has been extended to internal tagging of crustaceans (Wiles & Guan 1993, Caceci et al. 1999)

In addition to their use in conventional mark-recapture studies, PIT tags have the capability to be detected some distance from the reading antenna. The tags have detection ranges of up to 20 cm for the smallest tags with greater detection distances for larger tags. This offers the possibility to detect and identify tagged organisms in the natural environment without capture or handling. Fixed detector arrays have been used to monitor movements of tagged fish through fish passes (Castro-Santos et al. 1996, Lucas et al. 1999) and natural stream channels (Armstrong et al. 1996, Zydlewski et al. 2001). Recently portable detectors for searching rivers and streams for tagged fish have been developed (Roussel et al. 2000, Morhardt et al. 2000). There is a general compromise in PIT tagging studies between the size of tags and the detection range. Most studies have utilized 12-mm PIT tags as there small size permits their implantation into a wide range of species and age classes. There is increasing use in fisheries applications where remote detection is important of larger 23-mm PIT tags. These larger tags have a much improved detection range over 12 mm PIT tags. Detection distances of greater than 50 cm enable large areas of habitat to be effectively searched and they have proved highly effective in detecting and locating fish (Morhardt et al. 2000, Roussel et al. 2000, Zydlewski et al. 2001). Their large size precludes their internal use in most crayfish species although the potential exists for their internal use in a few crayfish species and other larger decapod species that grow to sufficient size.

3.3 The use and development of PIT tags for marking and studying movement of crayfish

Two novel techniques for tagging crayfish with PIT tags were developed and used to study the movement of crayfish i) internal tagging of crayfish with 12-mm (FDX) PIT tags and ii) external tagging and remote detection of crayfish with 23-mm (HDX) PIT tags

The internal implantation of PIT tags in crayfish has the potential to permit long term individual identification, avoiding the problem of loss of tag at moulting and allowing remote detection. The effect of PIT implantation was investigated in a laboratory study with signal crayfish. A portable detector was developed and its efficiency at searching various microhabitats was tested. In addition internal PIT tagging of a stream population

of white-clawed crayfish was carried out. This was principally to investigate the movement patterns of white-clawed crayfish, a full description of site and methods is contained in Chapter 5 but here aspects of the study which relate to the use of internal PIT tags to tag white-clawed crayfish are reported.

The ability to detect 23-mm PIT tags over relatively large distances has the potential to allow efficient detection and relocation of crayfish enabling the investigation of movement and dispersal patterns. A method for the external attachment of 23-mm PIT tags was developed and used to tag signal crayfish in a riverine population. A backpack reader was constructed and its efficiency and ability to relocate tagged crayfish was investigated. The movement patterns, dispersal, site characteristics and detailed methodology are described in Chapter 4, reported here are aspects of the study relating only to the PIT tagging methodology developed.

3.3.1 Methods

3.3.1.1 Internal implantation of 12-mm (FDX) PIT tags

Effects of tagging on captive signal crayfish

Signal crayfish, were captured in the River Wharfe, northern England during November 2000. Crayfish were acclimated to laboratory conditions for at least 20 days before tagging. The carapace length (CL), from the rostral apex to the posterior median edge of the cephalothorax, was measured to the nearest 0.1mm and crayfish were assigned to pairs matched for sex and size. Sixty crayfish were used (CL 33.7-61.4 mm), 34 males and 26 females. On the basis of preliminary assessment and past work (Wiles & Guan 1993), it was considered that crayfish smaller than 27-mm CL were not taggable with 12-mm PIT tags due to physical size limitations of the body cavity.

One individual from each size and sex matched pair of crayfish was tagged with a Trovan ID 100 PIT tag (nominally 12 x 2.1 mm PIT tags, 0.10 g in air; Trovan Ltd., Douglas, UK) whilst the other acted as a control. Tagging was carried out by holding the animal around the cephalothorax with the ventral surface uppermost and making an incision, using the tip of a sterile large gauge (diametre 2.5 mm) hypodermic needle, c. 3 mm wide and deep through the cuticle and underlying tissue at the base of the fifth pereopod (fourth walking leg). The tag was inserted through the incision, by gently pushing the tag anteriorally so that it came to rest underneath the digestive gland (hepatopancreas) and above the segmental musculature.

Crayfish were kept in individual tanks (50 cm x 30 cm x 30 cm), filled with de-chlorinated tap water, and provided with sections of plastic drainpipe for shelter. Water was changed at regular intervals (4-6 days). Crayfish were maintained at 15°C, a temperature at which they exhibit substantial feeding activity, with a light regime of 12 h: 12 h LD. Two months after tagging, to encourage crayfish to moult, the light regime was changed to 16 h: 8 h LD over a four week period, with light increased by an hour each week. Crayfish were fed *ad libitum* with slices of carrot and potato and weekly with pellets of amphibian food (protein 48%). Tanks were checked daily for mortality, tag loss and shed exoskeletons. Moulting date was recorded and the new CL was measured once the new exoskeleton had hardened. The experiment lasted for 6 months (182 days). Crayfish were tagged on 11 December 2000 and the experiment terminated on 11 June 2001.

PIT tag reader design

The prototype reader design (UKID Systems, Preston, UK) consists of a coil antenna, mounted on a pole to facilitate searching of the stream bed, connected to a decoding electronics module (Figure 3.1). The search head (diametre 180 mm) containing the electronic drive circuitry for the PIT tag energisation coil is potted in a waterproof housing. This is connected to a lightweight alloy tube (length 1.5 m), within which runs a cable connecting the search head to the decoding electronics. The decoding electronics are mounted in a compact lightweight plastic enclosure (26-cm long x 12-cm wide x 7-cm deep) with shoulder strap attachment. The reader unit weighs 800 g and the search antenna and pole 1900 g, total weight of the system 2700 g. It is a full-duplex (FDX) system operating at 125 kHz. The reader unit is operated by a three position toggle switch to allow off / momentary or continuous scanning of transponders. When detected, the transponder identity number is displayed on a 2 line x 16 character liquid crystal display. The reader has a "save" mode of operation that stores upto 3160 time/date stamped readings of transponder numbers for download to a personal computer via an RS-232 serial port. A socket for the connection of an external earpiece permits the operator to receive an audible indication of tag read in conditions of high ambient noise. The system is powered by an integral 1500 mAh NiMH battery pack which provides approximately 7 hours of continuous use. In addition an external battery pack (1500 mAh NiMH) can be attached to the reader extending the continuous run

time to 16 hours. A mains-powered, fast intelligent charger allows the internal batteries to be fully charged in less than 60 min.

Figure 3.1 Prototype 12-mm Passive Integrated Transponder (PIT) tag reader (UKID Systems, Preston, UK), shown with external battery pack (black casing). Pole with search head measures 1.5 m.

Trovan ID100 PIT tags (12-mm long x 2.1-mm diametre) were used in the laboratory experiment for assessing effects of tagging on crayfish, and UKID122GL PIT tags (12-mm long x 2.1-mm diametre; UKID Systems, Preston, UK) were used in the field detection testing. Both tags had similar detection ranges. The detection range varied with the orientation of the tag to the antenna and ranges of up to 150 mm were recorded when the tag was vertical (long axis of the tag perpendicular to the flat surface of the search head, measured as the distance from tag to antenna). Range was reduced by approximately 40% when the long axis of the tag was parallel to the flat surface of the search head. Range loss with tags in water or within the substrate was not apparent or was negligible.

Efficiency testing

An assessment was made of the ability of the reader unit to detect and locate tags in the field. Within a small river, the River Browney (NGR: NZ 257 406; depth < 1 m) an area of approximately 60 m^2 was surveyed, consisting of equal areas of small cobble (20 m^2), medium cobble (20 m^2) and large cobble (20 m^2). Within each microhabitat 25 PIT tags were placed by one operator beneath rocks in similar positions to where crayfish are normally found. The mean depth (MD) and mean maximal axis (MMA) of the rocks beneath which the tags were placed in each of the microhabitats were: small cobble (MD 26.6 mm, MMA 68.2 mm) medium cobble (MD 48.2 mm, MMA 130.4 mm) large cobble (MD 78.8 mm, MMA178.6 mm). In addition, tags were placed in artificial

burrows within a 30-m long stretch of bank. Burrows of lengths 5, 10 and 15 cm were made and tags were positioned 2.5 cm from the end of the burrow. Thus, tags were positioned at depths of 2.5 cm, 7.5 cm and 12.5 cm within the burrows. Twenty tags were placed in each of these burrow lengths. The area in which the tags were hidden was blind-searched by an operator unfamiliar with the site. When searching, the operator waded in an upstream direction, moving the antenna across the search area, just above the streambed, and across the submerged bank.

Tagging of a stream population of white-clawed crayfish

Five hundred and two white-clawed crayfish were captured and tagged in a 780 m section of Eller Beck, a tributary of the River Wharfe (NGR SE 977 617 – SE 983 622; see Section 2.3). Crayfish were tagged in two periods 14-31 August 2002 and 25 June–9 July 2003, with 382 and 119 crayfish tagged in each period respectively. Two hundred and forty one females (CL 27.3 – 42.7 mm) and 260 males (CL 27.7 – 46.0 mm) were tagged. Crayfish were tagged with either Trovan ID100 PIT tags or UKID 122GL PIT tags, both tags are glass encapsulated and identical size (12-mm long x 2.1-mm diametre). Tagging was carried out in the same manner as outlined for signal crayfish described above. Following tagging, crayfish were immediately returned to the stream. During 2002 and 2003, regular surveying of Eller Beck using a combination of trapping and night viewing was carried out (full details Chapter 4) to relocate tagged crayfish. When tagged crayfish were retrapped the tag insertion site on tagged crayfish was inspected, and a note made of crayfish that had moulted since tagging.

3.3.1.2 External tagging of crayfish with 23-mm (HDX) PIT tags

Portable reading unit

The portable reading unit (Figure 3.2) was constructed by incorporating a commercially available radio frequency identification system (Texas Instruments TIRFID S-2000) and was based upon the design of Roussel et al. (2000). The system consisted of a half-duplex reader module (TIRFID RI-RFM-008B) operating at 134.2 kHz, connected to a control module (TIRFID RI-CTL-MB2A). The reader/control modules were powered by a rechargeable 12-V DC, 10 Ah lead-acid gel battery, which provided in excess of 8 hours continuous run time on a single charge. Both modules were housed in a plastic box (280 mm x 180 mm x 140 mm). The instrumentation box and battery were attached to a rigid-frame rucksack. The reader module was connected to an open loop inductor

antenna that both generated an energising electromagnetic field and received transmitted signals from the tag.

a) b)

Figure 3.2 a) Portable 23-mm PIT reader in use b) the rechargeable 12-V battery, palmtop computer and reader and control module (viewed from left to right).

The antenna was constructed using 6 mm insulated fine copper multistrand (approximately 525 x 0.12 mm conductors) wire; 6 loops of the wire were wound to form a 80 x 55 cm rectangular inductor loop. The inductor coil was contained in PVC tubing (diametre 3.5 cm), with a 115 cm PVC handle to allow the movement of the antenna to be controlled by the operator. PVC was used as it is lightweight and non-ferrous, ferrous materials will interfere with and reduce the detection field.

A bank of tuning capacitors (TIRDIS RI-ACC-008) was connected to the circuit between the antenna and the reader module and was housed in the backpack; selection of combinations of capacitors allowed the antenna circuit to be tuned to the resonant frequency. The reader circuit was set up with a charge time of 50 ms and rest time of 50 ms so that tags that entered the antenna field for 100 ms were detected. A palmtop computer (Hewlett Packard HP200LX) was connected to the control module via a RS-232 serial cable. A custom software program (written in BASIC language by A. Haro, USGS, Conte Laboratory, MA, USA) continuously displayed and logged tag code data sent from the control module via the RS-232 interface, along with date and time information. The program provided the option that although the detector would repeatedly detect the same tag when it was within the field, the user could enter a time in seconds during which the program would not display the tag again after its initial detection. The palmtop computer was housed in a chest mounted waterproof,

transparent flexible case so that the operator could read detected tag codes as they were displayed. A piezoelectric buzzer was connected to a circuit on the control module so a loud tone was sounded whenever a tag was detected in the antenna field. The total weight of the complete system was approximately 5 kg.

The detection range (measured as the distance between the plane of the antenna loop and the tag, while holding the antenna horizontally above a PIT tag) varied with the orientation of the tag and with the location of the tag around the antenna (Figure 3.3) detection ranges of up to 60 cm when the tag was horizontal and up to 82 cm when the tag was vertical were recorded. The tag could be read within water and beneath the substrate without any loss of detection.

Efficiency trials

Before tagging efficiency tests of the system were carried out to detect tagged crayfish by concealing tags within the habitat to mimic tagged crayfish under refuges. A 20 m x 5 m area of riverbed containing a mixture of pebble, cobble and boulder habitat was searched for signal crayfish. In the positions in which crayfish were recorded a tag was placed. Particular attention was paid to searching and concealing tags beneath large cobble and boulders where crayfish were recorded. 40 tags were concealed in positions in which crayfish were recorded. The area was then blind searched by an operator unfamiliar with the site. During the efficiency trials single tags were concealed within each refuge even if more than one crayfish was recorded.

Scanning

Scanning was carried out by moving the antenna just above the substrate in a sweeping motion. It was found practical to scan 2m wide strips of the river bed. The operator could move at a slow walking pace whilst moving the detector antenna from side to side (Figure 3.4). During initial trials one of the main difficulties that lead to non-detection of tags was missing areas of river bed whilst scanning. Markers on the bank and within the river (marked stones) were important to orientate the operator and ensure all areas of river bed were scanned.

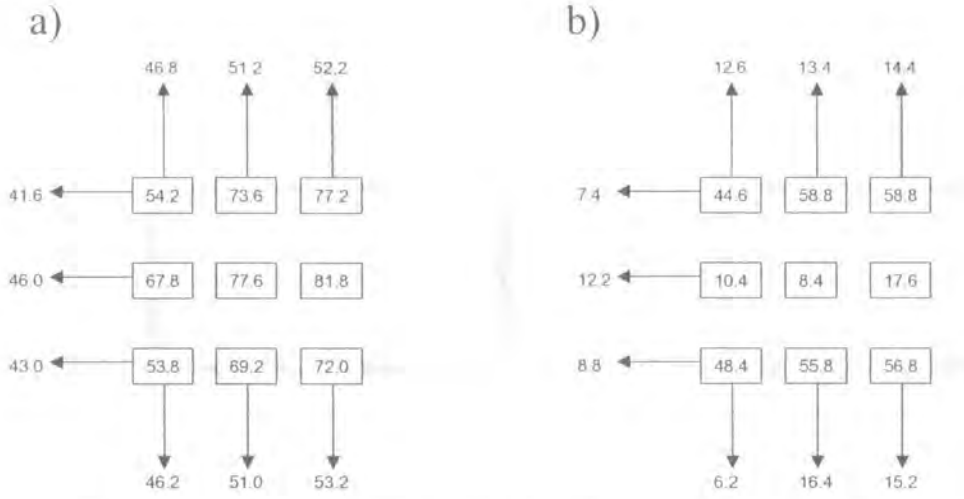


Figure 3.3 Maximum detection range of the portable PIT detector unit with TIRFID series 2000; RI-TRP-WEHP, (Texas Instruments, 23.1-mm long, 3.9-mm diametre) PIT tags a) perpendicular and b) parallel to the antenna loop. Boxed numbers refer to distance measured perpendicular below the antenna and unboxed numbers refer to distances measured on the same plane as the antenna. Distances are mean maximum detection distances (cm) of measurements made with five different PIT tags. Antenna loop measures 80 x 55 cm.

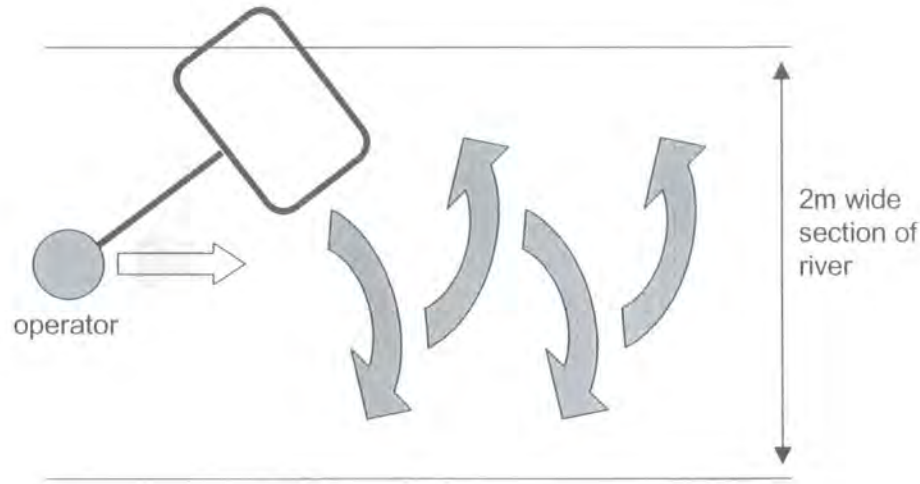


Figure 3.4 Method used to scan 2m wide transect of river bed with PIT detector.

Capture and tagging

Signal crayfish were captured by handsearching and tagged between 18 and 21 August 2003 from a 44-m stretch of river. Passive Integrated Transponder (PIT) tags (TIRIS series 2000; RI-TRP-WEHP) were used to track crayfish. Tags measured 23.1-mm long, 3.9-mm diametre, mass in air 0.6 g, and were attached to the cephalothorax. Tagging was restricted to crayfish of carapace length greater than 20 mm. This was the smallest size of crayfish it was possible to attach a tag to without restricting mobility of

the tail or overhanging the rostrum. Prior to attachment, in order to aid adhesive attachment, the surface of the encapsulating glass was abraded using emery paper. The tags were attached to the median line of the cephalothorax of crayfish using a combination of cyanoacrylate adhesive and dental acrylic (Figure 3.5). The dorsal surface of the cephalothorax was dried and cyanoacrylate adhesive applied to attach the tag in position. Dental acrylic was then used to fill around the lower portion of the tag to provide a strong robust means of attachment. Great care was taken to ensure that the animals' eyes, joints and antennae remained free from glue. Tagged crayfish were retained for approximately 30-mins until the acrylic was set. During this time the gills of the crayfish were kept moist by providing small amounts of water in the trays in which the crayfish were retained. On the 9 and 10 September 2003, after the completion of scanning, handsearching was carried out, and on the 9 September 30 traps were set in the central study area, to recover tagged crayfish and assess tag retention.

Figure 3.5 Signal crayfish tagged with 23-mm glass encapsulated Passive Integrated Transponder (TIRIS series 2000; RI-TRP-WEHP)

3.3.2 Results

3.3.2.1 Internal impantation of 12-mm (FDX) PIT tags

Survival and tag retention of captive signal crayfish

Although histological studies were not carried out, the tag insertion site appeared to heal within two weeks, but could be identified by slight pigmentation. Following moult there was no sign of the incision site. The position of tags was verified by x-radiography of three tagged crayfish (Figure 3.6), these showed little movement of the tag from the injection site.

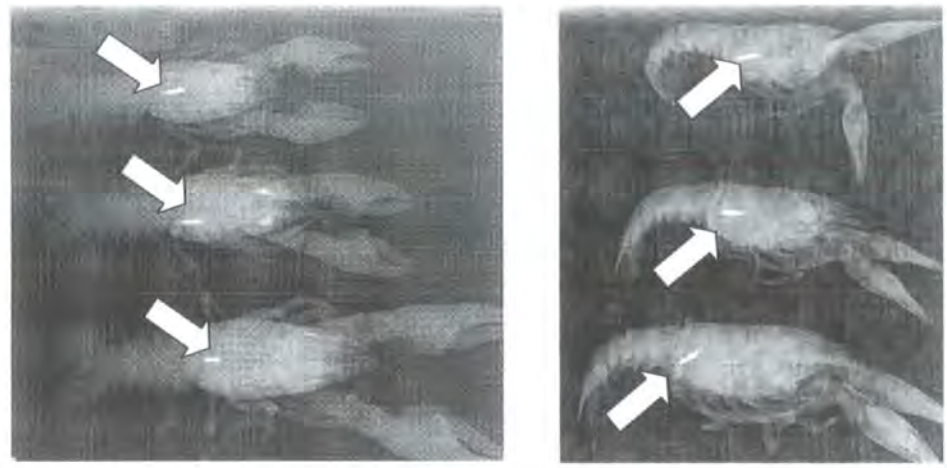


Figure 3.6 X-radiographs of three PIT tagged *Pacifastacus leniusculus*. Crayfish had been tagged for 6 months and undergone one moult before X-radiographs were taken. a) dorsal view b) lateral view. Arrows indicate position of tag which appears white on x-ray. Tag measures 12-mm in length.

Both control and tagged groups exhibited high survival during the 182 days of the experiment. Two tagged crayfish and one control animal died over this period, resulting in percentage survival of 93.3% of tagged crayfish, and 96.7% of the control group. There was no significant difference in mortality between tagged and control groups (Fisher exact test, $P > 0.05$). One mortality in the tagged group appeared to have been caused by the tagging procedure. Immediately after tagging the crayfish became comparatively unresponsive and it died within 24 hours of tagging. It appears that, in this case, the ventral nerve cord, which lies close to the ventral surface, may have been damaged. During the remainder of the experiment two crayfish died, one from each group. Reasons for mortality are unknown, but both cases occurred in the immediate pre-moult phase.

Over the duration of the experiment, tag retention was 100%. All tags remained operational throughout the experiment and the tag identification number could be read by passing the reader unit over the tagged crayfish.

Moulting of captive signal crayfish

All crayfish that moulted did so successfully without any apparent complications. During the course of the study 51 crayfish moulted (25 tagged, 26 controls), including 3 crayfish (1 tagged, 2 controls) that moulted twice. In pairs in which both crayfish moulted, the timing of first moult in tagged ($\bar{x}$ = 109 days post tagging) and control animals ($\bar{x}$ = 114 days post tagging) did not differ significantly (paired *t*-test, t = 0.77, d.f. = 22, $P > 0.05$) (Figure 3.7).

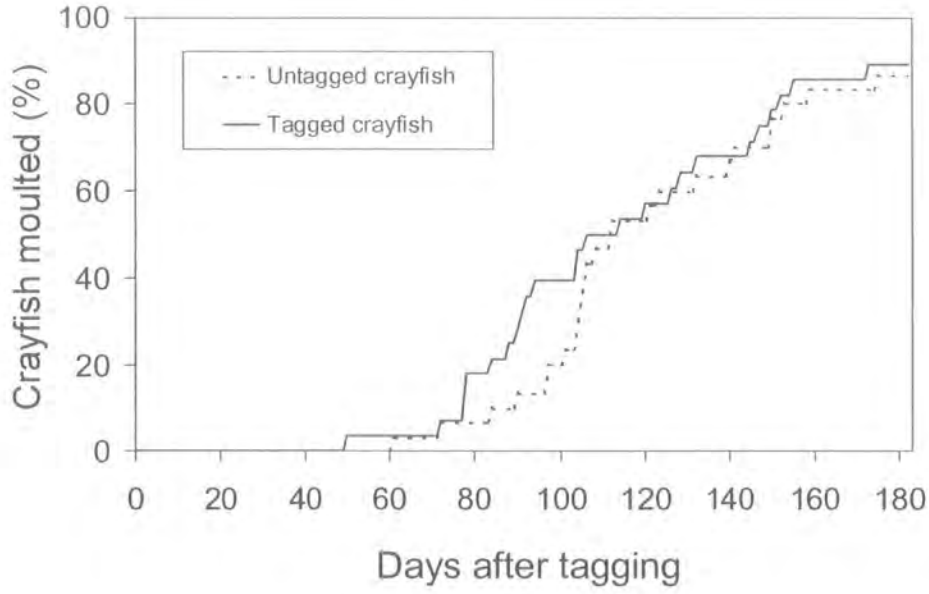


Figure 3.7 Timing of first moult during the experimental period for tagged and untagged *Pacifastacus leniusculus* held under laboratory conditions. Data are for all crayfish that survived to the end of the experiment (28 tagged, 29 untagged).

The moult increment (MI) and % moult increment (% MI) of tagged and untagged crayfish was not significantly different in males, females and both sexes combined (2-Factor ANOVA; MI $f_{3,57} = 0.866$, $P > 0.05$; % MI $f_{3,57} = 0.781$, $P > 0.05$). The growth of tagged crayfish was slightly reduced, by about 10% compared to untagged controls, although this difference (Table 3.2) was not significant.

Table 3.2. Per moult increment (MI), and percentage moult increment (% MI) of *Pacifastacus leniusculus* tagged with PIT tags and untagged controls retained under laboratory conditions. Data comprises 23 pairs of crayfish matched for size and sex in which both crayfish moulted.

	Initial CL, mm ($\bar{x}$ ± SD)	Post-moult CL, mm ($\bar{x}$ ± SD)	MI, mm ($\bar{x}$ ± SD)	% MI, mm ($\bar{x}$ ± SD)
Tagged (n = 23)	42.19 ± 4.61	45.99 ± 5.03	3.80 ± 1.18	9.04 ± 2.92
Males (n = 12)	42.61 ± 5.56	46.66 ± 5.88	4.04 ± 0.91	9.55 ± 2.21
Females (n = 11)	41.72 ± 3.50	45.26 ± 4.07	3.54 ± 1.42	8.47 ± 3.57
Controls (n = 23)	42.13 ± 4.23	46.32 ± 4.75	4.19 ± 1.08	10.08 ± 2.97
Males (n = 12)	42.51 ± 5.94	46.80 ± 5.71	4.29 ± 0.90	10.35 ± 2.81
Females (n = 11)	41.71 ± 3.15	45.79 ± 3.64	4.08 ± 1.28	9.78 ± 3.25

Efficiency of tag detection

The position of tags could be determined to within a 10-cm radius. In all microhabitats, including burrows, a high percentage (≥ 80%) of tags were detected and located (Fig. 3.8). There was no significant difference in the number of tags located within the different cobble classes (Fisher exact test, $P > 0.05$) or the different burrow depths (Fisher exact test, $P > 0.05$). Comparison of cobble classes combined with burrow classes combined, indicated that significantly more tags were located within the cobble classes than burrow classes (Fisher exact test, $P = 0.018$).

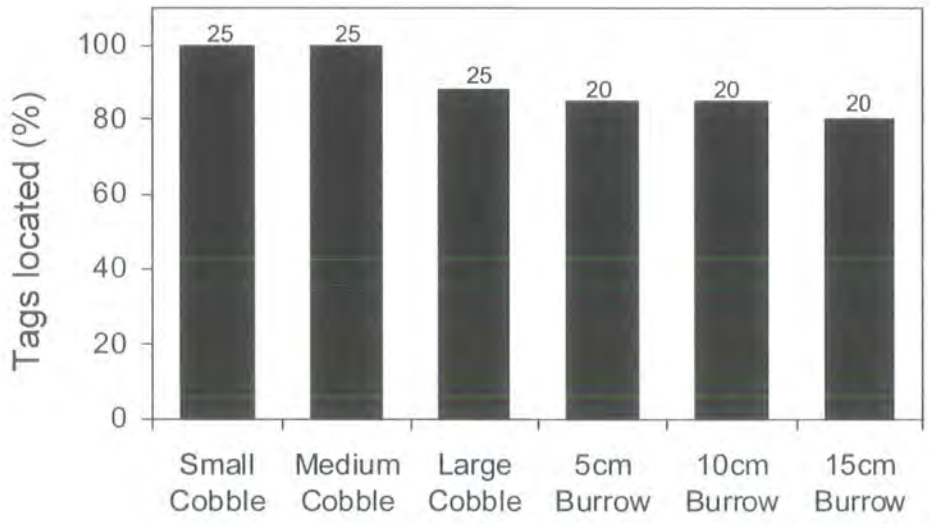


Figure 3.8 Efficiency of PIT tag detection depending on microhabitat. Tags within burrows were placed 2.5-cm from the extremity of the burrow to mimic a 5-cm long crayfish at the end of the burrow with the tag implanted in its body cavity. Each bar superscript denotes the number of tags placed within each microhabitat.

Field tagging of white-clawed crayfish

82% of PIT tagged crayfish were subsequently captured or relocated at least once after tagging. Crayfish were relocated and the PIT tag successfully interrogated up to 409 days after tagging when the study was terminated. No mortality directly caused by tagging was observed, although due to the immediate release of tagged crayfish observations were limited. All tagged crayfish when released swam or walked with no sign of mobility being impaired.

Premoult tag loss

Following tagging the insertion site of all recaptured crayfish appeared to heal successfully. A small discoloured mark was present where the insertion had been made but no infection was ever observed at the site. The discolouration at the insertion site persisted until crayfish moulted. This enabled an assessment of post tagging tag loss. No crayfish were recorded that had insertion mark but were not tagged. No tag failure of these crayfish was recorded. Tag loss during or post moult is possible but could not be assessed.

Moulting and breeding

Over the course of the study 163 crayfish were trapped and recorded as have moulted successfully and retained the tag, with several crayfish recorded moulting more than once. Berried females rarely enter traps, and only a small number of tagged berried females (5) were captured.

3.3.2.2 External tagging of crayfish with 23-mm (HDX) PIT tags

Efficiency testing

All 40 tags concealed within the habitat were detected when the area was blind searched. Additional trials were carried out by concealing tags beneath the largest boulders present at the site but tags could still be detected.

Field detection of tagged crayfish

The detector appeared successful at detecting tagged crayfish. Over 80% of crayfish tagged were detected at least once, and most were detected several times (full details of areas scanned are given in Chapter 4). Tag attachment did not appear to adversely affect movement or behaviour of crayfish. Following tagging crayfish were observed to walk or 'tail-flip' away and take cover under cobbles and boulders, their mobility did not appear to be restricted by tags with no perceivable difference in the observed movement of tagged and untagged crayfish. At the completion of the study, tagged crayfish were found in similar refuges and areas to untagged crayfish and tagged crayfish were found sharing refuges with untagged crayfish. The movement of crayfish did not appear to be

impaired by tagging with substantial movement of tagged crayfish away from the release location recorded.

Areas of river bed could be rapidly scanned for tagged crayfish. The 180-m central study stretch of river could be effectively scanned by a single operator, recording all detected crayfish, in about 3 hours. The non-uniform field produced by the detector and variation in the detection distance with orientation of the tag did not enable highly precise positioning of the tag. It was usually possible to identify the position of the tag to within 50 cm. However, when several tagged crayfish were in close proximity it was difficult to resolve the position to less than 1 m.

Tag retention

During scanning five tags were recovered from the substrate; no longer attached to crayfish. In all cases the tags were recovered without adhesive attached suggesting that the loss of the tags was due to the detachment of the tag from the adhesive rather than the adhesive becoming detached from the crayfish carapace. A total of 57 tagged crayfish were recaptured between 22 and 27 days after tagging. In addition 5 crayfish in which tag loss had occurred were recovered (adhesive still attached to carapace but no tag). An estimated tag loss of 8.7 % was calculated from number of crayfish captured with tags attached compared to number of crayfish captured without tag but evidence of tag attachment still remaining. Of recovered tags three of 62 tags had failed (they would no longer report their identity when interrogated). The reason for tag failure was not apparent with the glass encapsulation still intact. Moulting of crayfish will also lead to loss of tags, the number of tags lost due to moulting was minimised by carrying out the study during a period of low moulting frequency. Signal crayfish within the study area will frequently moult in the open and shed exoskeletons can be observed on the streambed (D. Bubb pers. obs.). All moulted exoskeletons encountered during scanning were checked for attached tags, a single moulted exoskeleton with attached tag was recovered.

3.3.3 Discussion

3.3.3.1 Internal implantation of 12-mm PIT tags

The initial laboratory studies and tag detection efficiency testing was conducted in 2001 and it was hoped that the system could be applied to a wild stream population of crayfish in 2002/03. For the system to operate effectively at detecting crayfish during the daytime, when they are within refuges, it is reliant on the substrate being relatively

small and crayfish utilising accessible (to the detector head) within-stream refuges. No streams within the study area were found to contain the combination of an abundant crayfish population and suitable substrate / refuge use to apply the system. As a compromise internal PIT tagging was carried out in a stream population of white-clawed crayfish. In this relatively abundant stream population most crayfish did not utilize within stream refuges but used burrows and refuges at the base of undercut banks that were not accessible to the PIT reader unit.

The main limitation of the UKID FDX tagging and reading system is the relatively short distance from the antennae which tags can be detected. This limits the system to stream environments in which the refuges used by crayfish are accessible to the scanner. The field trials of the reader unit suggest that if tags are within range of the antennae the system is efficient at searching for tags in the manner it would be employed in the field. The detection efficiency was lower in the burrow microhabitat classes compared to cobble microhabitats, possibly as it was found harder to position the antenna coil close to the substrate on vertical banks in comparison with the horizontal streambed. In environments in which large boulders and root masses are common it may be difficult to position the antenna close enough to tagged crayfish to detect them. Similarly the depth of crayfish burrows may be influential in determining if crayfish are detected. This may result in some size bias in the burrowing crayfish that are recorded, as larger crayfish tend to make deeper burrows (Guan 1997). Signal crayfish are capable of burrowing to depths of over 30 cm, which could potentially place tagged crayfish out of the detection range. Use of a larger search head and antenna coil could enable faster searching of a given area, although for use of a fully enclosed coil as used in this study, increased size would result in greater resistance to flow and reduced ability to search around rocks and other likely refuges. This could be solved by using an 'open coil' design such as that of Roussel et al. (2000) in which the antenna coil is protected by plastic piping and which could be placed over rocks of smaller radius than the coil. Recent technological advances and the development of '12-mm supertags' with increased detection ranges of upto 30 cm have the potential to improve the effectiveness of remote detection of internally PIT tagged crayfish. This may reduce the limitation that the short detection distances currently place on the application of the system.

Internal PIT tagging of crayfish had several benefits: it permits repeated non-destructive identification of individuals, has a theoretically indefinite life span, negligible tagging

mortality, high tag retention, and no apparent long-term effects on growth and survival of tagged animals. Internal PIT tagging has also been used successfully in the laboratory without ill effect on prawns tagged in the abdominal musculature (Caceci et al. 1999). The laboratory trials of this study support the preliminary findings of Wiles & Guan (1993) that PIT tagging does not adversely affect growth or survival of signal crayfish. Growth and moulting of captive tagged crayfish appeared normal with no significant difference between the growth of tagged and control crayfish. This contrasts with a reduction in growth of 15.4 - 18.3 % when marking crayfish externally by punching and clipping holes in uropods, telson and pleura (Guan 1997).

The survival of captive tagged and control crayfish was high. The death of one crayfish immediately after tagging suggests the insertion of PIT tags may cause a low level of acute tagging mortality. Care needs to be taken to ensure that the tag is not inserted too close to the median line, along which the ventral nerve cord runs. It is possible that relative inexperience when conducting laboratory tagging of crayfish contributed to the mortality of the tagged laboratory crayfish. There was no apparent acute mortality caused when tagging within a wild population of white-clawed crayfish. Wiles & Guan (1993) reported a high level of tagging mortality in small crayfish (<25 mm CL) when using 13-mm x 2-mm tags, but in large crayfish they did not report any tagging mortality. In the light of the findings of Wiles & Guan (1993) and observations of the size of the body cavity of crayfish carapace less than 27 mm the current studies were restricted to crayfish of carapace length greater than 27 mm.

The field tagging of white-clawed crayfish suggest that internal PIT tagging is appropriate for long term marking of individuals within wild crayfish populations. There were no apparent effects on white-clawed crayfish of PIT tagging although this is only based on incidental observations and no direct tests of tag induced mortality or interference with breeding, growth and moulting was conducted. Crayfish are relatively long-lived organisms with signal crayfish aged over 15 years reported (Belchier et al. 1998). A tag which can be used to recognise individuals over several years is likely to be beneficial for future studies.

3.3.3.2 External tagging of crayfish with 23-mm (HDX) PIT tags

Following the initial development of the system, and construction of the detector it was hoped to use the system to compare the movement, interactions and spatial behaviour of signal and white-clawed crayfish in an area of the river in which they are both present. However the areas of the river containing both species (Chapter 2) proved unsuitable for using the system. In the areas where populations of both species of crayfish existed, as dictated by the progressive downstream spread of signal crayfish there were also large areas of deeper water above waist depth that could not be scanned by wading, as this would risk submerging the detector. Additionally water releases from Grimwith reservoir at the proposed time of the study discoloured the water to such a degree that the collection of crayfish was difficult and wading would have been dangerous. As a compromise a site at which the entire river bed could be scanned effectively and which contained an abundant signal crayfish population was utilised.

At the site chosen the system allowed a large number of crayfish to be tracked and fine scale information on the movements to be gathered. Aside from the initial disturbance caused when catching and tagging crayfish disturbance to the crayfish was minimal. Disturbance of the riverbed during scanning was minimised by careful positioning of feet and the avoidance of stepping on unstable rocks and boulders which were likely to provide a refuge for crayfish. The low level of disturbance contrasts with conventional mark-recapture studies in which repeated searching or trapping must be carried out to recover crayfish. The two main methods for recapturing crayfish, handsearching and trapping both limit the number of recaptures. Trapping is highly selective and ineffective for collection of smaller age classes (CL<35 mm) whilst handsearching is very time consuming and repeated handsearching is likely to lead to disruption of the habitat. The proportion of tagged crayfish relocated by external PIT tagging was high (89%) in comparison with previous crayfish mark-recapture studies (17%, Guan & Wiles 1997; 15% Light 2003; 10% Robinson et al. 2000; 1% McCreesh 2000). The backpack PIT detector allowed large areas of river bed to be relatively quickly scanned for tags and made it possible to search all parts of the study area including areas that were not accessible for handsearching.

The efficiency of the system at detecting individual tags (and crayfish) was high, most tags were located if they fell within the area over which the detector head was passed.

The efficiency of the system at detecting tags declined when more than one tag was within the same area. This is likely to have reduced the frequency with which some of the tagged crayfish were detected. Throughout the study the density of tagged crayfish in the area, wher they were caught and released, was high. Crayfish in areas were there were few other tagged crayfish appeared more likely to be detected on each scan whilst records from crayfish which appeared to remain in the high density release area were more sporadic. The problem of tags going undetected when there are several in the same area is analogous to the situation of 'sitter' fish that is encountered in fixed array PIT detection stations at fish passes. The tag which is closest to the antenna will be detected even if other PIT tags are also in the detection field. When tags are close together there may also be the problem of interference between the two tags which may prevent the detector from receiving the identification codes from the tags. These problems could be lessened by tagging crayfish over a wider area to reduce the density of tagged crayfish present in any one area, but would necessitate scanning of a larger area of riverbed.

The use of external tags has the disadvantage in crayfish that it is only suitable for use over relatively short durations as once crayfish moult tags are be lost. This is of particular importance for studies involving smaller crayfish which moult several times a year compared to the one or two moults undertaken by larger adults. In addition to the loss of tags through moulting, in this study an estimated 8.9% of crayfish shed tags. The majority of this tag loss appeared to be the result of failure of the adhesive to attach securely to the glass encapsulation of the tag. Whilst the level of tag loss was not excessive the method of tag attachment could be improved if a more suitable adhesive could be found which provided a firm attachment to both the tag and crayfish. The glass used on PIT tags is very smooth as it is intended to be biocompatible; it is therefore less suitable for external attachment. Lost tags could potentially influence the results when tracking, as crayfish that shed their tags will be recorded as not moving unless the tag is recovered. The relatively high level of electronic tag failure of approximately 5 % may be due to Texas TIRIS series 2000; RI-TRP-WEHP ECO tags being utilised, much lower tag failure rates have been found with non ECO tags of <0.01 % (A. Haro pers. com.). Due to their external attachment on the cephlothorax of crayfish the tags may be subject to a certain amount of physical stress which may increase the level of tag electronic failure if the electronic circuits are not robust.

3.3.3.3 Conclusions

The techniques developed here provide additional methods for the study of the spatial behaviour of crayfish. They add to the previously developed marking methods and radiotelemetry techniques, offering alternative methods that can be utilised to address question relating to behaviour, movement and population studies of crayfish. Their feasibility is dependant on the research questions being addressed and the habitat and behaviour of crayfish in the area being studied.

Table 3.3 Main characteristics of two most widely utilised methods for studying spatial behaviour of crayfish (radiotelemetry and branding/punching) and the two novel techniques developed as part of this study.

Method	Size range which has been successfully tagged	Maximum remote detection range	Duration of mark	Cost of mark*
Radiotelemetry	CL > 30 mm	100's metres	Until crayfish undertake moult or may be limited by battery lifespan (c. 2-3 months)	£80
Branding/Punching unique marks on exoskeleton	CL >15 mm	Reliant on capture and visual inspection	Several moults although may become less distinct with later moults	-
Internal 12-mm PIT tags	CL >27 mm	20 cm	Potentially indefinate	£2
External 23-mm PIT tags	CL > 20 mm	80cm	Until crayfish undertake moult	£2

* does not include cost of equipment required to detect or read tag.

CHAPTER 4. DISPERSAL AND MOVEMENT OF SIGNAL CRAYFISH (AGED >1+) DETERMINED BY EXTERNAL PASSIVE INTEGRATED TRANSPONDER (PIT) TAGS

This chapter investigates the short term movement and dispersal behaviour of signal crayfish within a high-density population. The use of external large PIT tags, a novel technique for studying movement in crayfish, enabled high numbers of repeat locations to be obtained and crayfish of age 1+ to be tagged.

4.1 Introduction

The signal crayfish is a highly invasive species (Chapter 1). It has been widely introduced in Europe outside its natural range where it is threatening the native crayfish species and the wider aquatic ecosystem (Holdich 2003, Chapter 1,2). Considerable investment and effort has been made in determining the best approach and management and control strategies for invasive crayfish species (Rogers & Holdich 1998, Holdich 1999, Lodge et al. 2000b, Peay 2001).

An understanding of dispersal patterns, enabling population expansion is fundamental to a considered approach of how to manage invasive species. In many groups of animals there is a strong sex and age bias in the animals that undertake the largest movements and disperse (Hemker et al. 1984, Logan et al. 1986, Caudill 2003), the pattern of population range expansion is likely to be strongly influenced by these groups of animals. In crayfish various authors have reported conflicting patterns of movement with sex and size. The movement and dispersal of signal crayfish is not well understood and only a limited number of studies have investigated this (Abrahamsson 1981, Guan & Wiles 1997b, Kirjavainen & Westman 1999, Light 2003). The most extensive study conducted on movement of signal crayfish (Guan & Wiles 1997b) was limited to relatively large (CL>35mm) crayfish; they reported no difference in movement between the sexes and no influence of size. Recently Light (2003) reported that larger signal crayfish moved greater distances and were more likely to move downstream, however this was based on a limited number of recaptures. An understanding of the movement ability and comparative role that the different sexes and age classes contribute to dispersal in signal crayfish is likely to be of importance in designing any possible control or management strategies.

The aim of this study was to use large (length 23 mm) externally attached passive integrated transponders (Chapter 3) to examine and investigate sex and size differences in the pattern movement of signal crayfish within an established signal crayfish population in the River Wharfe.

4.2 Methods

4.2.1 Study site

The study was centred upon a 180-m section (here after referred to as the 180-m central study stretch) of the upper River Wharfe, northern England (54° 05' N 2° 02' W, NGR: SD 980663). The 180-m central study stretch consists of the central area of a long glide. The upstream end of the glide is bordered by an area of riffles and then a waterfall (vertical drop approximately 1-m), and the downstream end by an area of riffle. The river is 20 – 30 m wide, shallow on the right side (looking downstream) and deeper on the left side (maximum depth 0.55 m under summer base level river flows). The substrate is predominately compacted cobble and pebble. The areas close to the left and right bank have large cobble and boulder substrate. In these areas the cobble and boulder is less compacted and embedded than the central area of the river. Water velocities along the 180-m central study stretch are generally low (<0.33 m s^{-1} measured during low flow conditions 5 cm from substrate; OTT C31 Impeller Current Metre).

To enable accurate locations of detected crayfish to be determined, the 180-m central study stretch was marked out into 2-m sections. Marked canes were placed at the upstream end of each 2 m section on the bank and painted rocks were placed every 5 m across the river.

The study site only contained signal crayfish. The site is approximately 1 km downstream from the source of signal crayfish in the Wharfe (confluence of White Beck). Signal crayfish are well established, having been at the site for over 10 years. Although no absolute density estimates were made, standardised effort searches suggest that the density of crayfish at Grassington and the study site were similar. Quantative surveys in 2002 at Grassington using modified Surber sample quadrats (0.49 m^2) estimated the density of signal crayfish to be approximately 8 crayfish m^{-2} for all age groups combined.

4.2.2 Capture and tagging

Signal crayfish were captured and tagged between 18 and 21 August 2003 from a 44-m stretch of river. 22 sections (60 – 104 m downstream from the upstream end of 180-m central study stretch) were searched for crayfish. Within these sections, the area closest to the left bank that provided the most suitable habitat for crayfish was searched. Crayfish were captured by handsearching; stones were moved aside from the bed of the river by hand and any crayfish with a carapace length greater that about 20 mm that were concealed beneath were collected. Care was taken to return all stones to their original position once the area had been searched. During tagging each 2-m section of the river was searched by two experienced surveyors. The catch from each 2-m section was processed together then returned to the centre of the 2-m section. To minimise disruption to crayfish returned to the river after tagging, the catch from one 2-m section was tagged while the next 2-m section of the river was searched.

Passive Integrated Transponder (PIT) tags (TIRFID; RI-TRP-REHP, Texas Instruments) were used to track crayfish. Tags measured 23.1-mm long, 3.9-mm diametre, mass 0.6 g. The tags were attached to the cephalothorax of crayfish using a combination of cyanoacrylate adhesive and dental acrylic. Tagged crayfish were retained for approximately 30-mins until the acrylic was set. During this time the gills of the crayfish were kept moist providing small amounts of water in the trays in which the crayfish were retained. Tagged crayfish were sexed, the carapace length, the unique tag identification code and any injuries recorded. A full description of the tagging method is provided in Chapter 3; Section 3.3.1.2.

During tagging only crayfish CL > 20 mm were captured, as this was the minimum size that could be tagged. After the termination of scanning on the 6th September, on the 9th and 10th September additional handsearching was carried out to capture all sizes of crayfish present and attempt to recover tagged crayfish. In addition 30 traps were set on the night of the 9th September equally spaced along the 180-m central study stretch as a further attempt to recover tagged crayfish.

4.2.3 Scanning

The portable reading unit was constructed by incorporating a commercially available radio frequency identification system (Texas Instruments TIRIS S-2000) and was based upon the design of Roussel et al. (2000). A full description of the reading unit is

provided in Chapter 3; Section 3.3.1.2. The 180-m central study stretch was scanned daily for 15 days from 23 August – 6 September 2003. During scanning the antenna head was swept over the river bed just above the substrate. Two metre wide transects across the river were scanned using the method developed in Chapter 3; Section 3.3.1.2. When a tag was detected the tag number was recorded and the tag assigned to a 1 m^2 grid location, the position of which was identified by reference to the markers on the riverbank and within the river. All scanning took place during daylight hours when crayfish were observed to be inactive; the recorded locations therefore represent daytime refuge sites.

Initially the entire riverbed of the 180-m central study stretch was scanned. After 5 days of scanning it was apparent that most crayfish were recorded within unembedded large cobble and boulder habitat that was present only in limited areas. The presence of unembedded large cobble (128 - 256 mm longest axis) and boulders (>256 mm) was mapped in 2 x 2 m squares across the 180 m central study stretch. The distribution of this habitat and the position of all new locations of crayfish detected in the five initial days of tracking was mapped (Figure 4.1). Of the 459 crayfish locations recorded, only 7 were not within the unembedded large cobble and boulder habitat. Therefore on subsequent days only the unembedded large cobble and boulder habitat was scanned.

There was extensive movement of tagged crayfish out of the 180-m central study reach. To enable information on the movements of these crayfish to be gathered scanning was extended out of the 180-m central study reach on 10 days. This scanning was restricted to areas of unembedded large cobble and boulder habitat. The dates and areas scanned are displayed in Figure 4.2.

4.2.4 Analysis of daily movements

When crayfish were relocated on one or more subsequent days the distance moved was calculated to provide a measure of daily movement. Due to the possibility of repeatedly locating lost tags (Chapter 3; Section 3.3.3.2) the analysis of daily movements excluded those crayfish for which no movement was recorded over the 14 days of tracking. During scanning crayfish were assigned to a 1-m^2 grid square. In the analysis crayfish were assumed to be in the centre of the metre square. A crayfish was only considered to have moved if it moved a distance of 2 m or greater. This was to avoid considering

crayfish that were on the edge of a $1m^2$ square and could be picked up in adjacent squares on subsequent days as being classified as moving.

4.2.5 Environmental conditions

Water temperature at the study site was measured at 60-min intervals continuously throughout the study using Tinytalk temperature loggers (Orion Components, Chichseter, U.K.). The flow in the upper Wharfe was recorded at Addingham Gauging Station, the nearest continuous gauging station, 21 km downstream of the study site.

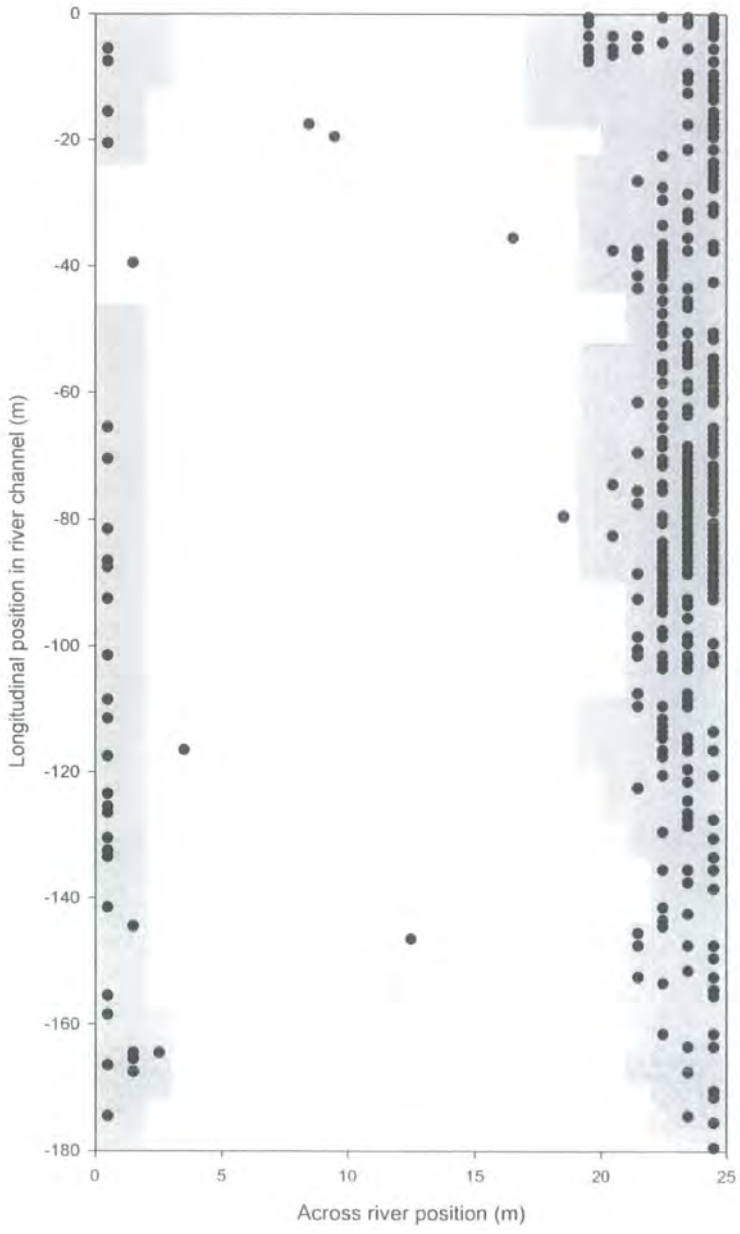


Figure 4.1. Locations of crayfish recorded during scanning between 23 and 27 August 2003 and distribution of unembedded large cobble and boulder habitat (represented by shading) within the 180-m central study stretch.

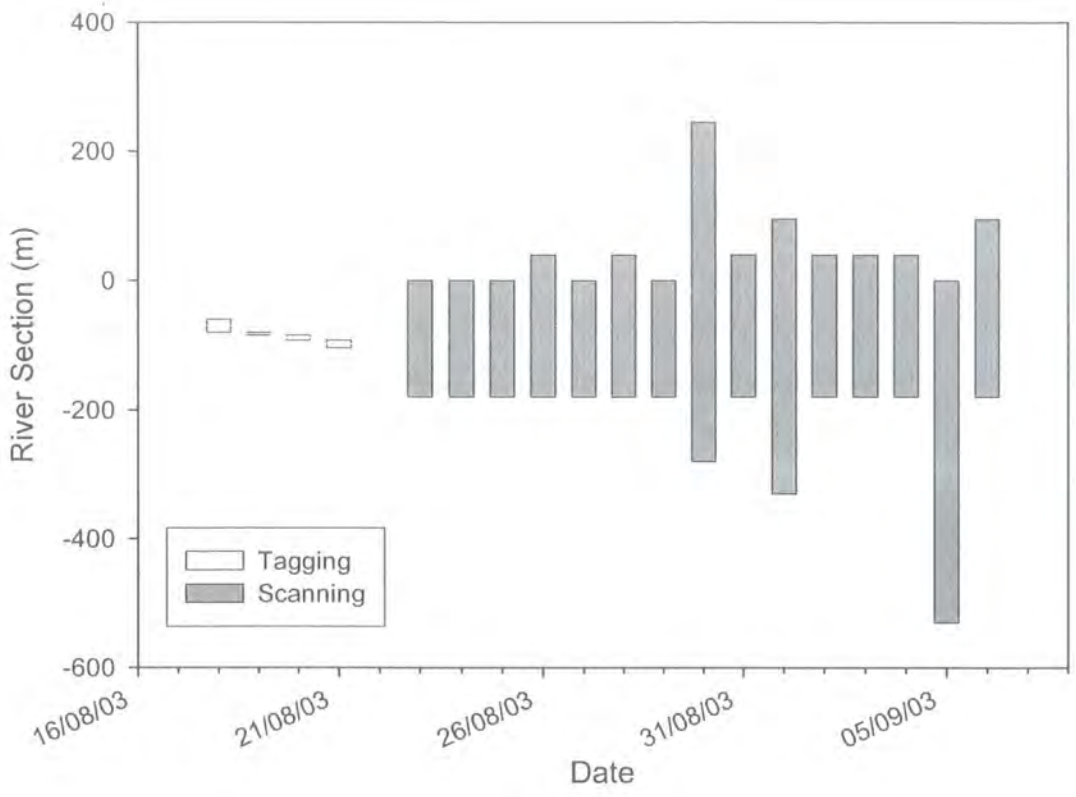


Figure 4.2. Dates of tagging and scanning and areas scanned. 0 to –180 is the 180-m central study stretch.

4.3 Results

4.3.1 Environmental conditions

Environmental conditions (flow and temperature) during the study were relatively constant. Discharge during most of the study period was relatively stable and low except for a small peak in discharge that occurred between tagging and the start of scanning. Water temperature fluctuated by several degrees diurnally with mean daily temperature ranging from 11.25 °C to 16.8 °C (Figure 4.3).

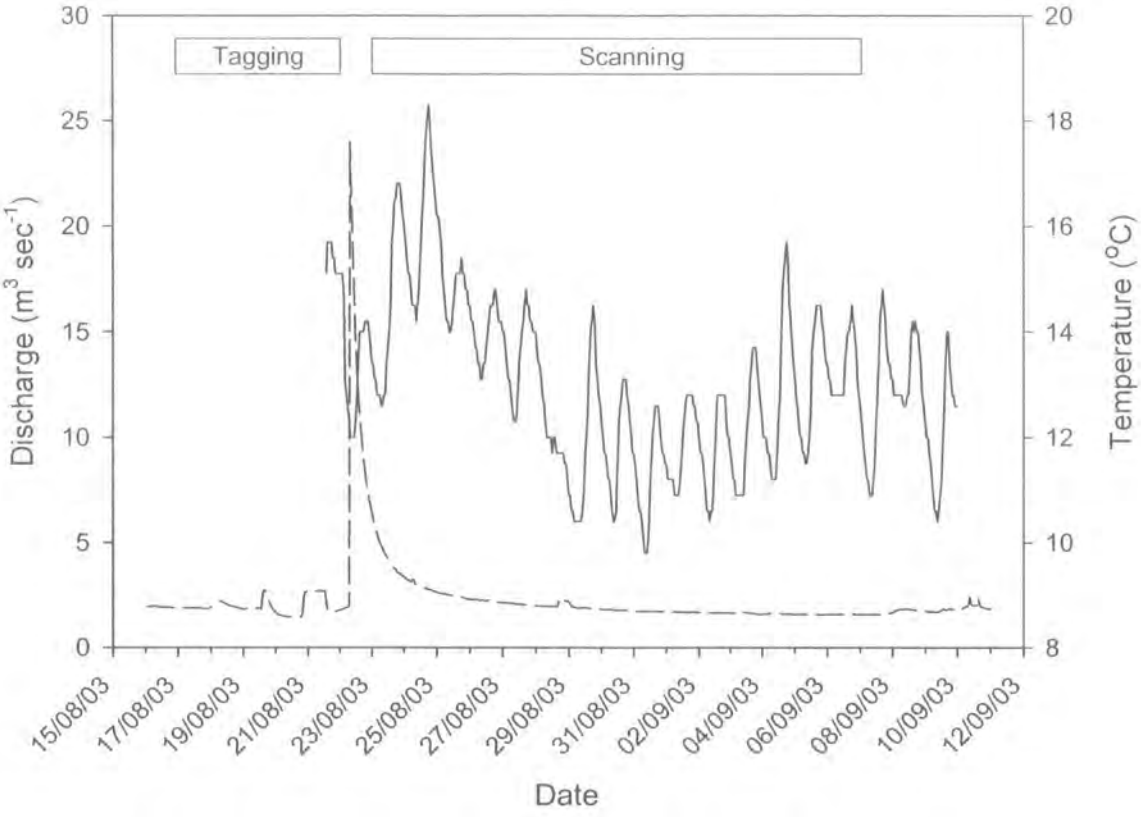


Figure 4.3. River discharge (dashed line) and temperature (solid line) of the River Wharfe. Discharge measured at Addingham flow gauging weir and temperature measured at study site.

4.3.2 Size and age structure

A total of 599 crayfish were captured during PIT tagging, trapping and handsearching. Figure 4.4 shows the size distribution of all crayfish captured in the study area. On the basis of the size-frequency distribution the individual age classes cannot be reliably distinguished with the exception of the 0+ age class (juvenile crayfish which hatched in the spring of 2003). At the time of the study the 0+ age class appears to have carapace lengths of <18 mm.

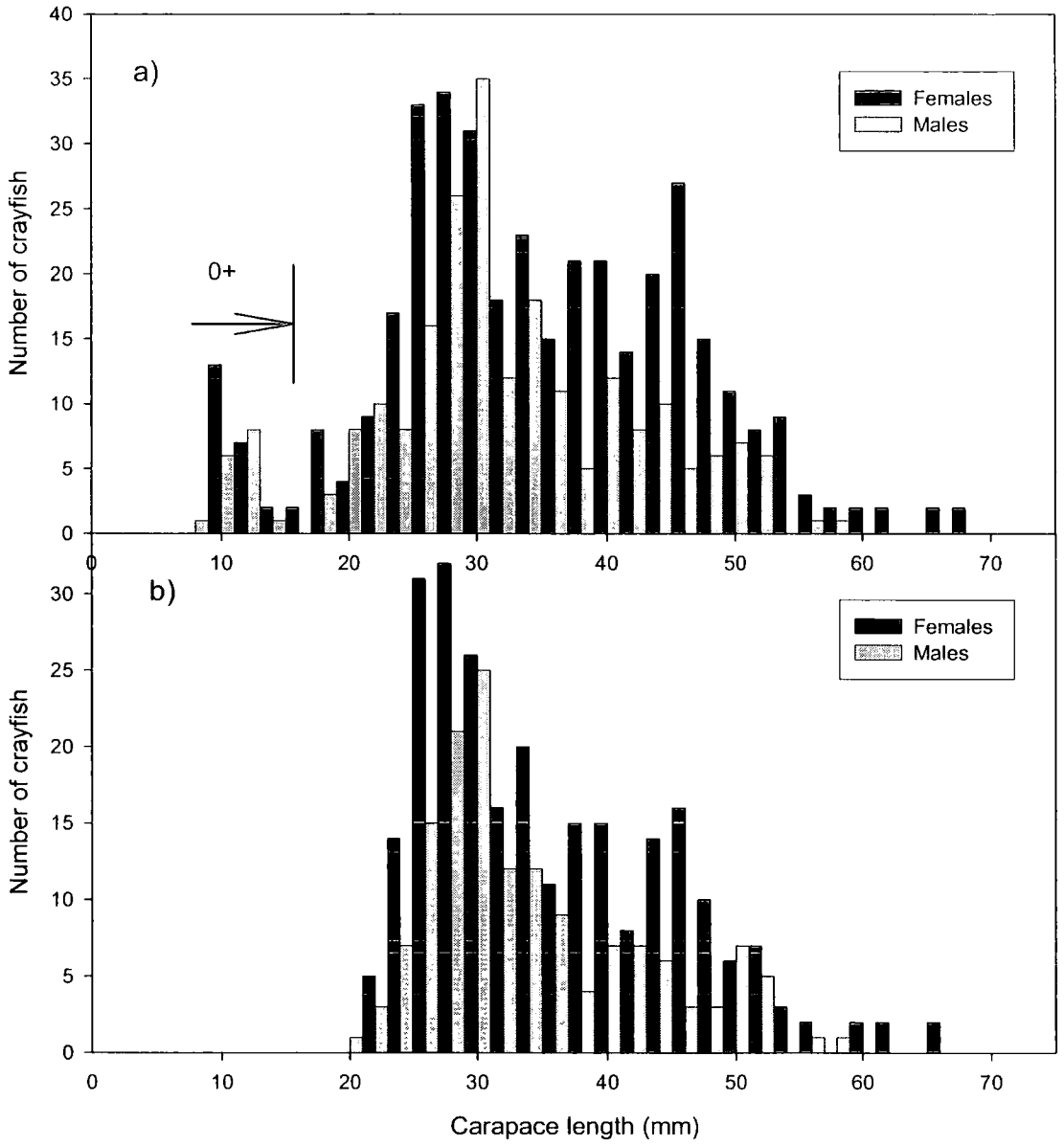


Figure 4.4 Size distribution of a) all crayfish captured within River Wharfe external PIT study area during PIT tagging, handsearching and trapping (23/8/03 – 10/9/03) b) crayfish tagged with 23-mm PIT tags.

A total of 406 (257 females, 149 males) crayfish were PIT tagged. Tagged crayfish ranged from carapace length (CL) 21.0 mm to CL 67.3 mm. The average size of tagged crayfish was CL 36.1 mm. Figure 4.4 b) shows the size distribution of all PIT tagged crayfish. The crayfish tagged with PIT tags are all believed to be age 1+ (hatched in spring 2002) and older. The sex ratio of all crayfish captured (males 224: females 375) and tagged crayfish only (males 149: females 257) was significantly biased towards females (Chi-Squared Test with Yates' correction for continunity; all crayfish χ^2 = 37.56 d.f.=1, $P<0.01$; tagged crayfish χ^2 = 28.20 d.f.=1, $P<0.01$).

4.3.3 Maximum movement

Of the 406 signal crayfish tagged 363 (89%) were subsequently located at least once. There was considerable dispersal of tagged crayfish from the release location, with maximum recorded movement of a tagged crayfish from release location of 375m. The largest movements made by crayfish were in a downstream direction; the movement of crayfish upstream appeared to be limited by the waterfall. Several crayfish were recorded at the downstream side of the waterfall no crayfish were recorded upstream (Figure 4.5).

For all crayfish located once or more the maximum distance that they moved from their release location was calculated. Since the maximum distance from release location was significantly correlated with the date on which crayfish were located (Spearman Rank Correlation $r_s = 0.243$, $n = 363$, $P < 0.001$), the maximum distance that each crayfish had moved from the release location per day since release was calculated. There was considerable variation in the maximum distance per day that crayfish moved from their release location (Fig 4.6). The frequency distribution of distance moved fitted with that expected from a negative binomial distribution. General Linear Models were constructed (Genstat, version 6.0, VSN International Ltd, U.K.) with a negative binomial error function. With maximum distance/day tracked as the response and size, sex, injury entered as predictors into the model. Full factorial models were initially constructed then least significant factors removed. None of the predictors size, sex (Fig. 4.7) and injury was significantly related to the distance moved.

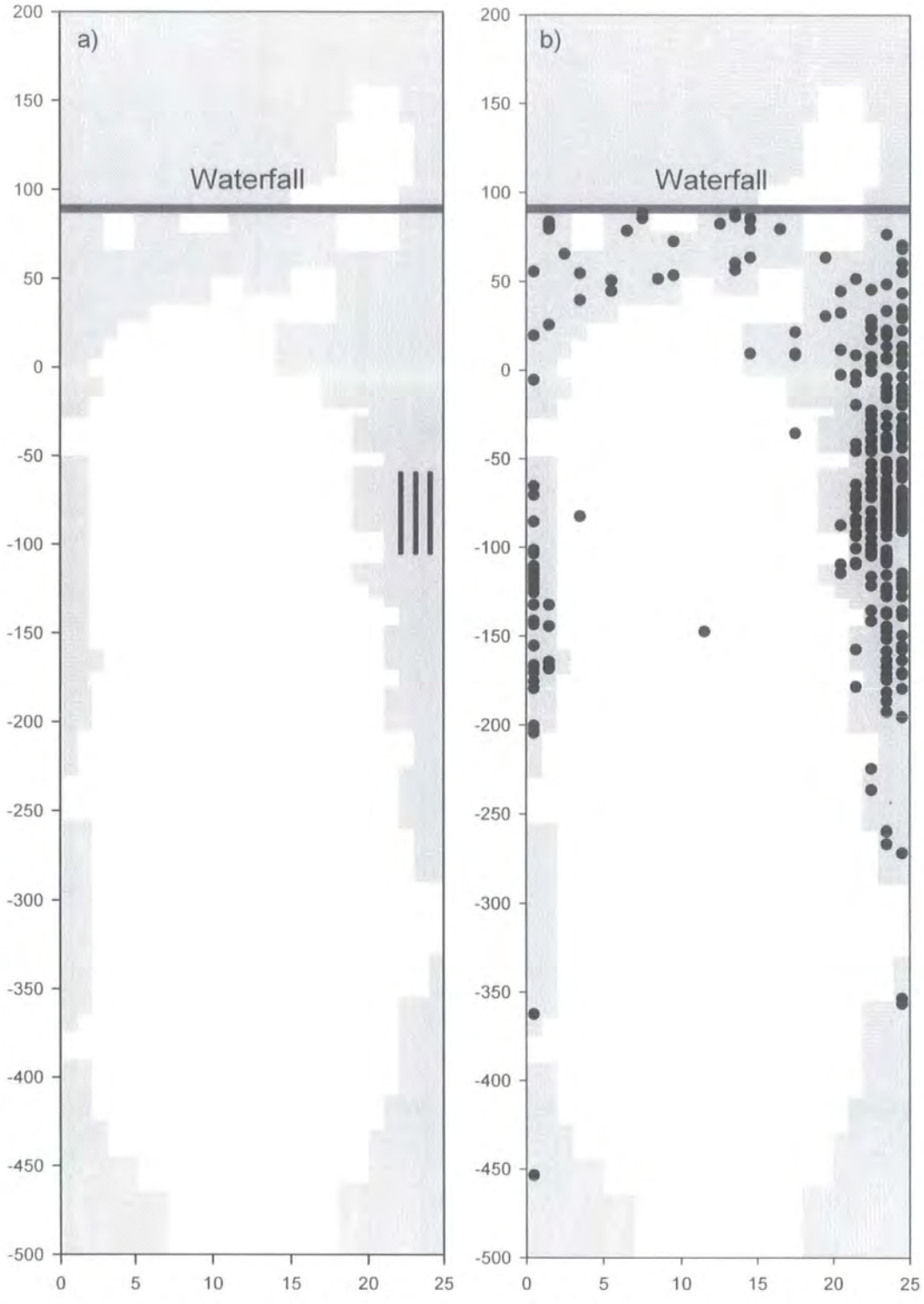


Figure 4.5 Locations of crayfish a) released after tagging shown by three parallel lines b) at maximum distance from release location recorded during scanning between 23 August and 6 September 2003. The distribution of unembedded large cobble and boulder habitat (area scanned) is represented by grey shading.

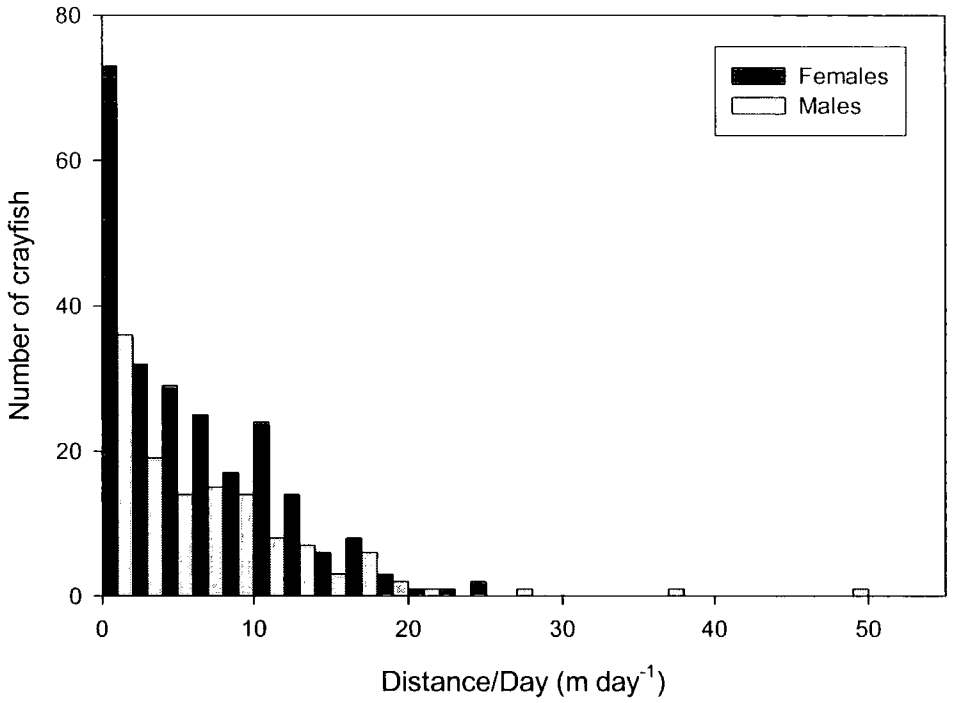


Figure 4.6 Frequency distribution of maximum distance moved from release location per day between release and detection.

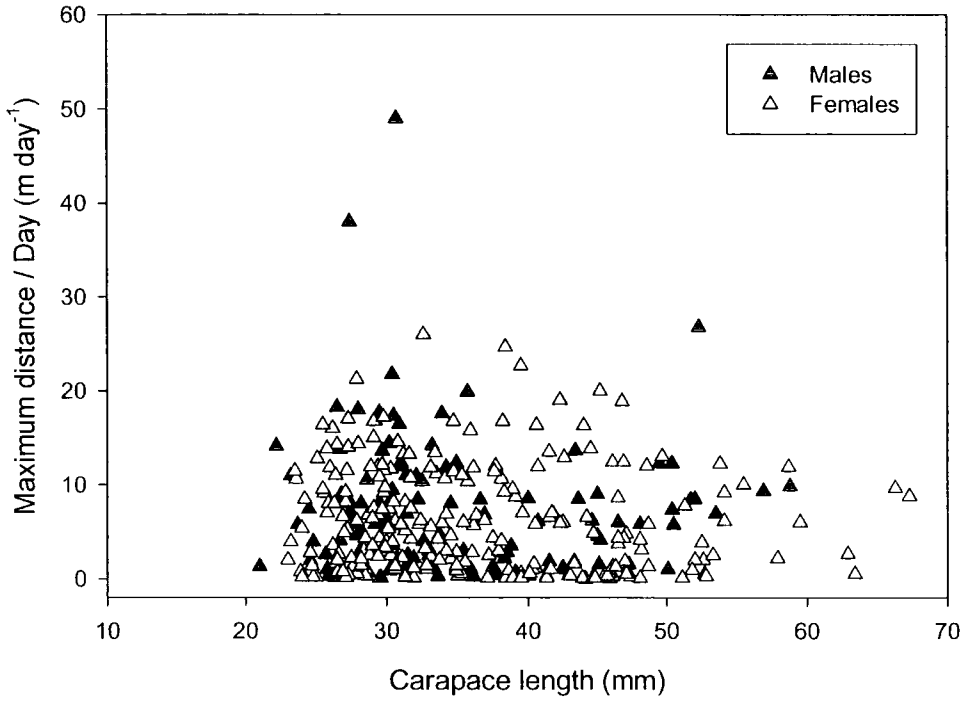


Figure 4.7 Maximum distance moved from release location per day between release and detection and carapace length of crayfish.

4.3.4 Daily movements

Crayfish were located on subsequent days in 1207 instances. Short (< 2 m) or no movement between days prevailed. Over 68 % of the time no movement (< 2 m) was

recorded. Most crayfish movements were over a relatively short distance (< 20 m) although crayfish were capable of making large movements with a maximum overnight movement of greater than 90 m (Fig. 4.8).

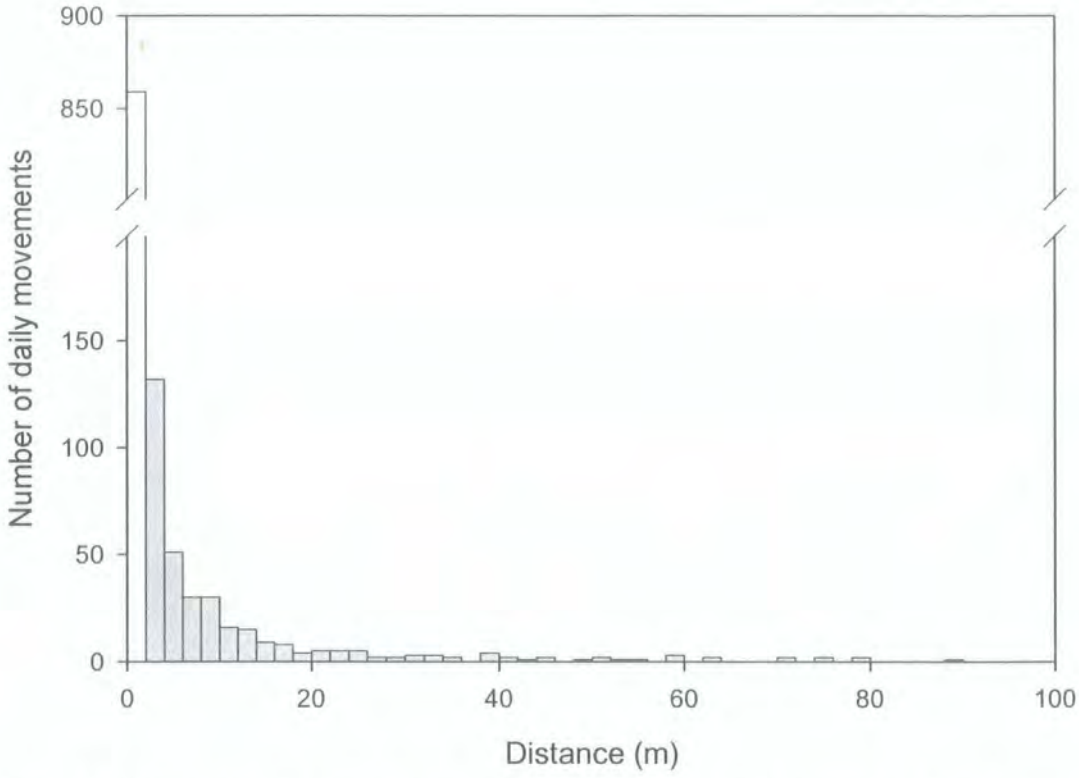


Figure 4.8 Distribution of daily movements made by PIT tagged crayfish. Unshaded column represents crayfish considered not moving (< 2 m).

The pattern of movements of crayfish with respect to previous movements was investigated. The likelihood of crayfish moving was significantly related to their previous movement. Crayfish which were recorded as being static for a night were more likely to remain static on the subsequent night, whilst crayfish which moved previously were more likely to move again (Figure 4.9; Chi-squared Test $\chi^2 = 98.96$, d.f. = 3, $P < 0.01$). When crayfish made movements on subsequent nights the distance moved by crayfish was positively and significantly correlated with the distance moved previously (Spearman Rank Correlation $r_s = 0.234$, $n = 235$, $P < 0.001$). Whilst the distance moved was significantly related to previous movement the direction moved by crayfish was not significantly associated with the direction of previous movement. When crayfish made movements on subsequent nights 89 (44.7%) moved in the opposite direction to that previously whilst 110 (55.3%) moved in the same direction (Chi-Squared Test with Yates' correction for continunity $\chi^2 = 2.01$ d.f. = 1, $P > 0.05$).

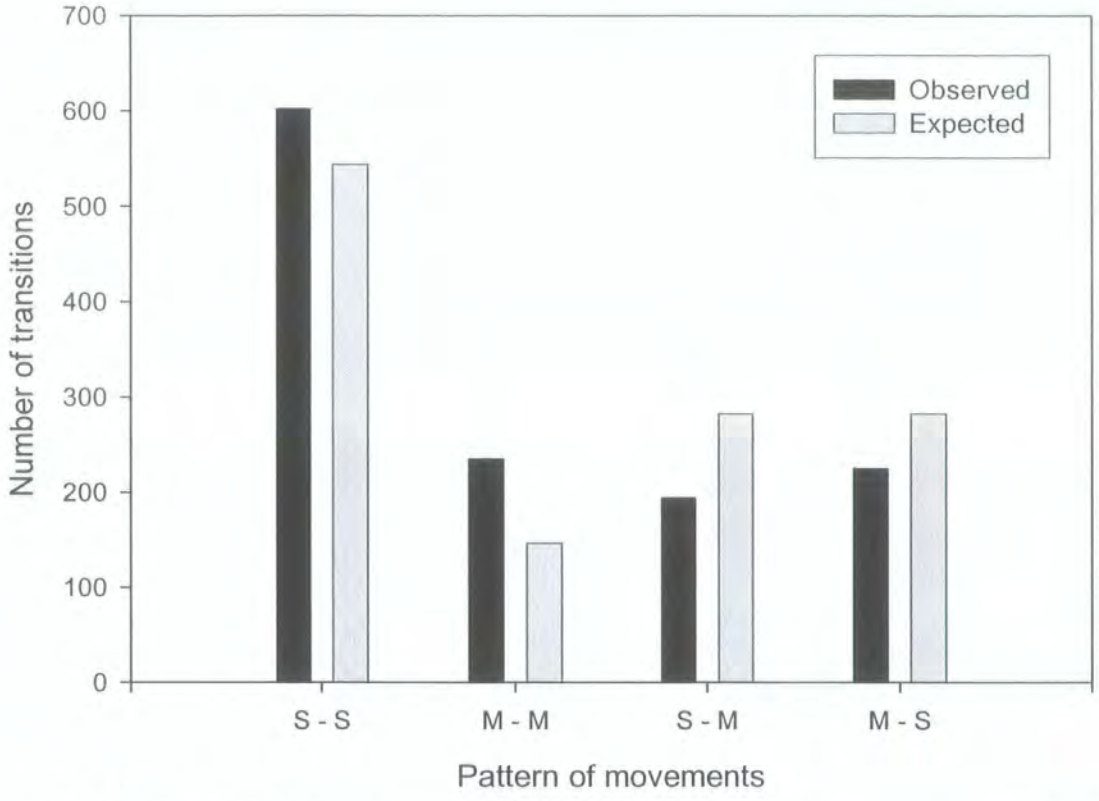


Figure 4.9 Expected and observed pattern of transition of movements of crayfish recorded on subsequent days. S-static, M-moving.

4.4 Discussion

The study demonstrated that both sexes and all age groups tagged were capable of making substantial movements. There was a general pattern of most crayfish moving relatively short distances with a small number of individuals making larger movements. During the period that fieldwork was conducted there did not appear to be any tendency for either sex or age class to move greater distances. This is in agreement with Guan & Wiles (1997b) who reported no difference between the movement recorded in males and females and the sizes studied. However Guan & Wiles (1997b) study was restricted to large adult crayfish of carapace length greater than 35 mm, in contrast to this study in which all age classes were tagged with the exception of 0+ crayfish. The degree to which these small (0+) crayfish contribute to dispersal is unknown. The difficulties involved in marking and capturing this size of crayfish makes the study of movement of this potentially important age class problematic. The lack of a pattern of movement in relation to both size and sex suggests that both sexes and all crayfish older than1year may contribute to the dispersal of signal crayfish. Control measures such as trapping

which are restricted to large adult crayfish may have limited success in reducing dispersal from an area.

The transition between crayfish moving and remaining still suggests that the movements of crayfish may not be random. Crayfish appear to undertake periods of movement indispersed with static periods. Although the causal factors behind movements was not investigated, movements may reflect searching behaviour for refuges or food and once a suitable refuge or food source is located crayfish remain relatively static. A similar pattern of non-random transitions between moving and remaining static has been reported in the freshwater crab *Potamon fluviatile* (Gherardi et al. 1988).

The study was restricted to a limited period and therefore may not be representative of annual patterns of movement. It was carried out during summer when water temperatures were approaching their annual high. Previous studies have reported that crayfish activity and movement is positively related to water temperature (see Chapter 6, Flint & Goldman 1975, Abrahamsson 1981, Lozán 2000, Barbaresi & Gherardi 2001), suggesting that the distances and rate of dispersal recorded here may be greater than if the study was carried out during other periods of the year.

The behaviour of crayfish may have been different if carried out during other periods of the year. At the time of the study females were not carrying young or eggs, no mating activity was taking place and few crayfish were moulting. These factors have been reported to influence the activity (Brown 1979, Abrahamsson 1981) and possibly wider scale movement of crayfish. Discharge throughout the study was relatively stable; all movements by crayfish appeared to be active movements with no passive movements occurring during the low flows. The influence which high discharge may have on movements of crayfish and frequency of passive movement in high flows could not be investigated.

The waterfall that was present at the upstream extent of the site appeared to form a barrier to the movement of tagged crayfish. Whilst a number of crayfish moved upstream to the base of the falls none appeared to move upstream over the waterfall. The long term significance of the waterfall in preventing movement upstream past it is unknown but at least in the short term it appeared to prevent upstream movements of crayfish. If waterfalls such as this prevent the movement of signal crayfish they have the

potential to limit the upstream expansion of signal crayfish in some river systems. However it has been suggested that signal crayfish will circumvent in-river barriers by climbing out of the water (Holdich 2003), and weirs and falls may only provide temporary restrictions to upstream movement.

The movements recorded in this study may be biased towards crayfish making short movements and underestimate the number of long distance movements made by crayfish. Although the movement of crayfish upstream appeared to be limited by the presence of a waterfall the downstream end was unconfined. It is possible that some crayfish moved downstream out of the area that was scanned and their positions were not detected. However the pattern of detections (Figure 4.5) and the shape of the frequency distribution curve (Figure 4.6) strongly suggest that over the timescale studied, probably very few locations of crayfish were missed.

CHAPTER 5. MOVEMENT OF WHITE-CLAWED CRAYFISH IN A SMALL ERODING UPLAND STREAM

This chapter investigates the long-term movement and dispersal behaviour of white-clawed crayfish within a small upland stream. The use of internal PIT tags enabled permanent marking of crayfish and relocations of crayfish after extended (> 1 year) periods of time.

5.1 Introduction

Within the context of the conservation of white-clawed crayfish in Great Britain there is increasing recognition of the importance of upland streams in northern England for this species. Abundant stream populations of white-clawed crayfish exist in rivers in the north east of England (e.g. Aire, Ure, Swale, Wansbeck, Bubb & Lucas 2004, Environment Agency unpublished information, D. Bubb unpublished information). With the comparatively slow upstream colonisation by signal crayfish of upland rivers and tributaries (Chapter 2), the timescale over which headwater stream populations of white-clawed crayfish are threatened by invasion by signal crayfish may be longer than riverine populations. In addition a number of stream populations distributed across a catchment may be less vulnerable to single pollution events. Streams may have the potential to provide refugia for white-clawed crayfish, especially in catchments free of signal crayfish or in instances where natural or artificial barriers separate the two populations (Holdich et al. 2004).

Increasing interest and attention has been placed on reintroductions of white-clawed crayfish and a number of introductions have taken place (Spink & Frayling 2000, Kemp et al. 2003, Rogers 2003). Upland streams distant from signal crayfish populations have been suggested as potential refugia sites at which introductions could be conducted (Priestley 2003). The success of reintroduction programs and wider conservation of white-clawed crayfish populations is likely to be reliant on an understanding of the movement patterns and spatial behaviour of crayfish within these habitats. Studies of the spatial behaviour of white-clawed crayfish in upland streams are limited (although see Robinson et al. 2000). Upland streams tend to be of higher gradients with highly variable flow regimes than lowland streams, factors that may be important in influencing the spatial behaviour and dynamics of crayfish populations (Robinson et al. 2000, Light 2003).

Investigations of the spatial behaviour of crayfish have predominantly been concerned with movements during summer months when water temperatures are highest and crayfish are most active (e.g. McCreesh 2000, Robinson et al. 2000, Light 2003). The restriction of studies to a single season has the potential to conceal biologically significant behaviour occurring over the unstudied period of the year. The use of internal PIT tags in this study permitted the permanent marking of crayfish enabling the movement patterns of individual white-clawed crayfish to be investigated over an extended (> 1 year) period. The aim of the study was to investigate and examine the spatial behaviour of white-clawed crayfish in a natural upland stream. Whilst the principle concern was movement, information on the characteristics of the white-clawed crayfish population was gathered and is also presented here.

5.2 Methods

5.2.1 Study site

Eller Beck is a small low order eroding headwater stream. Eller Beck rises from Linton Moor at an altitude of approximately 300 m. It runs for about 5 km before joining Linton Beck which flows into Captains Beck which in turn flows into the River Wharfe (see Figure 2.4, Chapter 2), approximately 3 km downstream from the confluence of Eller and Linton Beck.

White-clawed crayfish are present throughout most of Eller Beck (Chapter 2). In this study work was conducted on a 1.8 km section of Eller Beck (NGR SD 974616 - 987623; Figure 5.1) where white-clawed crayfish are relatively abundant. Within this area the gradient is relatively high (1:45) and the stream consists predominantly of shallow riffle sections interspersed with glides and occasional pools (maximum depth 1 m). The wetted stream width varies from 0.5 m to 4.8 m (during summer base flow) but for most of its length is between 1.5 and 2.5 m wide. The substrate is principally composed of gravel and cobble, with occasional boulder. As a result of the eroding nature of the stream, large areas of the bank are heavily undercut. The crayfish population within Eller Beck appears to use refuges created by the undercut bank. Attempts to capture crayfish by handsearching during 2002 were of very limited success (<2 crayfish person hours^{-1}) with very few crayfish utilising instream refuges beneath cobbles and boulder. In 2003 algae coated much of the bed in areas of slower flowing water during the summer, this did not occur in 2002. The stream is fairly open with little

riparian vegetation; the area bordering the stream consists mostly of grazed rough pasture. Mature deciduous trees shade a small section (Figure 5.1), and for part of the study stretch the stream forms a deep channel and is heavily shaded by the banks and overhanging vegetation. A small manmade weir is present; this has a vertical drop of about 25 cm. During August 2003 engineering work was conducted on this weir temporarily removing the vertical drop on the downstream edge.

Using Ordnance Survey Landline data (1:10,000 scale) as a template, the stream was mapped in fine detail to enable accurate positioning of crayfish. The stream was divided into 3 m sections (distances measured along midline of stream). When crayfish were located they were assigned to a 3 m section following reference to the detailed map.

The exposure of crayfish to predators may influence their behaviour. A grey heron *Ardea cinerea* was frequently observed feeding in Eller Beck. Bullhead *Cottus gobio*, brown trout *Salmo trutta* and stoneloach *Barbatula barbatula* were present within Eller Beck. Whilst they have been described as predators of crayfish (Hogger 1988) it is unlikely that they would eat crayfish of the size tagged in this study (CL > 25 mm). Potential terrestrial predators include American mink *Mustela lutreola* and stoats *Mustela erminea* (Hogger 1988, Armitage 2001). Although mink are present in the upper Wharfe catchment, and stoats observed in the area around Eller Beck, no evidence of their presence along Eller Beck was found. Areas of fine damp sand and mud along the stream banks were frequently checked for footprints but none was ever recorded.

5.2.2 Environmental conditions

Throughout the duration of the study temperature and pH of Eller Beck were recorded regularly (usually every week) by Scott Doherty Associates environmental consultants as part of a monitoring programme for the adjacent quarry. In addition water temperature was measured at 60 min intervals from April to September 2003 using a Tinytalk temperature logger.

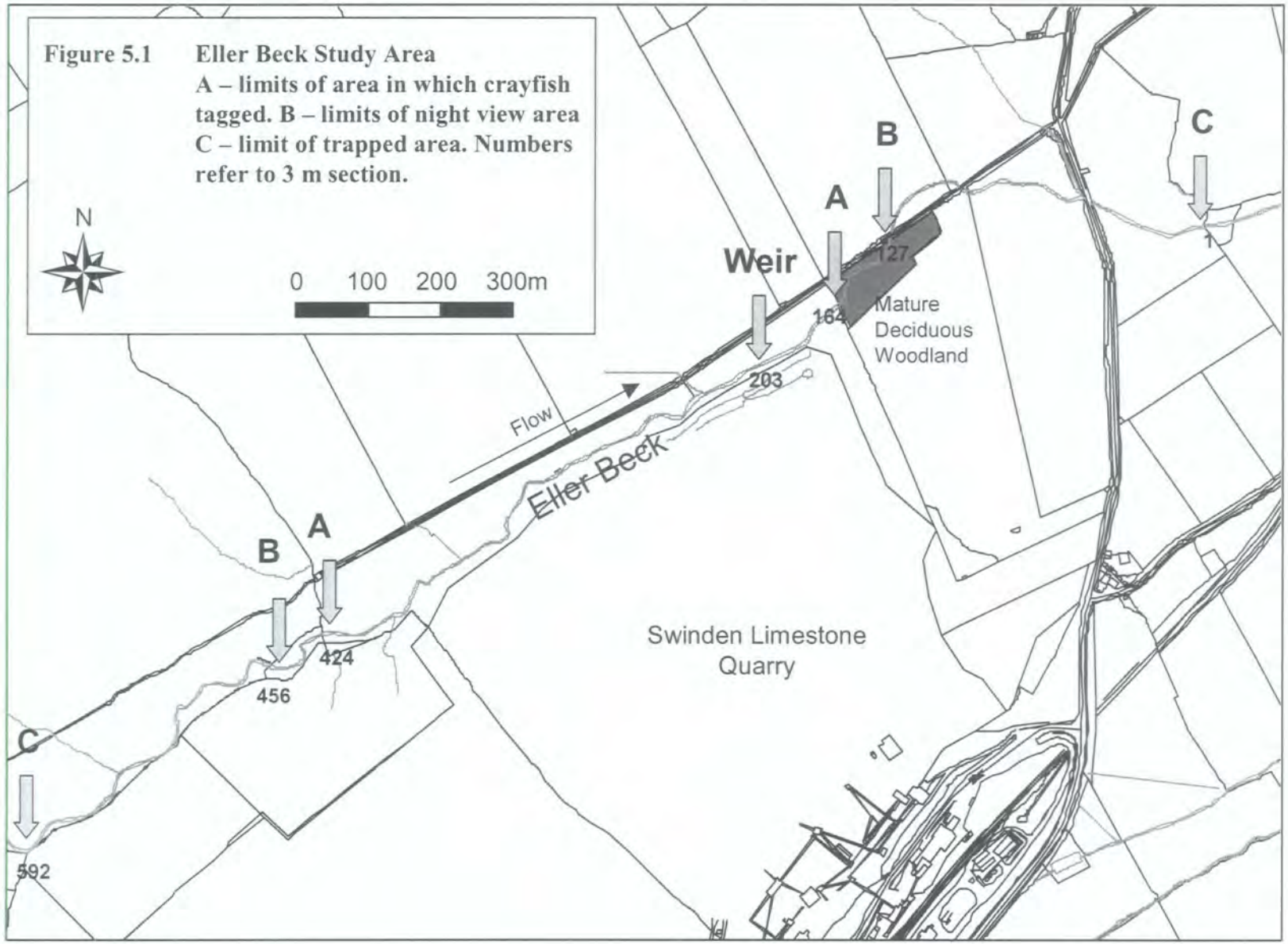


Figure 5.1 **Eller Beck Study Area**
A – limits of area in which crayfish tagged. B – limits of night view area C – limit of trapped area. Numbers refer to 3 m section.

5.2.3 Tagging

Crayfish were tagged in two periods. Most crayfish were tagged from 14 to 31 August 2002 with additional crayfish tagged in 2003 during 25-26 June and 8-9 July. All tagged crayfish were from the middle 780 m of the study reach (Sections 164 to 424; Figure 1). Crayfish for tagging were captured by a combination of night hand capture and trapping, predominantly the former. Night hand capture was performed using torches to scan the streambed for active crayfish. Observed crayfish that appeared large enough to be tagged (carapace length >27 mm) were captured either by hand or using a small hand net. Crayfish were tagged by torchlight and immediately returned to the capture location. Crayfish traps (Swedish Trappys™) baited with fresh liver were set overnight; catches were processed the following morning with tagged crayfish returned to the section of the stream in which the trap had been set.

Crayfish were tagged using either Trovan ID100 PIT tags (Trovan Ltd., Douglas, UK) or UKID 122GL PIT tags (UKID System, Preston, UK). Both tags are glass encapsulated and are identical in size (12-mm long x 2.1-mm diametre). Tagging was carried out by holding the crayfish around the cephlothorax with the ventral surface uppermost and making an incision, using the tip of a sterile large gauge (diametre 2.5 mm) hypodermic needle, c. 3 mm wide and deep through the cuticle and underlying tissue at the base of the fifth pereopod (fourth walking leg). The tag was inserted through the incision, by gently pushing the tag anteriorally so that it came to rest underneath the digestive gland (hepatopancreas) and above the segmental musculature (for full description of tagging method see Chapter 3; Section 3.3.1.1). The individual identification code, sex, carapace length, injuries and missing or regenerating chelae were recorded for all tagged crayfish. Following tagging, crayfish were immediately returned to the stream at or close to (< 1 m) the capture location.

5.2.4 Recapture/Relocation

Crayfish were re-located by a combination of night viewing and trapping. A total of 15 recapture/relocation sessions of fieldwork were conducted during the study. The details and timing of survey work conducted during each fieldwork session are provided in Table 5.1. All fieldwork was carried out during periods of low flow, when water clarity was high.

Night view

In order to ensure that crayfish were active when visual night searches were carried out night survey work was not commenced until a minimum of 1 hour after sunset. During night viewing sections 127 to 456 were walked slowly in an upstream direction by two surveyors with torches. Although a variety of torches were used during night viewing surveys, they were always sufficiently powerful to illuminate the stream bed in the deepest areas. The entire wetted stream bed was searched for visible crayfish. The antenna head of the long handled PIT detector (see Section 3.3.3.1 for description) was passed over any crayfish seen. If the crayfish was tagged the identification number of the crayfish was recorded along with the 3m section in which the crayfish was observed.

Trapping

Trapping was conducted using plastic Swedish Trappy™ crayfish traps baited with fresh liver. The traps are circular mesh tubes (mesh size 2 cm, length 50 cm, diametre 21 cm) with an inverted conical entrance at each end. To improve efficiency and effectiveness of the traps, especially for small crayfish, they were modified by wrapping a fine mesh (<3 mm) around the tubular part. Traps were set during late afternoon or evening and emptied the following morning. Traps were placed in areas of slow moving water, regularly spaced along the stream. Due to the limited number of traps available (9 in 2002, 30 in 2003) trapping of the entire study length was carried out over several nights. In 2002 and 2003 during all trapping sessions traps were set from sections 127 to 456. In 2002 45 trap-nights were fished in each fieldwork session (except session 3) whilst in 2003 60 trap-nights were fished in each fieldwork session. In addition during 2003 on 5 fieldwork sessions traps were set upstream (sections 457 to 592) and downstream (sections 0 to 126) of the central study area, 30 trap-nights were fished upstream and 30 trap-nights downstream. All trapped crayfish were scanned for PIT tags. If the crayfish was tagged the identification number of the crayfish was recorded. The carapace length, sex, injury, and evidence of *Thelohania contejeani* (Porcelain disease) was recorded for all untagged crayfish. Individuals in white-clawed crayfish populations are frequently infected by the microsporidian parasite *T. contejeani*. In the latter stages of infection it is easily recognised, striated muscle blocks in the body are infested and appear white, as compared to the normal translucent muscle (Brown 1979).

Table 5.1. Details of timing and survey methods used during each recapture/relocation fieldwork session. Sections refers to numbered 3m sections over which traps were set. Dates refer to date on which traps were set.

Session	Date	No. Traps	Sections	Night View
1	11-Sep-02	9	164-258	Y
1	12-Sep-02	9	259-335	Y
1	13-Sep-02	9	336-412	Y
1	14-Sep-02	9	413-456	N
1	16-Sep-02	9	127-163	N
2	21-Sep-02	9	413-456	N
2	22-Sep-02	9	336-412	N
2	23-Sep-02	9	259-335	Y
2	24-Sep-02	9	164-258	Y
2	25-Sep-02	9	127-163	N
3	09-Oct-02			Y
3	10-Oct-02			Y
4	14-Apr-03	30	127-299	Y
4	15-Apr-03	30	300-456	Y
5*	30-April	30	127-299	N
6	29-May-03	30	127-299	Y
6	30-May-03	30	300-456	Y
7	11-Jun-03	30	127-299	Y
7	12-Jun-03	30	300-456	Y
8	24-Jun-03	30	457-492	Y
8	25-Jun-03	30	300-456	N
8	26-Jun-03	30	127-299	Y
8	28-Jun-03	30	1-126	N
9	07-Jul-03	30	457-492	N
9	08-Jul-03	30	300-456	N
9	09-Jul-03	30	127-299	Y
9	10-Jul-03	30	1-126	Y
10	22-Jul-03	30	457-492	Y
10	23-Jul-03	30	300-456	N
10	24-Jul-03	30	127-299	Y
10	25-Jul-03	30	1-126	N
11	05-Aug-03	30	457-492	Y
11	06-Aug-03	30	300-456	N
11	07-Aug-03	30	127-299	N
11	08-Aug-03	30	1-126	Y

Session	Date	No. Traps	Sections	Night View
12	20-Aug-03	30	457-492	N
12	21-Aug-03	30	300-456	N
12	22-Aug-03	30	127-299	Y
12	23-Aug-03	30	1-126	Y
13	02-Sep-03	30	300-456	Y
13	03-Sep-03	30	127-299	Y
14	16-Sep-03	30	127-299	Y
14	17-Sep-03	30	300-456	Y
15	30-Sep-03	30	300-456	Y
15	01-Oct-03	30	127-299	Y

* Session 5 aborted due to heavy overnight rain and rise in stream discharge. Low numbers of crayfish were captured and information is not included in analysis of CPUE but is included where movements are considered.

5.2.5 Abundance

An estimate of the abundance of white-clawed crayfish (>27 mm) within Eller Beck was made using the modified Petersen formula (equation 5.1) with normal approximation of the confidence interval (equation 5.2) following the recommendations of Krebs (1989).

$$\hat{N} = \frac{(M+1)(C+1)}{R+1} - 1 \qquad (5.1)$$

$$\left(\frac{1}{\frac{R}{C} \pm \left\{ 1.96 \left[\sqrt{\frac{(1-f)(R/C)(1-R/C)}{C-1}} \right] + \frac{1}{2C} \right\}} \right) M \qquad (5.2)$$

where $\hat{N}$ is estimated population size

M is number of animals marked in the first sample

C is the number of individuals captured in the second sample

R is the number of individuals in second sample that are marked

f is the estimated fraction of total population sampled in the second sample i.e R/M

5.3 Results

5.3.1 Environmental conditions

During the study a mean pH of 8.2 (SD 0.3; Min 7.2, Max 8.8) was recorded. There was a seasonal pattern of highest water temperatures in mid-summer (Maximum temperature 25.4 °C) and lowest temperatures (Minimum temperature 1.2 °C) recorded in mid-winter. Diurnal fluctuations in water temperature of several degrees were recorded throughout the summer (Figure 5.2).

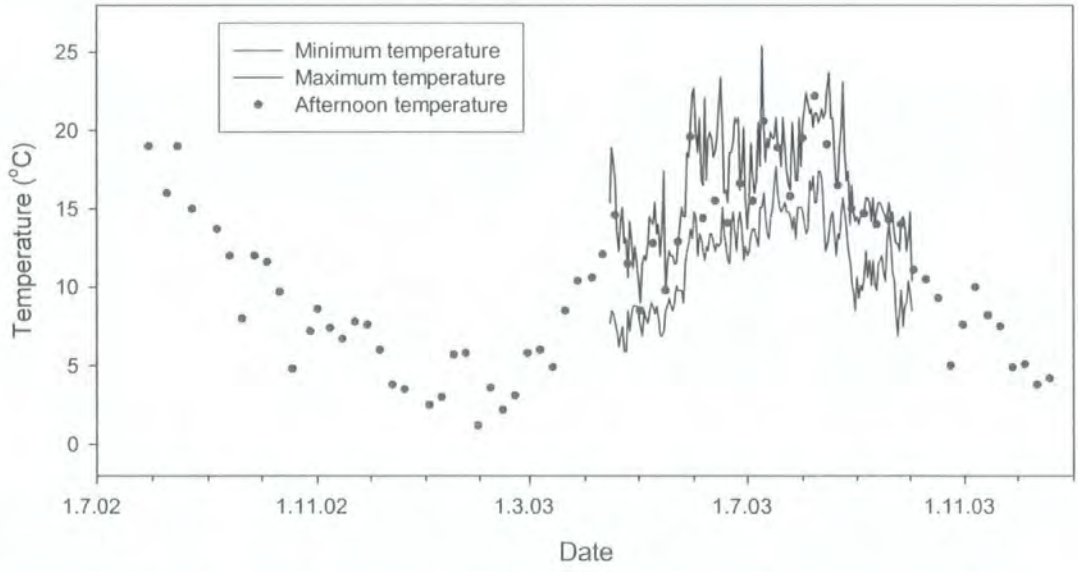


Figure 5.2 Water temperature of Eller Beck, Minumum and maximum daily temperature recorded by Tinytalk temperature logger (Hourly readings). Afternoon temperature recorded by Scott Doherty Associates environmental consultants.

5.3.2 Population characteristics

Size distribution of tagged crayfish

A total of 501 white-clawed crayfish were tagged; 382 crayfish (217 females, 165 males) were tagged from 15-31 August 2002 and 119 crayfish (24 females, 95 males) were tagged on the 25-26 June and 8-9 July 2003. Male crayfish ($\bar{x}$ CL = 37.3mm) captured during tagging were significantly larger than female crayfish ($\bar{x}$ CL = 33.7mm) captured (t = -11.8, d.f. = 495, $P < 0.001$). The size frequency of tagged crayfish is displayed in Figure 5.3. On the basis of the size-frequency distribution, and lack of information of size-frequency of crayfish carapace length < 27 mm, the individual age classes cannot be reliably distinguished. Information from other studies of white-clawed crayfish in England suggest that crayfish of carapace > 27 mm are likely to be in the 3+ age class and older (Brown 1979, Pratten 1980, Hogger 1988) and all tagged crayfish

will be mature adults. Female white-clawed crayfish are generally considered to be mature when their carapace length exceeds 25 mm and males mature when their carapace length exceeds 22 mm (Pratten 1980, Brewis & Bowler 1983)

The level of injury (crayfish with missing or regenerating chelae) in tagged crayfish was 16.8% with no significant difference between the levels of injury in males (16.5%) and females (17.0%) (Chi-Squared Test with Yates' correction for continunity $\chi^2 = 0.0005$, d.f. = 1, $P > 0.05$).

Timing of breeding

Although berried females and females carrying young were rarely trapped, a small number were caught thus allowing an estimate of the timing of breeding within Eller Beck to be made. Mating appeared to occur in late September and October, as females were captured with spermatophores in early October (1/10/03). Fieldwork was not carried out later than this so it is not known when egg laying occurred. In the wild, ovigerous females usually appear about a month after mating is first observed (Ingle 1974, Brewis & Bowler 1985), whilst captive white-clawed crayfish have been described spawning several days after mating (Matthews & Reynolds 1995). In both years young became independent in mid July. Berried (egg carrying) females were recorded through April, May and June in 2003. Females were recorded with attached young on 18/7/02 and 7/7/03 but not on 25/7/02 and 22/7/03.

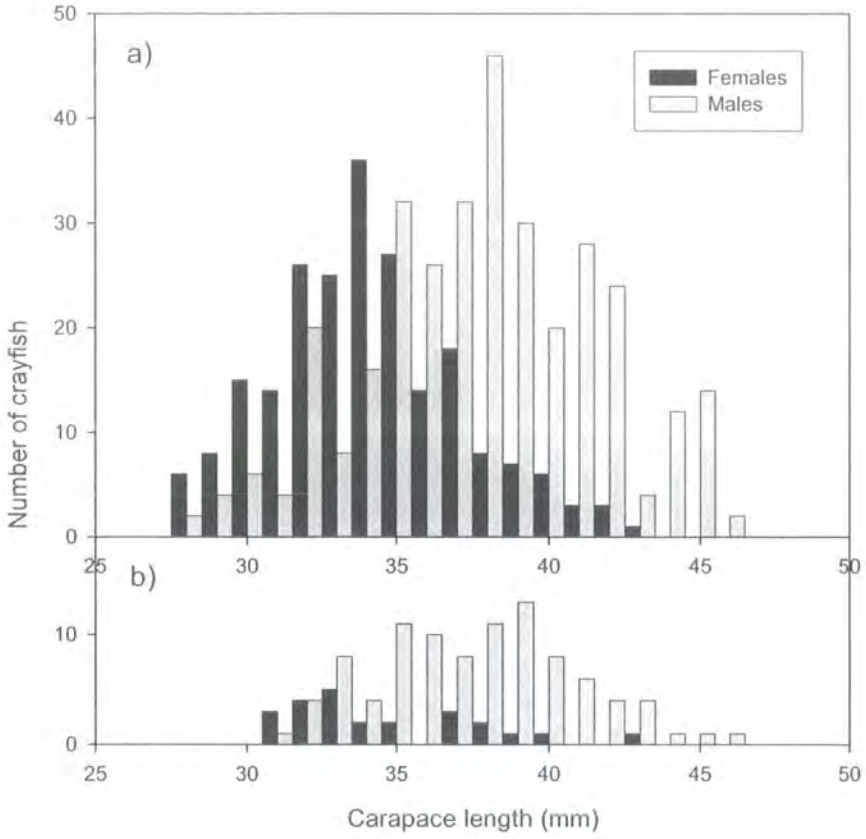


Figure 5.3 Size distribution of internally PIT tagged white-clawed crayfish tagged a) from 14 to 31 August 2002 b) 25-26 June 2003 and 8-9 July 2003.

Infection by <u>Thelohania contejeani</u>

The proportion of trapped crayfish that were recorded exhibiting signs of *T. conteheani* varied from 1.67% to 9.02% with a mean of 5.94%. A peak of infection appeared to occur in mid to late summer with the lowest levels recorded in April to May (Figure 5.4)

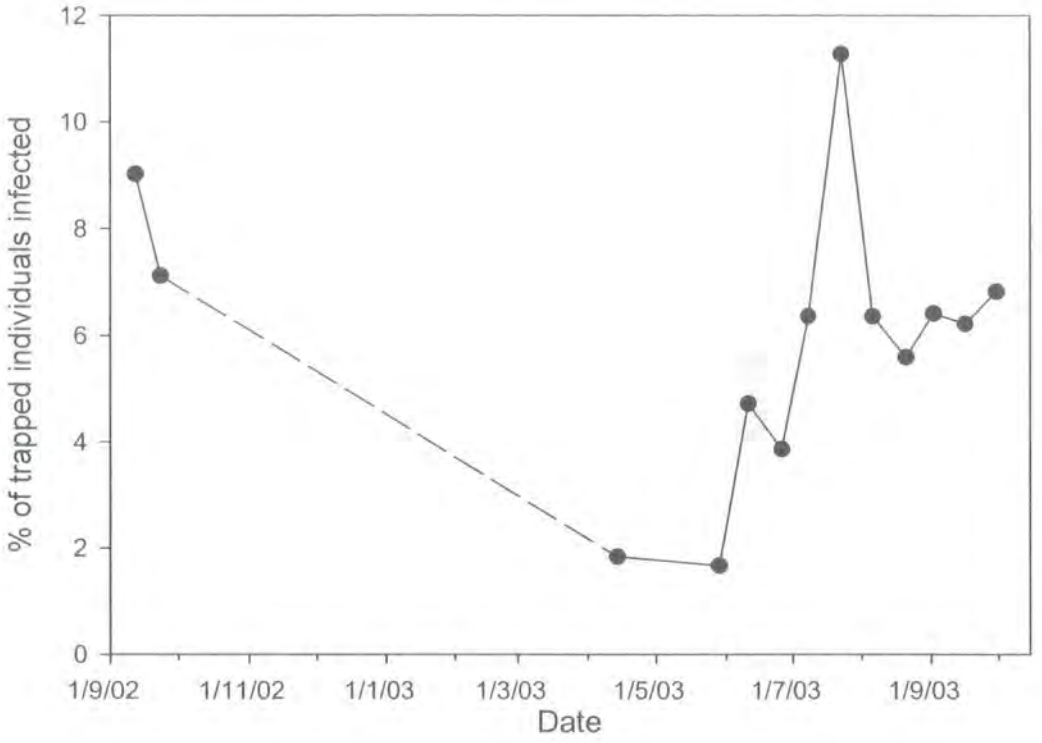


Figure 5.4 Seasonal changes in the percentage of crayfish trapped showing visible signs of *Thelohania contejeani* infestation.

Abundance and density of crayfish

A modified Petersen formula (equation 5.1) and normal approximation to the binomial confidence interval (equation 5.2) was used to estimate crayfish abundance (CL > 27 mm) using data from the first session of trapping (11-14 September) after tagging (14-31 August) in 2002.

11 - 14 September 2002	$M = 382$	$\hat{N} = 888$ (95% C.I. 791, 1017)
	$C = 254$	
	$R = 109$	

The mean width of Eller Beck (sections 164 - 424) was 2.03 m (measured every 3 m) giving an estimated wetted stream area of 1583.4 m^2. The density of adult crayfish (CL > 27 mm) within Eller Beck was estimated at 0.56 (95% C.I. 0.50,0.64) crayfish m^{-2}.

Seasonal changes in catch per unit effort (CPUE)

Variation in catches is only considered in the 2003 field season, during which the positions and numbers of traps used during each fieldwork session were kept consistent.

Over the 2003 field season there was a large amount of variability in the numbers of crayfish trapped (Figure 5.5). The number of males trapped fluctuated from CPUE of 2.13 crayfish trap-night^{-1} on 22 - 23 August to a CPUE of 0.32 crayfish trap-night^{-1} on the 31 September – 1 October. Female CPUE varied from a minimum of 0.233 crayfish trap night^{-1} on 25 - 26 June to a maximum of 1.5 crayfish trap-night^{-1} on 5 – 7 August. There was a general pattern for males of maximum catches from mid June to mid September with lower catches before and after this. The seasonal pattern in females was more marked; catches peaked from August to mid-September.

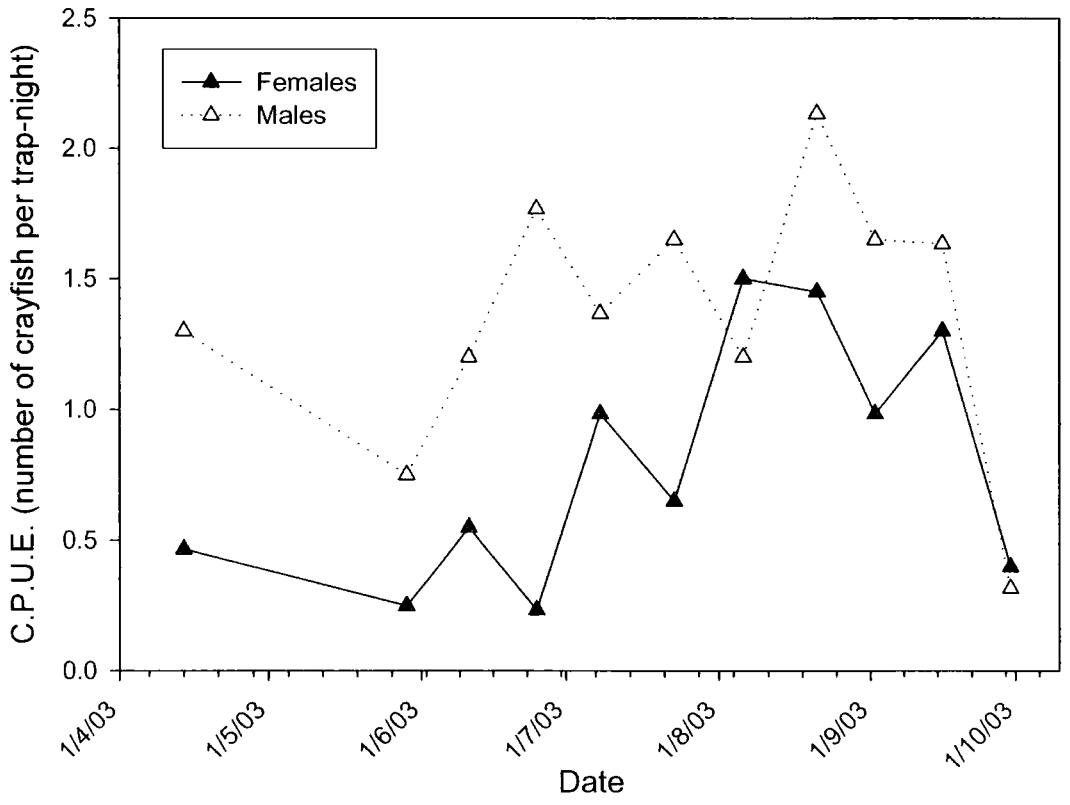


Figure 5.5 Variation in catch per unit effort of white-clawed crayfish recorded during 2003 in Eller Beck.

Sex ratio

When all trapping sessions are considered together there was a bias in the sex ratios of catches with a total of 1200 males compared to 848 females trapped (this includes individuals repeatedly trapped). The ratio of the sexes trapped was highly variable. Males predominated all catches in early summer up to August. From August onwards the numbers of females and males trapped was similar albeit with a large amount of variation between samples (Figure 5.6).

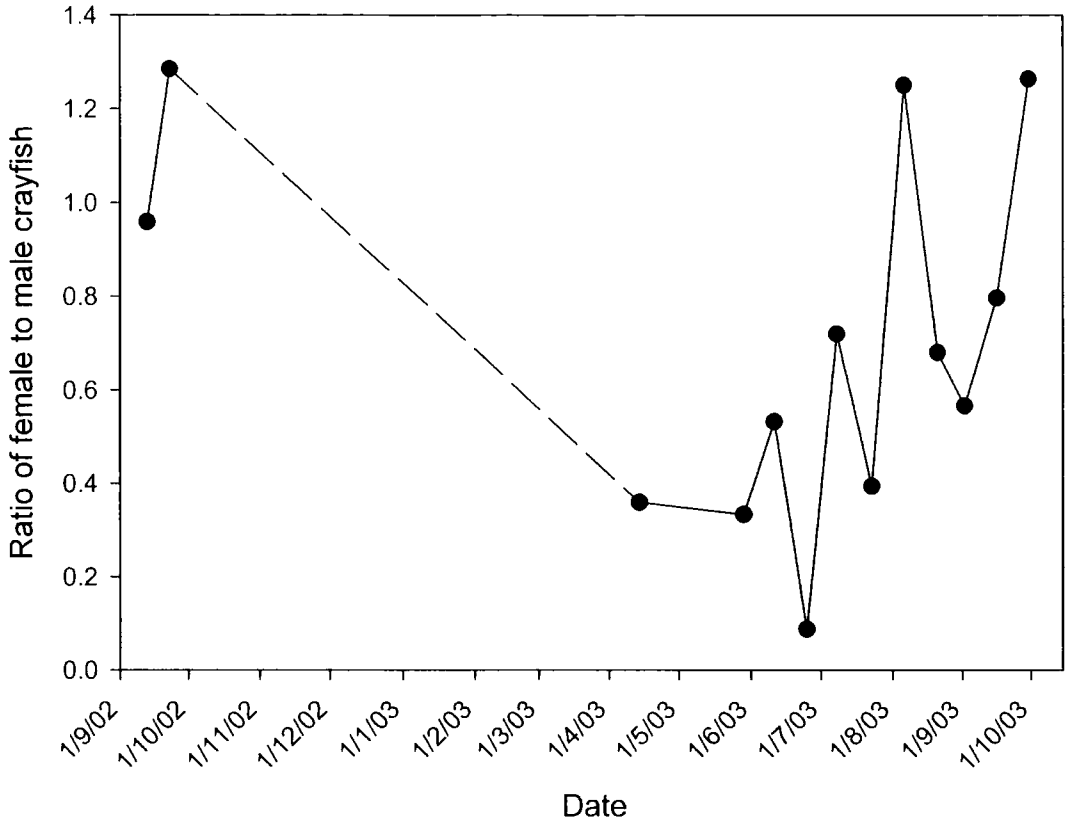


Figure 5.6 Variation in the sex ratio of crayfish trapped in Eller Beck. Data from sections 127 to 456. Each record relates to 45 trap-nights in 2002 and 60 trap-nights in 2003.

5.3.3 Movements

The absolute relocation rate of PIT tagged crayfish was 82.6%; 413 of the 501 tagged crayfish were located at least once after tagging. The interval between tagging and the last relocation ranged from 1 to 412 days with a median of 238 days. The number of times crayfish were relocated varied between 1 and 15 times with a median of 3.

The movement patterns shown by PIT tagged crayfish were very variable. Figure 5.7 demonstrates a selection of the movements recorded. The movements of all crayfish in which more than 8 relocations were recorded are given in Appendix 2. Individual crayfish were capable of making large (> 100 m) movements upstream and downstream (e.g Crayfish 3202, E6FB; Figure 5.7). The greatest absolute distance moved was 734 m upstream and 918 m downstream in 335 and 304 days respectively. Most crayfish made occasional large movements, but crayfish would often appear to reside and be repeatedly located in the same area for several weeks or months (e.g. Crayfish 4519, 9286; Figure 5.7).

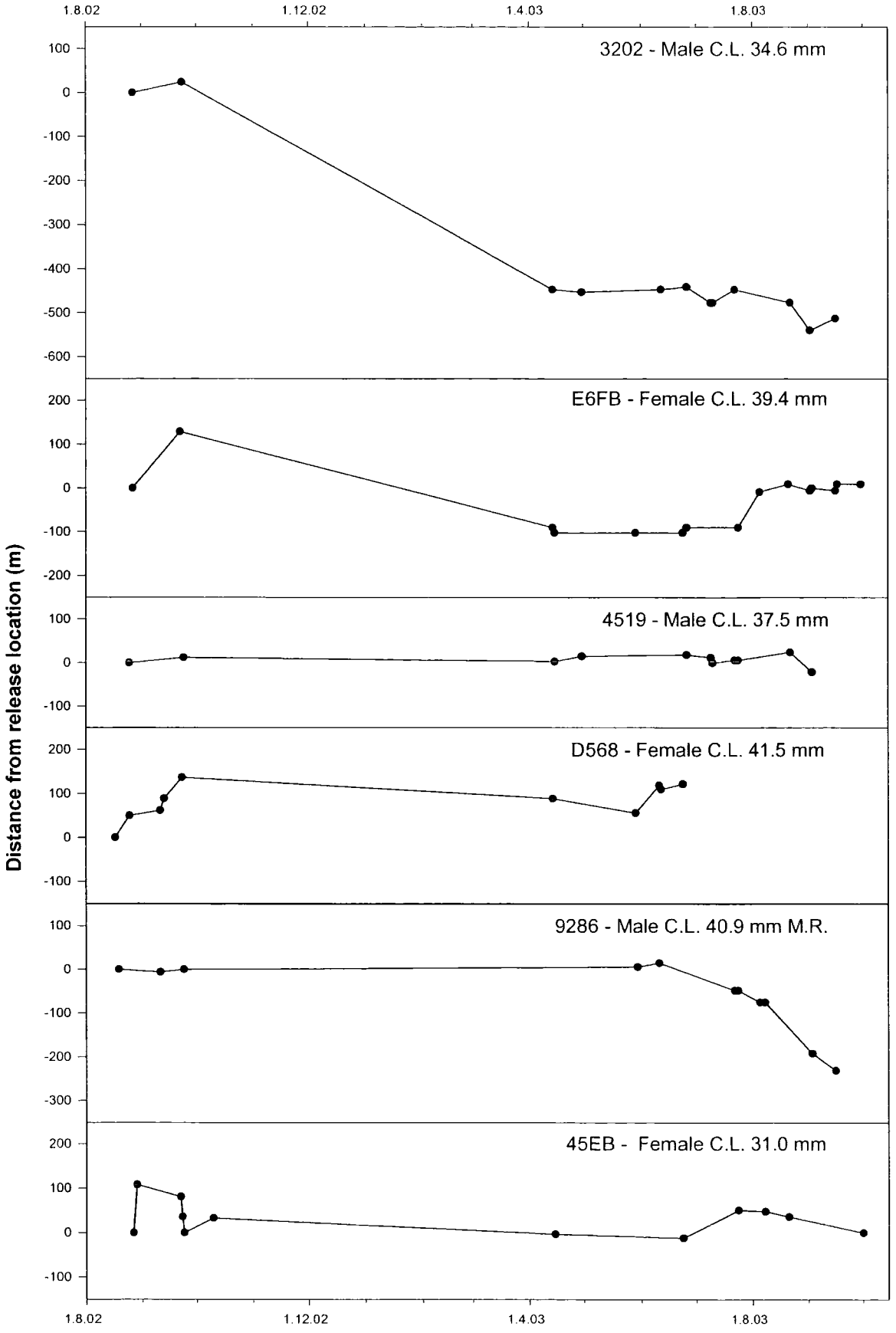


Figure 5.7 Example tracks of 6 internally PIT tagged white-clawed crayfish. Y axis represents distance crayfish moved along Eller Beck; positive values represent upstream movements and negative values downstream movements from release location.

From the movement patterns of the 49 crayfish (Appendix 2) examined in detail there is little evidence of crayfish returning to previously occupied areas of the stream. Once a crayfish had moved from one area to another it was rare for it to subsequently be recorded in the area it had moved from.

Annual rate of movement

To ensure that calculations of net annual distance moved were representative, and included all seasons they were restricted to 219 crayfish which were tagged in 2002 and relocated in 2003. The median time between tagging and relocation for this group of animals was 358 days. A negative exponential model was fitted to the empirical data (SigmaPlot 2000; Figure 5.8), this offered improved fit to the data compared with fitting Poisson and inverse power models. The majority of crayfish did not move large distances with 53.4% of crayfish moving less than 100 m. Although a few crayfish were recorded moving large distances of over a kilometre, 92.7 % of crayfish moved less than 500 m. The median annual distance moved was 84.8 m $year^{-1}$ (25 % Quartile 34.6 m $year^{-1}$, 75% Quartile 229.9 m $year^{-1}$), equivalent to annual net movement of 0.233 m day^{-1} (25 % Quartile 0.095 m day^{-1}, 75% Quartile 0.630 m day^{-1}).

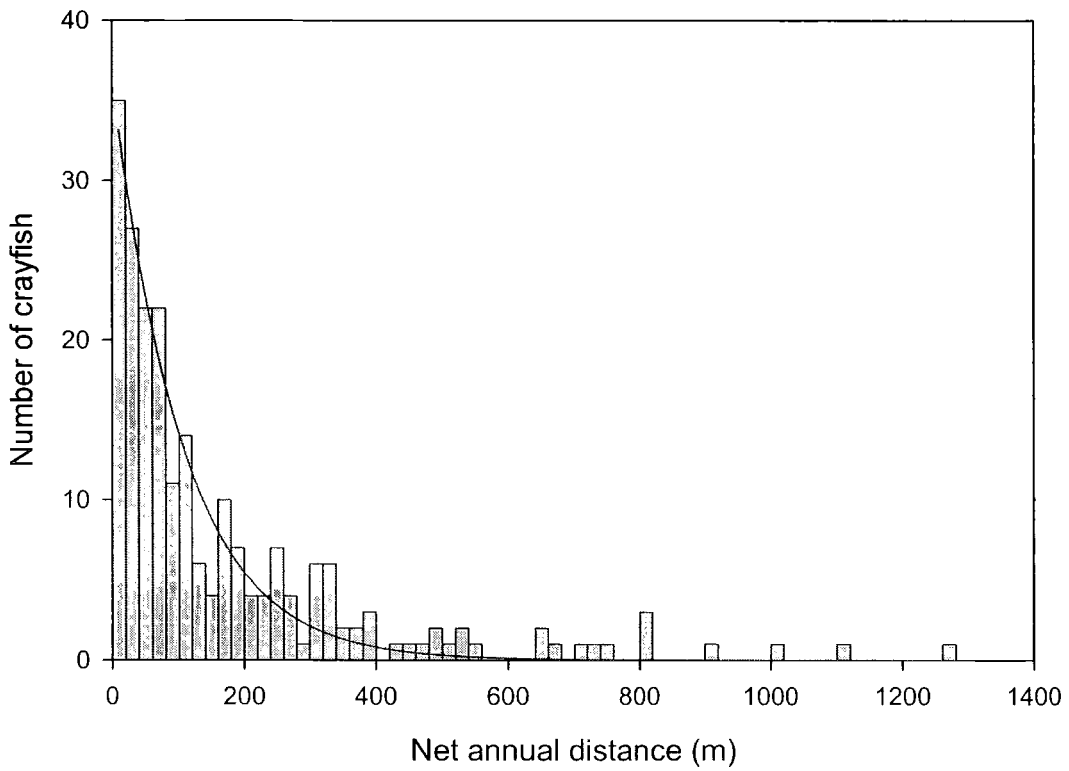


Figure 5.8 Net annual distance moved of 219 PIT tagged white-clawed crayfish, tagged in 2002 and relocated in 2003. Negative exponential line fitted ($y = 36.46 \exp^{-0.0095X}$) $R^2 = 0.9389$, $F = 1000.7$, d.f. 1,65, $P < 0.0001$.

Influence of size, sex and injury on movement

In a multifactor model sex, size, injury, number of days between tagging and final relocation, sex x days and size x days were all significantly related to the distance between release location and final relocation (Table 5.2). Uninjured crayfish tended to move further than injured crayfish (Figure 5.9). There was a significant interaction between sex and days (Figure 5.10a), for crayfish which were tagged and relocated over a short period of time, females tended to move greater distances than males, however for those crayfish which were tagged then relocated over longer periods of time the reverse was the case and males tended to move greater distances. There was also a significant interaction between days and carapace length (Figure 5.10b). Larger crayfish tended to move greater distances but this difference became less pronounced with increasing time between tagging and final relocation (Figure 5.10b)

Table 5.2 ANCOVA model (normal error structure) of distance moved (log transformed) between tagging and final relocation. All potential interactions were evaluated and non-significant ($P > 0.05$) factors were left out.

Factor	*t*	d.f.	*F*	*P*
Sex	7.38	1	54.59	< 0.001
Injury	-12.58	1	158.34	< 0.001
CL	2.97	1	8.82	0.003
Days	3.18	1	7.72	0.006
Sex x Days	-5.36	1	28.82	< 0.001
CL x Days	-2.21	1	4.88	0.028
Whole Model		6,404	40.12	< 0.001
			$R^2 = 0.364$	

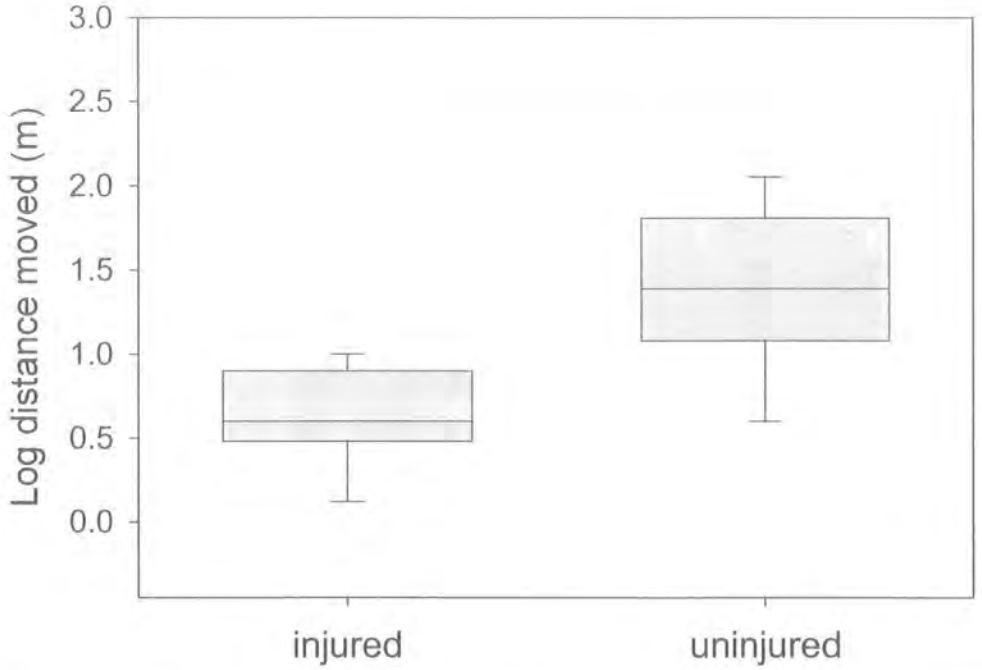


Figure 5.9 Comparative distance moved (log transformed) between tagging and final relocation of injured (missing or regenerating chelae) and uninjured crayfish. Median, 10, 25, 75 and 90 percentiles shown.

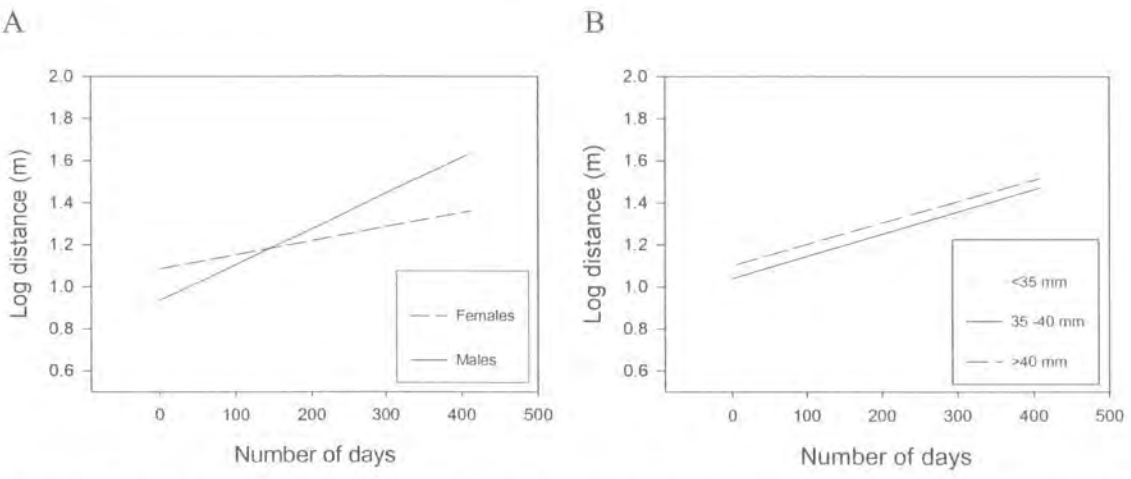


Figure 5.10 Plot of distance moved (log transformed) and number of days between tagging and final relocation of a) males and females and b) three size classes.

Direction of movements

At the final recorded location of all tagged crayfish which were relocated, significantly more were recorded downstream compared to upstream from their release location; 267 had moved downstream, 122 upstream and 24 had not moved from their release location (Chi-Squared Test with Yates' correction for continunity $\chi^2 = 54.05$, d.f. = 1, $P <$

0.001). The distribution of upstream and downstream movements from tagged location to final location is shown in Figure 5.9. Crayfish that moved downstream from the release location moved significantly greater distances (Mann-Whitney $U = -4.11$, $P < 0.001$). Median distance moved downstream was 72 m (25% quartile = 25.5 m, 75% quartile = 207 m) and median distance moved upstream was 42m (25% quartile = 15.0 m, 75% quartile = 80.25 m).

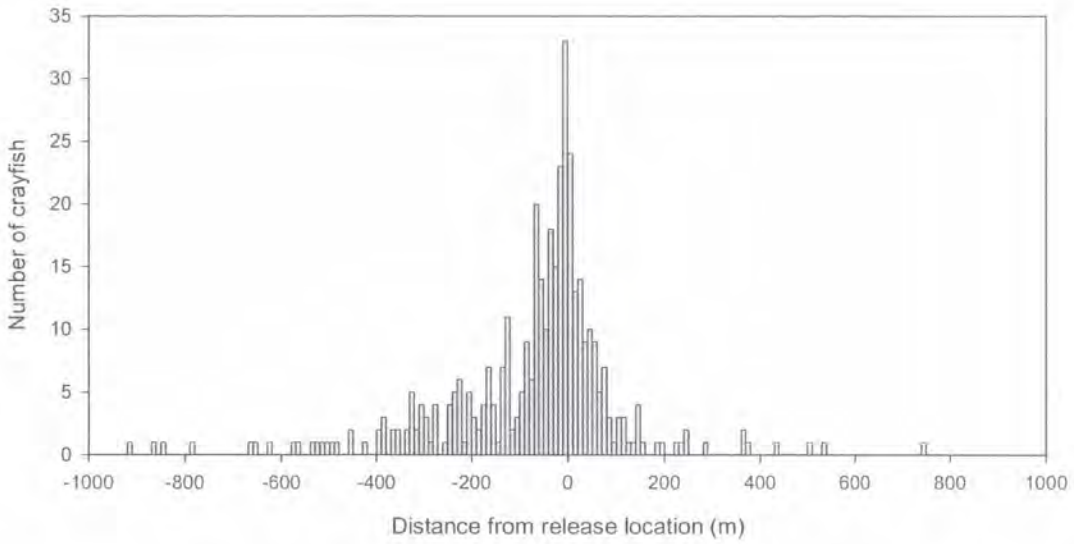


Figure 5.9 Final recorded position of 389 relocated PIT tagged white-clawed crayfish. Distance from release location shown. +ve values represent upstream and –ve values represent downstream. 24 crayfish which were only relocated at release location are not shown.

The upstream movement of crayfish appeared to be limited by the presence of a small weir at section 203. A single crayfish was recorded moving upstream past the weir, whilst 33 crayfish were recorded moving downstream over the weir (Figure 5.10). The single upstream movement of a crayfish occurred between 15 April and 5 August 2003. During this time engineering work was carried out on the weir, and rocks and rubble were piled up on the downstream side of the weir, removing the vertical drop.

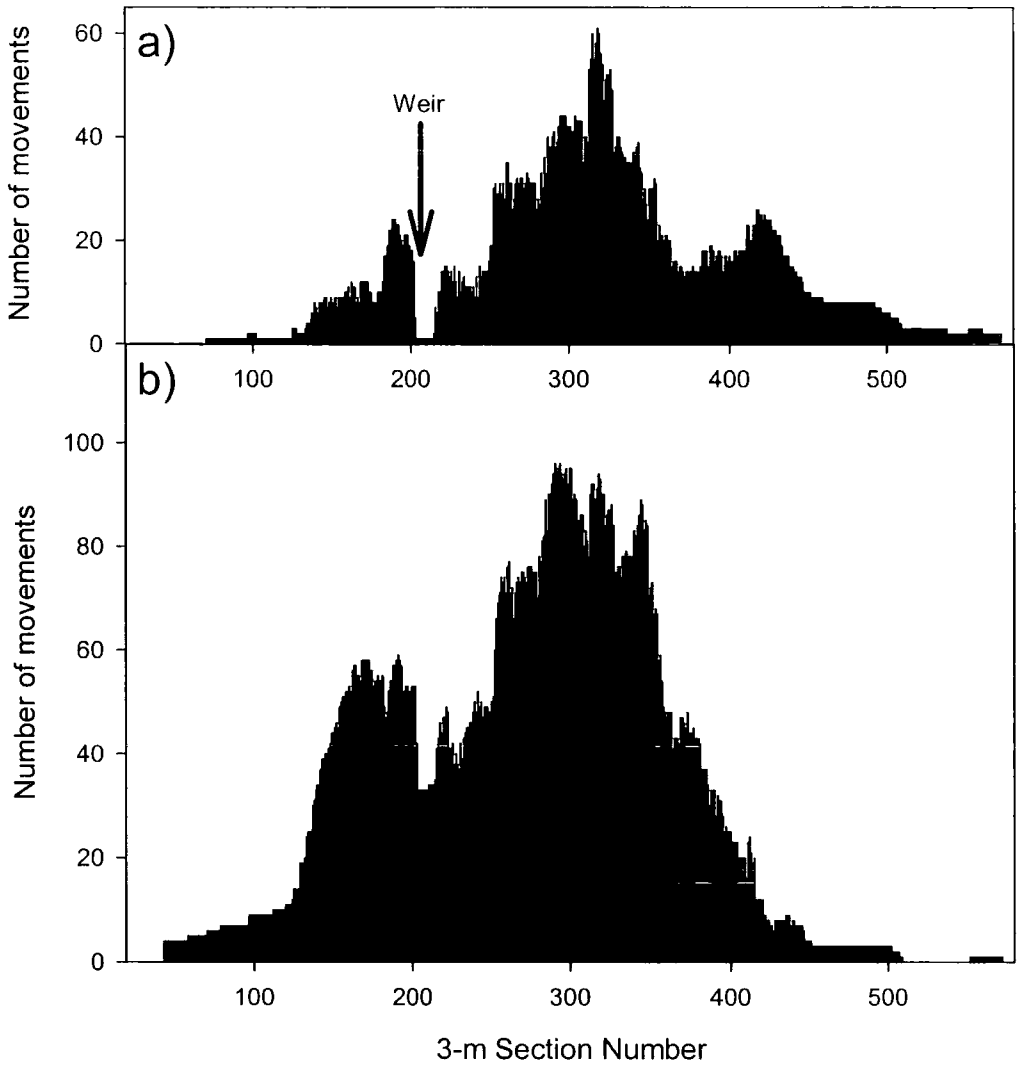


Figure 5.10 Total numbers of movements of crayfish recorded between 3-m sections a) in an upstream direction b) in a downstream direction

When the median position of relocated crayfish is considered there appeared to be an overall tendency for crayfish to move downstream over the winter period but to remain in the same position throughout the summer (Figure 5.11). Between October 2002 and April 2003 the median position of relocated crayfish changed from 6 m downstream on the 9-10 October 2002 to 51 m downstream on the 14-15 April 2003. Over the 2003 summer field season the median position of crayfish appeared relatively constant although with a high degree of variability between fieldwork sessions. If the 49 crayfish that were relocated 8 or more times are considered 84% were recorded moving

downstream between the last recorded location in 2002 and the first recorded location in 2003.

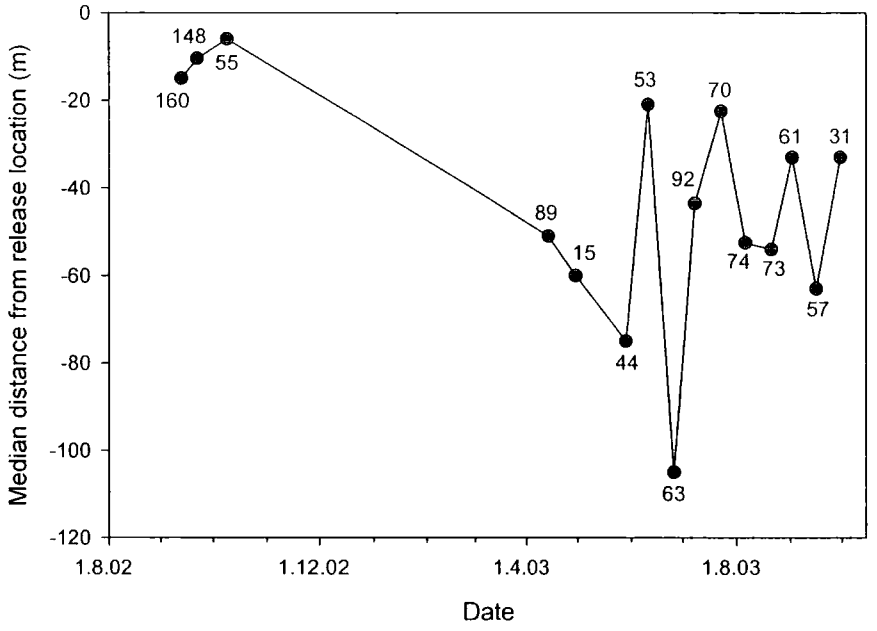


Figure 5.11 Median distance of relocated crayfish from release location. Numbers denote number of PIT tagged crayfish relocated during each fieldwork session. Only crayfish tagged in 2002 are included.

5.4 Discussion

Population information

Obtaining accurate density estimates of crayfish populations is difficult due to the behaviour of crayfish and sampling biases and difficulties involved in the various sampling methods used. Comparisons between density estimates are difficult (see reviews in McCreesh 2000, Nyström 2002) due to the range of methodologies that have been used, and variations in the section of the population sampled. The estimate of 0.56 crayfish m^{-2} calculated in this study is restricted to adults CL > 27 mm due to a combination of the use of traps which generally only catch crayfish CL > 25 mm (Brown & Brewis 1979, Byrne et al. 1999) and the use of internal PIT tags to mark crayfish which is restricted to crayfish CL > 27 mm (Chapter 3). It is therefore only representative of a subset of the population, the true density of crayfish will be considerably higher than this. Although difficult to estimate as no assessment of the relative abundance of the different age classes was made in Eller Beck, information from other studies suggests that the actual density of crayfish may be tentatively estimated at around three or four times that recorded for crayfish CL > 27. Peay (2002)

reported the proportion of the white-clawed crayfish CL > 25 mm in a stream population in northern England was 33%. The proportion of the white-clawed crayfish population made up of juveniles > 13 mm (age class 1+) has been recorded at between 50% and 66% (Brown & Bowler 1977, Robinson 1997) in streams in northern England.

Published densities of white-clawed crayfish are variable. Brown & Bowler (1977) found maximum densities of 7 crayfish m^{-2} in an aquaduct in northern England. Mees (1983 cited in Byrne et al. 1999) reported densities of up to 7 crayfish m^{-2} in streams in central England whilst Arrignon & Roché (1983) recorded densities of 3 crayfish m^{-2} in a Corsican stream. Demers (1979) recorded densities of 1.1-2.5 crayfish m^{-2} in French rivers. All these studies only considered crayfish of carapace length > 13 mm excluding age 0+ crayfish. Byrne et al. (1999) have reported very high densities of 9 – 97 crayfish m^{-2} in Irish stream populations using similar traps to those used in this study and mark-recapture techniques. Whilst examination of the CPUE in these Irish streams (3.05-5.95 crayfish trap $night^{-1}$) suggests that densities are higher than those recorded in Eller Beck, the calculations of density do not take into account the limited area of stream trapped and the likely immigration and emigration of crayfish into the area (supported by low numbers of recaptures). This violation of the assumptions of the model used to calculate density appears to have lead to unrealistic density calculations. In fixed area surveying using quadrates Robinson (1997) recorded density of 0.41 crayfish m^{-2}, Peay (2002) recorded 6.69 crayfish m^{-2}, and Byrne et al. (1999) 24.06 crayfish m^{-2}. These estimates may be subject to large biases due to habitat preferences shown by crayfish. The selection of the areas surveyed and the positioning of the quadrat will be highly influencial in determining the numbers caught and calculated density.

The Petersen model used to calculate the population estimates made in this study assumes that the population is closed, and that crayfish do not move into and out of the study area. This is not strictly the case as crayfish were able to move into and out of the area that was used for calculating the density. However given the short time between tagging and relocation, and the low levels of movement recorded during the study for the purposes of the calculation of abundance, it was felt that the population could effectively be considered closed. Trapping outside of the tagging area during summer 2003 recorded few tagged crayfish suggesting that movements out of the tagged area in the few weeks during which density estimate was calculated were limited.

The seasonal changes in CPUE and sex ratio recorded in this study are likely to reflect the biases involved when using traps. Traps have been widely reported to only collect a subset of the population (Brown & Brewis 1979, Abrahamsson 1981, Holdich & Domaniewski 1995, Byrne et al. 1999). The varying trap catches recorded in this study can partially be explained by changes in activity associated with seasonal changes in water temperature, but additional factors such as moulting and breeding are also likely to be influencial. The numerical dominance of males trapped in early summer may reflect the ovigerous status of females at this time of year, during which time they have been reported to be relatively inactive and less likely to be trapped (Brown & Brewis 1979).

The microsporidian parasite *Thelohania contejeani* is widespread in populations of white-clawed crayfish (Evans & Edgerton 2002, Holdich et al. 2004). The level of infection in Eller Beck (mean 5.94%) was similar to that recorded by Brown (1979) of 6.5%. The significance of the seasonal variation in proportion of crayfish infected is not known. It may reflect low over-winter survival of infected individuals or seasonal pattern of infection. The life cycle of microsporidians is poorly understood (Edgerton et al. 2002). Whilst it has been suggested that they are transmitted by cannibalism of infected tissues there are no reports of successful transmission by this means (Evans & Edgerton 2002). Infection by *T. contejeani* is fatal although the development is often prolonged, with an average time span of 1 year between crayfish exhibiting recognisable signs and death (Brown 1979). The effect of the levels of infection recorded in Eller Beck on the population dynamics and its importance as a source of mortality within the population is not known.

Movements

The repeated relocation of some individuals within the same area of stream over the course of several weeks or months suggests that some of the crayfish in Eller Beck show a certain level of site fidelity. Previous studies have suggested that white-clawed crayfish maintain an 'ephemeral home range' (Robinson et al. 2000) on a weekly timescale with occasional movements to new areas of stream. The movements patterns recorded in this study are in general agreement with this pattern although the length of stationary phases appeared to be greater than previously reported. Crayfish did not appear to return to previously occupied areas of stream once they had moved to a new area.

The levels of daily net movement (median 0.233 m day^{-1}) recorded in this study are lower than have been reported from other studies of the spatial behaviour of white-clawed crayfish (0.93 m day^{-1} McCreesh 2000, 1.26 m day^{-1} Robinson et al. 2000). The low levels of movement may reflect the timescale and timing of study. The information from this study relates to animals tracked over all seasons whilst previous studies have been limited to a restricted summer period. Movement and activity of crayfish over winter when water temperatures are low has been reported to be greatly reduced (Chapter 6, Flint & Goldman 1975, Abrahamsson 1981, Lozán 2000, Barbaresi & Gherardi 2001), and there are reports of white-clawed crayfish going into torpor over winter (Brewis & Bowler 1982). Both of these factors may have an impact on the levels of movement recorded.

The high gradient of Eller Beck may also contribute to low levels of movement recorded. During night-view surveys it was observed that crayfish were almost always restricted to the slower moving pools and glides. However, it is clear from the movements of individual crayfish and occasional observations that they do move over riffle areas. The permeability of riffles to movements may be reduced leading to an increased tendency for crayfish to remain in the same pool or glide section and contributing to the low levels of movement recorded.

The high gradient of the stream and large numbers of riffles may also contribute to the observed pattern of more frequent and longer movements downstream. Directional movements of crayfish have been previously reported but these have usually suggested that crayfish are able to maintain their general position. Light (2003) reported female signal crayfish tended to move upstream early in early summer and downstream in late summer whilst Momot (1966) recorded predominantly upstream movements of *Orconectes nais* and interpreted this as recolonisation in an intermittent stream. Henry (1951 cited in Light 2003) found a pattern of downstream movements in spring and upstream movements in autumn. Other studies (Hazlett et al. 1979, Gherardi et al. 1998, Guan & Wiles 1997b) have found no bias in direction of movements suggesting general maintenance of position against active or passive displacements. In this study whilst there appeared to be a tendency for crayfish to move downstream over winter, there was no compensatory redistribution movements of crayfish upstream in spring and summer. The apparent tendency for downstream movement to be made over winter may possibly

be linked to high flows and low temperatures. The lower temperatures associated with late autumn, winter and early spring are likely to limit the metabolic capacity for locomotion of crayfish. This may reduce the ability of crayfish to move upstream, especially against the elevated flows that often occur over winter.

The presence of a comparatively small weir acted as a barrier within the stream apparently preventing any upstream movements by white-clawed crayfish. Crayfish were frequently observed in the area beneath the weir but the only individual recorded as moving upstream past the weir appears likely to have moved over it when engineering work was being carried out which temporarily removed the vertical drop. The importance of barriers in limiting movements of white-clawed crayfish is unknown. The results from this study suggest that the presence of even a comparatively small barrier may have a major impact on movements of crayfish. In areas where expansion of white-clawed crayfish populations is occurring and when reintroduction schemes are considered barriers may have a major impact on the successful upstream colonisation. Removal of barriers or measures to improve the ability of white-clawed crayfish to traverse barriers may be required to enable connectivity within a system.

The weak tendancy for larger crayfish to move greater distances may reflect a number of factors. It may be the result of greater areas searched for resources, with greater absolute energy requirements of larger crayfish or it may be due to increased locomotory ability. A similar pattern of increased distance moved by larger white-clawed crayfish was described by Robinson et al. (2000), but not by McCreesh (2000). The lack of pattern found by McCreesh (2000) may reflect the limited size range of crayfish tagged in that study compared to both this study and Robinson et al. (2000).

The tendency for females tracked over short periods to move greater distances than males tracked over similar short time periods of time may be a reflection of increased energy demands and the need for a more proteic diet in the phase of vitellogenesis as has been reported in river crab *Potamon fluviatile* (Gherardi et al. 1988). Those crayfish tracked only for short periods of time are animals which where only tracked during a single summer and not overwinter. The reduced movement of females with increasing time tracked may reflect the species life cycle. Females that were tracked for long periods of time were crayfish which were tagged in 2002 and relocated in 2003, the period that they were tracked for would have included the overwinter period when they

are likely to be ovigerous. The activity of ovigerous females has been described as 'limited' (Gherardi et al. 1998) and McCreesh (2000) described a pattern of restricted movement by radiotracked ovigerous female crayfish with increased movement following young becoming independent.

The decreased movement of crayfish with missing or regenerating chelae has not previously been reported. It is possible that the decreased movement reflects changes in dominance and lower ability of crayfish with missing chelae to obtain shelters if they are previously occupied reducing the likelihood of injured crayfish making movement to different areas. The possession of a suitable refuge or shelter is a key resource for crayfish survival (Lodge & Hill 1994). Communication in crustaceans often involves the display of chelae, and they perform an important role in agonistic and aggressive interactions with the chelae playing a major role in the acquisition and retention of shelters (Mariappan et al. 2000). In white-clawed crayfish, Gherardi et al. (2000a) showed that crayfish missing one chela have a lower hierarchical rank.

CHAPTER 6. SPATIAL AND TEMPORAL MOVEMENT PATTERNS OF ADULT SIGNAL AND WHITE-CLAWED CRAYFISH

This chapter describes the movement and dispersal of radiotagged crayfish within upland riverine populations. The seasonal movement pattern of signal crayfish and the influence of environmental factors is described. In addition the comparative spatial behaviour and microhabitat use of syntopic white-clawed and signal crayfish is described.

6.1 Introduction

In an ecological context, information about movements and activity is important in contributing to an understanding of habitat requirements, patterns of resource utilization and potential for interspecific interactions. Previous studies on movement and colonisation by signal crayfish have been predominantly concerned with populations in lakes and lowland rivers (Abrahamsson 1981, Guan & Wiles 1997b, Kirjavainen & Westman 1999). The spatial behaviour of signal crayfish under the more variable and rapidly changing conditions in upland rivers is mostly unreported. Most crayfish species are capable of substantial active movements against flows, this ability may be particularly important in rivers and streams for range expansion. The impact of flood events may be important; upstream movements of the crayfish *Orconectes nais* to depopulated areas following floods have been recorded (Momot 1966). High flows may contribute to downstream expansion of populations through passive movements, but may also cause flood related mortality (Parkyn 2000, Robinson et al. 2000) and reductions in density (Light 2003).

A thorough understanding of the spatial and temporal patterns of movements in signal crayfish is relevant to understanding their colonisation abilities. Investigations of the spatial behaviour of crayfish have predominantly been concerned with movements during the summer when water temperatures approach their maximum. Interpreting annual dispersal patterns from studies conducted over a restricted period of time may conceal important components within the lifecycle of crayfish. The spatial behaviour of crayfish during autumn and winter has received little attention. This includes the time when breeding and egg laying occurs and hence has the potential to influence the movement patterns of adult breeding crayfish. In addition, the effect of seasonal variation in temperature and the impact high flows may have on the behaviour of crayfish has not been investigated.

An important component determining the invasiveness of species is the rate at which they disperse (Mooney & Drake 1989), and Ehrlich (1989) considers vagile behaviour to be characteristic of invasive species. Signal crayfish are considered to be highly invasive species (Holdich et al. 1995). This contrasts with white-clawed crayfish which are generally considered relatively non-invasive with population expansion occurring only slowly (Peay 2002). Whilst various studies have investigated the spatial behaviour of white-clawed and signal crayfish (see Chapter 3), all studies have been restricted to locations where the two species do not coexist. Differences in study sites, methodologies, duration and timing make comparisons between the movement of signal and white-clawed crayfish problematic. The presence of both white-clawed and signal crayfish within the 'mixed zone' in the River Wharfe allowed the spatial behaviour of white-clawed and signal crayfish to be compared directly. In addition to comparisons of their spatial behaviour the comparative microhabitat use of signal and white-clawed crayfish was also investigated. The degree of overlap in habitat use by the two species may influence the degree of interspecific interactions and the potential for competition between the two species. Laboratory studies have suggested that signal crayfish are dominant to white-clawed crayfish and competition for shelters has been suggested to contribute to the observed replacement. The replacement of white-clawed crayfish by signal crayfish occurs relatively rapidly in the River Wharfe (Chapter 2) and at other sites (Holdich et al. 1995, Holdich & Domaniewski 1995), whilst various factors have been suggested as contribution to the observed replacement, there are no field-based studies addressing which mechanism(s) may be the primary cause(s) and if there is overlap in the habitat use of the two species.

The objectives of this study were to a) measure the extent of movement of adult signal crayfish at fine spatial and temporal scales in upland rivers, to establish their relationship with environmental conditions and model dispersal behaviour b) compare the movements of signal crayfish from populations of varying densities and c) compare the spatial behaviour and habitat use of sympatric white-clawed and signal crayfish. All measurements concerning movements and dispersal at the study sites on the Wharfe and Ure were made by radio-telemetry. Although limited to the study of adult crayfish, this method has the capacity to provide data on the movement patterns of animals on a fine spatial and temporal scale. Moreover it can provide such data where the likelihood of recapture of marked individuals is very low, so it is highly appropriate for the study of

movements during winter and in expanding low-density populations, such as at the Ure site.

6.2 Methods

Radiotelemetry data collection was separated into five site-season specific component studies: (i) River Wharfe, winter 2000/01, (ii) River Ure, summer to autumn 2001, (iii) River Ure, summer 2002, (iv) River Wharfe, summer 2002 and (v) River Wharfe, summer 2003.

6.2.1 Study Sites

Fieldwork on the Ure was centred upon a 1 km section of river (NGR: SE 266780 – SE 265787) surrounding the site of introduction of signal crayfish. Fieldwork on the Wharfe was carried out at two sites. Radiotracking during winter 2000/01 and summer 2002 was carried out at the same site, hereafter referred to as Grassington site and radiotracking during summer 2003 was carried out further downstream, at a site hereafter referred to as Barden Bridge site. At the Grassington site radiotracking was centred on a 1.5 km section of river (NGR: SD 993644 – SE 000634) approximately 5 km downstream from the source of introduction of signal crayfish. At the Barden Bridge site fieldwork was centred on a 1 km section of river (NGR: SE 053578 – SE 054568) approximately 15 km downstream from the source of introduction.

At the Ure and Grassington sites only signal crayfish were present whilst at the Barden Bridge site both signal and white-clawed crayfish were present. At the Grassington site the signal crayfish population is well established, having been present for over 10 years (Chapter 2). The length of time signal crayfish have been present at the Barden Bridge site is not precisely known but it appears to be approximately 5 years (Chapter 2). Densities of crayfish varied considerably between the three sites. The highest densities of signal crayfish were present at the Grassington site, with lowest densities at the Ure site. Although quantitative surveys were not carried out standardised effort handsearching (capturing all size classes of crayfish) was conducted at all sites allowing comparisons of relative densities. At the Grassington site handsearching in 2002 recorded 55 signal crayfish person-hours^{-1}, at the Ure the average catch (over the study site) by handsearching in 2003 was 9.6 signal crayfish person-hours^{-1} (Chapter 2). At the Barden Bridge site in 2003 30 signal crayfish and 15 white-clawed crayfish were captured in an hour of handsearching by one person.

The rivers in all study areas are approximately 30 m wide. The Ure and Barden Bridge sites are bordered for much of their length on both sides by deciduous woodland. The Grassington site is bordered on one side by woodland with pasture predominant on the other. At all sites the substratum varies from large boulders on exposed bedrock to silt, although cobble is the dominiant substrate. The sites include areas of riffle, glide and pools with deeper water. The Grassington site is partially regulated by a weir at the downstream end of the study site.

6.2.2 Environmental measurements

Water temperature at the study sites was measured at 60 min intervals during the study periods using Tinytalk temperature loggers (Gemini Data Loggers, Chichester, U.K.). The flows in the Upper Wharfe and Ure were measured at Addingham and Kilgram gauging stations, respectively. Although the gauging stations are several kilometres downstream from the study sites the pattern of discharge between the study sites and gauging weirs are very similar (River height at Grassington and discharge at Addingham $r^2 = 0.8932$, River height at Mickley weir (2 km upstream from Ure site) and discharge at Kilgram $r^2 = 0.9615$).

6.2.3 Capture and radiotagging

Large crayfish for radiotagging were caught by handsearching in accessible areas of the river. Stones were moved aside from the bed of the river by hand and any large crayfish that were concealed beneath were collected. The carapace length (CL) of crayfish, from the rostral apex to the posterior median edge of the cephalothorax, was measured to the nearest 0.1 mm using vernier calipers. The wet mass of crayfish was measured to the nearest 0.1 g using an electronic balance. Excess water was removed from crayfish prior to weighing.

Table 6.1. Details of crayfish tagged during the five periods of radiotracking (for full details see Appendix 3)

Site and year	Duration	Number tagged	Number successfully tracked (M:F)	Track duration* (days) mean (S.D.)	Carapace length* (mm) mean (S.D.)	Mass* (g) mean (S.D.)
Grassington 2000/01	October – February	20 PL	18 (9:9)	120 (10.4)	45.7 (6.9)	36.9 (21.8)
Ure 2001	August - September	15 PL	15 (3:12)	32.9 (7.7)	42.8 (5.3)	32.8 (8.5)
Ure 2002	June – August	14 PL	12 (5:7)	29.3 (7.2)	34.7 (17.9)	48.1 (8.1)
Grassington 2002	June – August	21 PL	19 (9:10)	47.3 (21.4)	44.1 (3.6)	28.0 (6.5)
Barden Bridge 2003	July – August	15 PL 20 AP	15 (8:7) 20 (11:9)	32.6 (3.7) 23.1 (10.0)	46.1 (8.2) 38.5 (2.2)	36.1 (24.5) 17.6 (3.4)

PL – Signal crayfish, AP – White-clawed crayfish. * of individuals successfully tracked for > 5 days.

Radio transmitters (type PIP powered by an Ag 392 battery; Biotrack, Wareham, UK) were used to track crayfish. Tags measured 17 x 8 x 6 mm, with a whip antenna length of c. 10 cm and were potted in dental acrylic. Frequencies between 173.700 and 173.950 MHz, with a nominal spacing of 10 kHz were used to identify individual crayfish. The radio tags had a lifespan of over three months. In order to maximize tag life, pulse length was limited to 15 ms, with a pulse period of 2 s, giving a predicted minimum life of 2.9 months, although achieved life was generally greater than this. Tags were attached using a combination of cyanoacrylate adhesive and dental acrylic. All tags were attached to chelae of crayfish (Figure 6.1) with the exception of three crayfish radiotagged during summer 2003 River Wharfe. The chelae of these three crayfish (two female white-clawed crayfish and one female signal crayfish) were too small to attach the radiotransmitter, instead the tag was attached to the cephlothorax. Before attaching the transmitter the chela (or cephlothorax) was dried. Cyanoacrylic adhesive was applied to attach the tag in position, and dental acrylic was used to fill crevices round the tag and provide a strong, robust means of attachment. Care was taken to ensure that the joints on the chela were free from glue and that full mobility of the chela was retained. Tags were preferentially attached to the chelae rather than cephalothorax, because attachment to the cephalothorax would increase body depth and it was felt that this was more likely to influence the mobility of crayfish in refuges.

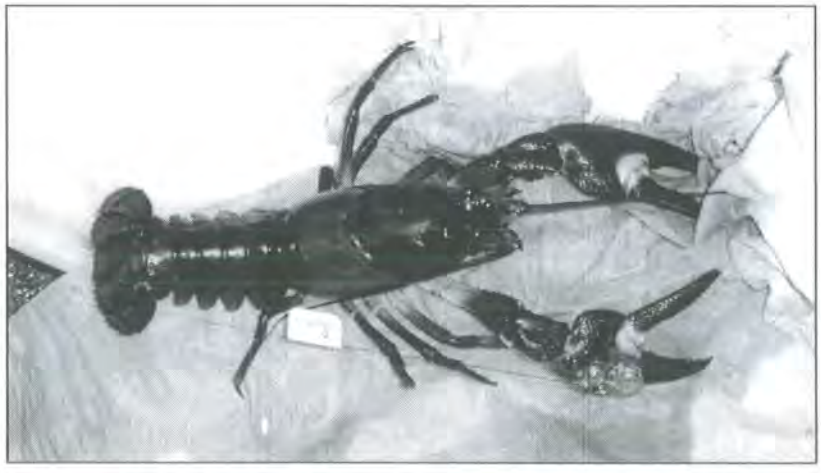


Figure 6.1 Male signal crayfish tagged with radiotransmitter (type PIP, Biotrack)

Crayfish were retained for about 30 minutes until the acrylic was set. During each tracking session except Barden Bridge 2003 crayfish were returned close (usually < 1 m) to the capture location. During Barden Bridge tracking in 2003 when both signal and white-clawed crayfish were tracked simultaneously, crayfish were released in four areas

of the river with approximately 25% of tagged crayfish of each species released at each location. Total tag mass was not more than 1.8 g, which represented 1.4-15.1 % of body mass. This is a similar tag mass:body mass ratio as in other telemetry studies of crayfish (Bohl 1999, Schütze et al. 1999, Robinson et al. 2000, Gherardi & Barbaresi 2000, McCreesh 2000) none of which reported interference with behaviour or survival.

6.2.4 Tracking

Crayfish were tracked over the study using a combination of a modified Yaesu FT290R receiver (Argus Electronics, Great Yarmouth, UK), a Mariner M57 receiver (Mariner Radar, Lowerstoft, UK) and a Biotrak BT-256 Sika receiver (Biotrack, Wareham, UK) all with a collapsible three-element Yagi antenna. Tagged crayfish could be detected at a distance of 50-100 m with the Yagi antenna held at head height. Once a signal was detected the direction of the strongest signal was followed until the fieldworker was close to the crayfish. In the case of the Biotrack and Mariner receivers as the distance to the tag declined and the signal strength increased, the gain was adjusted to decrease the arc over which the signal could be detected. The Yaesu receiver did not have a manually controlled gain, therefore to allow precise locations to be recorded the receiver was either detuned away from the tag frequency or the Yagi antenna was replaced with a 0.1 m length of coaxial cable to reduce the gain. Using these methods when water levels permitted entry to the river (> 75 % of the time) the positions of radiotagged crayfish could be located to within one metre. The accuracy of location was reduced to within 5 m when the position of crayfish was assessed by triangulation from the bank. When crayfish were located their positions were recorded with reference to riverside features that had been marked on a scale map of the area. Their position upstream or downstream of the release location was calculated.

During tracking on the Ure and Wharfe in 2002 and Wharfe in 2003 the positions of crayfish were recorded every other day. On the Ure in 2001 intensive tracking every other day was carried out during September and less frequently, usually twice a week, in August. During the winter tracking in the Wharfe, crayfish were usually tracked once or twice a week. All tracking was carried out during daylight hours; locations therefore represent daytime refuge sites but are indicative of long-term movements. This was confirmed by periodic night-time visits.

Not all crayfish tagged were successfully tracked. During the study on the Wharfe in winter 2000/01, the radiotags on two crayfish are believed to have become detached soon after tagging (<14 days). During fieldwork in summer 2002 two crayfish each at the Wharfe and Ure sites moulted soon after tagging (<10 days) and so lost their radio transmitters. The results from these crayfish are not included in the analysis.

During winter 2000/01 in order to compare local activity, on a standardised basis, over the full period of study, signal strength measurements were made over 4 hours beginning 30 minutes after sunset. Local activity levels were monitored during 10-min time periods using changes in signal strength as an index of activity (Lucas & Batley 1996, Robinson et al. 2000). Crayfish were classified as active (1+ changes) or inactive (0 changes) based on the number of variations in signal strength recorded. Changes in transmitter antenna orientation relative to the receiver antenna that occur due to movements of the whole animal or of the chelae, are responsible for observed variations in signal strength (Robinson et al. 2000). Thus these measurements reflect behaviour patterns such as feeding and aggressive interactions as well as locomotion. Tests with non-moving tags and resting crayfish during the day, further validated the applicability of these night-time local activity measurements. Local activity of between 7 and 18 individual tagged crayfish was monitored in each session (mean number of crayfish monitored per session 14.2). The percentage of crayfish that were active was calculated and compared with temperature.

6.2.5 Tracking methodological rationale and data analysis

The quantification of the areas utilised by radiotracked animals is often achieved through home range analysis (White & Garrot 1990), where home range is defined as the area or volume repeatedly traversed by an animal during activities such as feeding, resting and reproduction. However, this analysis was not applicable to the movement of crayfish recorded during this study in which crayfish were repeatedly located at the same position with occasional movements to a new refuge and no return to previously occupied locations (see Figure 6.1). The analysis of home ranges may be applicable to crayfish if their nocturnal positions are recorded whilst they are foraging (e.g Armitage 2000) however in this study only the daytime positions were recorded. The analysis of the pattern and extent of movements by radiotracked crayfish was based on distances moved from release location. For each radiotracked crayfish, the total linear range was calculated. This was the difference between the maximum distance upstream and

downstream recorded throughout the period a crayfish was tracked. In several of the radiotracking periods the number of days which individual crayfish were tracked for varied. Because in the Ure, Summer 2002 and Grassington, Summer 2002 tracking sessions, linear range was correlated with the duration that crayfish were tracked for (Spearman Rank Correlation, $r_s = 0.634$ (Ure) $r_s = 0.684$ (Wharfe) both $P < 0.05$) to compare the relative movement of individuals tracked over different durations, the range was divided by the number of days for which the crayfish was tracked (range per day tracked).

6.2.5.1 Pattern of dispersal of signal crayfish

Many studies have sought regression equations that best describe the distributions of dispersal distances (e.g. Kot et al. 1996). Negative-exponential functions are commonly used to model the shape of the curve describing the distance moved by marked individuals (Hill et al. 1996, Conrad et al.1999). The frequency distribution of dispersal recorded in this study showed a typical negative exponential shape. Therefore the negative-exponential function was used to describe the movements made and dispersal of individuals. In the context of lotic environments dispersal is essentially bi-directional, upstream or downstream, but the factors (especially flow) influencing directional movement make separate comparison of the direction of dispersal a sensible approach. In the analysis of dispersal data separate models were fitted to the upstream and downstream components. Data were linearly transformed using a semi-ln plot, analysed using regression analysis, and the upstream and downstream regression lines compared. The upstream and downstream range of tagged animals was used to provide a measure of the dispersal potential of the tagged crayfish, and to allow comparison of upstream and downstream dispersal. The analysis of ranges includes signal crayfish data from both rivers and all seasons. The relatively small number of signal crayfish tagged during each seasonal component necessitated this although when conducting concurrent tracking on both rivers no differences in spatial behaviour were observed (see results). The integration of these data provided a realistic data set of the dispersal opportunities of signal crayfish occurring during different environmental conditions over the annual cycle. Whilst the comparison of upstream and downstream ranges includes signal crayfish tracked for differing durations, at different seasons and sites, it is considered appropriate as each radiotagged signal crayfish provides a paired sample of an upstream range and a downstream range.

6.2.6 Microhabitat use of signal and white-clawed crayfish

During the radiotelemetry study in 2003 at the Barden Bridge site the following abiotic variables were recorded at each unique location at which a radiotagged crayfish had been located: depth, water velocity, degree of shading and substrate. All measurements were made during stable baseflow conditions. At each location a $1m^2$ square quadrat was placed on the substrate. Water velocity and depth were measured at the center of the quadrat. Water velocity was measured over a 30 second period with a OTT C31 impeller current metre (OTT Messtechnik GMBH & Co., Kempten, Germany) at 5 cm from the substrate level, depth with a ranging pole to the nearest 5 cm. The degree of riparian shading was assessed on a qualitative scale ranging from 1 to 5, with 5 being heavily shaded by low overhanging branches and 1 unshaded open water. The proportion cover within the quadrat of six categories of substrate was visually estimated. The following substrate categories based on a modified Wentworth scale were used; 1-silt and sand (diametre <2 mm), 2-gravel (2-16 mm), 3-pebble (16-64 mm), 4-small cobble (64-128 mm), 5-large cobble (128-256 mm), 6-boulder (>256 mm). A substrate index (I) (modified from van Snik Gray & Stauffer 1999) was calculated from the sum of the percentage cover (n) of each substrate category (S): $I = \Sigma n S$. The index therefore ranges from 100 (area consisting of 100% silt/sand) to 600 (area 100% boulder) and increases with substrate size.

The ability to analyse habitat use statistically from telemetry data in this study was compromised because measurements collected on individuals are not independent and individual replication was limited. Furthermore, certain habitat variables, such as water velocity, depth and substratum are frequently collinear and interrelated. To overcome these limitations the data is presented graphically in a manner similar to the approach used by David & Closs (2003). The individual habitat variables used by each crayfish are pooled within species and converted to proportions. Using this approach, the comparative use of each habitat variable (velocity, depth, shade, substrate) can be assessed directly. The degree of overlap in habitat use by signal and white-clawed crayfish was assessed using principle component analysis (PCA). Principle component analysis was performed on all the crayfish microhabitat records. Factors included in the PCA were water velocity, depth, shade, substrate index, % boulder, % large cobble. Biplots of the two most important principle components were constructed and the maximum convex polygons containing all observations were calculated. This allowed a

comparison of the range of microhabitats used by signal and white-clawed crayfish to be made and gave an indication of the degree of overlap.

6.3 Results

6.3.1 Signal crayfish movement and dispersal

6.3.1.1 Movement patterns

In all periods of radiotracking a similar pattern of movement of signal crayfish was observed. Crayfish would usually remain in the same location for days to weeks, and then move to a new location associated with a refuge (Figure 6.2). No signal crayfish were recorded returning to refuges that they had previously occupied after they had moved to a different refuge. In all tracking periods there was a large variation between individuals in the total amount of movement recorded between refuges (Figure 6.3). The maximum distance moved by any one crayfish was 790 m and the minimum was 0 m during total tracking periods of 74 and 127 days respectively.

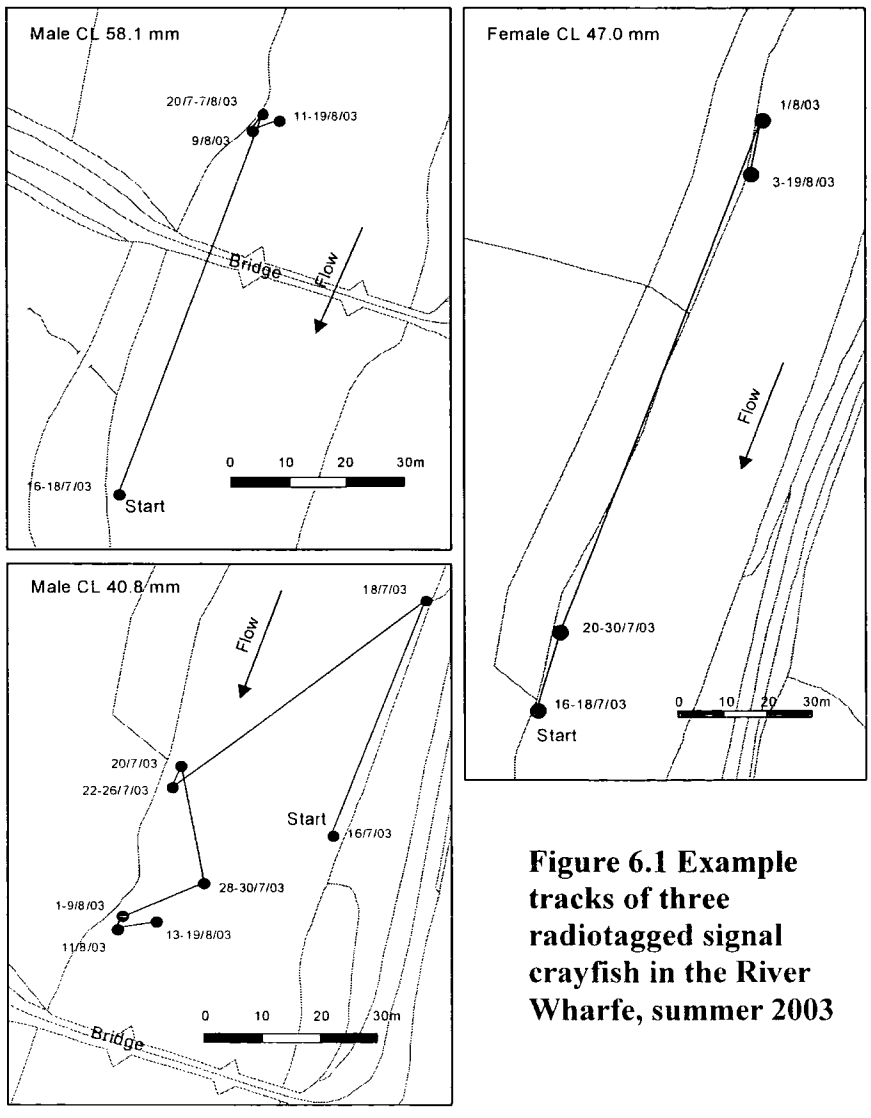


Figure 6.1 Example tracks of three radiotagged signal crayfish in the River Wharfe, summer 2003

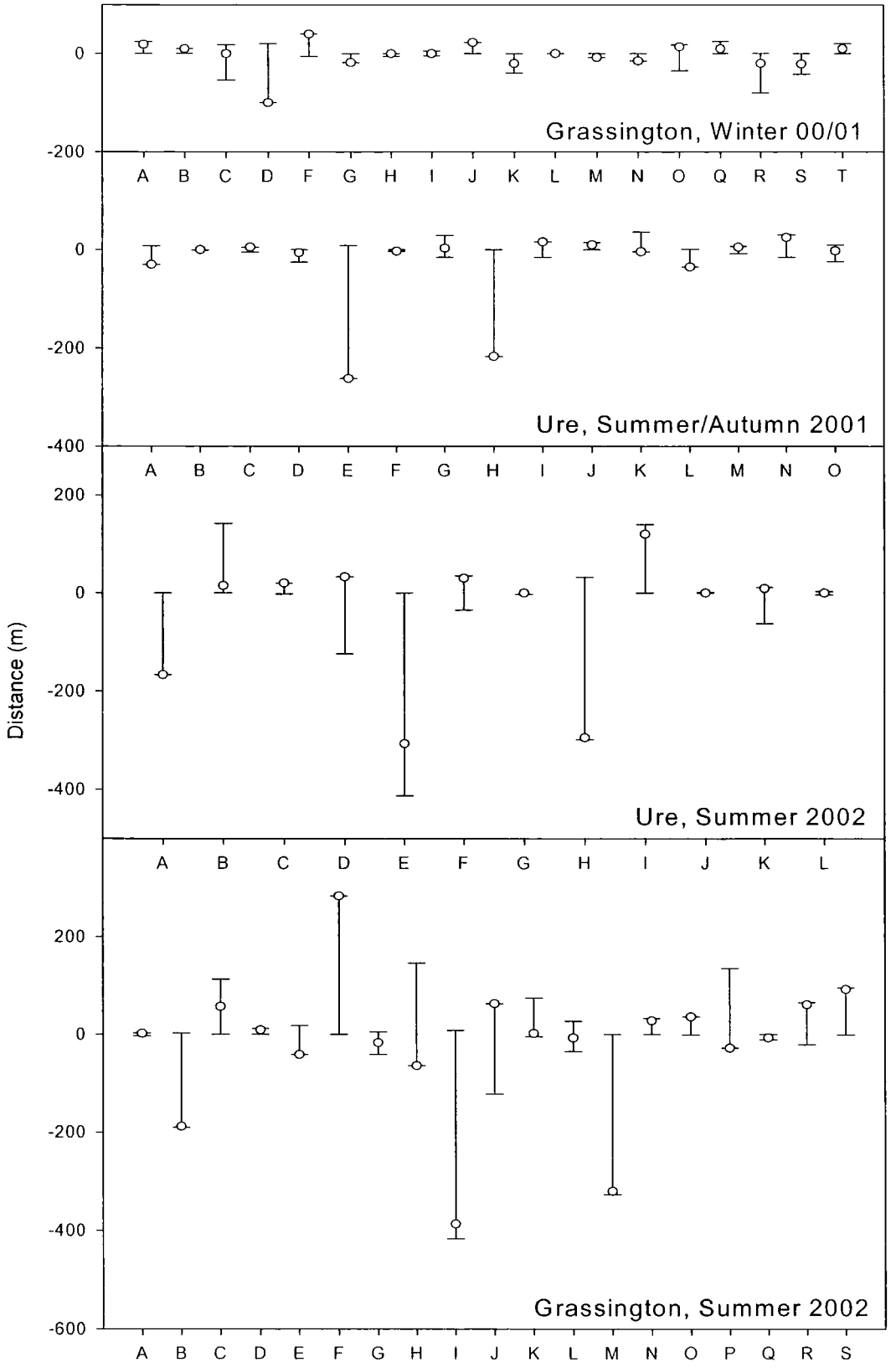


Figure 6.3 The upstream and downstream range of movement of radiotracked signal crayfish in first four radiotracking sessions. Circles represent final position and attached bars represent maximum distance moved upstream (+) and downstream (-). The release location is represented by 0 m on the vertical axis. (Details of Barden Bridge 2003 tracking session given in Figure 6.12)

6.3.1.2 Site and seasonal changes in movements of signal crayfish

There were significant differences between the amount of movement of signal crayfish recorded in the different tracking periods (Kruskal-Wallis $K_4 = 33.6$, $P < 0.001$). Maximum movements were recorded during mid-summer (July-August) with a decline in recorded movements during late summer (August-September) and further declines in winter (Figure 6.4). A comparison of the two radiotracking sessions carried out concurrently at Grassington and in the Ure in summer 2002 and the session carried out at Barden Bridge in summer 2003, showed no significant difference in either the daily distance moved (Kruskal-Wallis $K_2 = 0.46$, $P > 0.05$) or range per day tracked (Kruskal-Wallis $K_2 = 2.5$, $P > 0.05$). Hence during summer, there seemed to be no clear difference in the spatial strategies of adult signal crayfish from the three populations of contrasting densities.

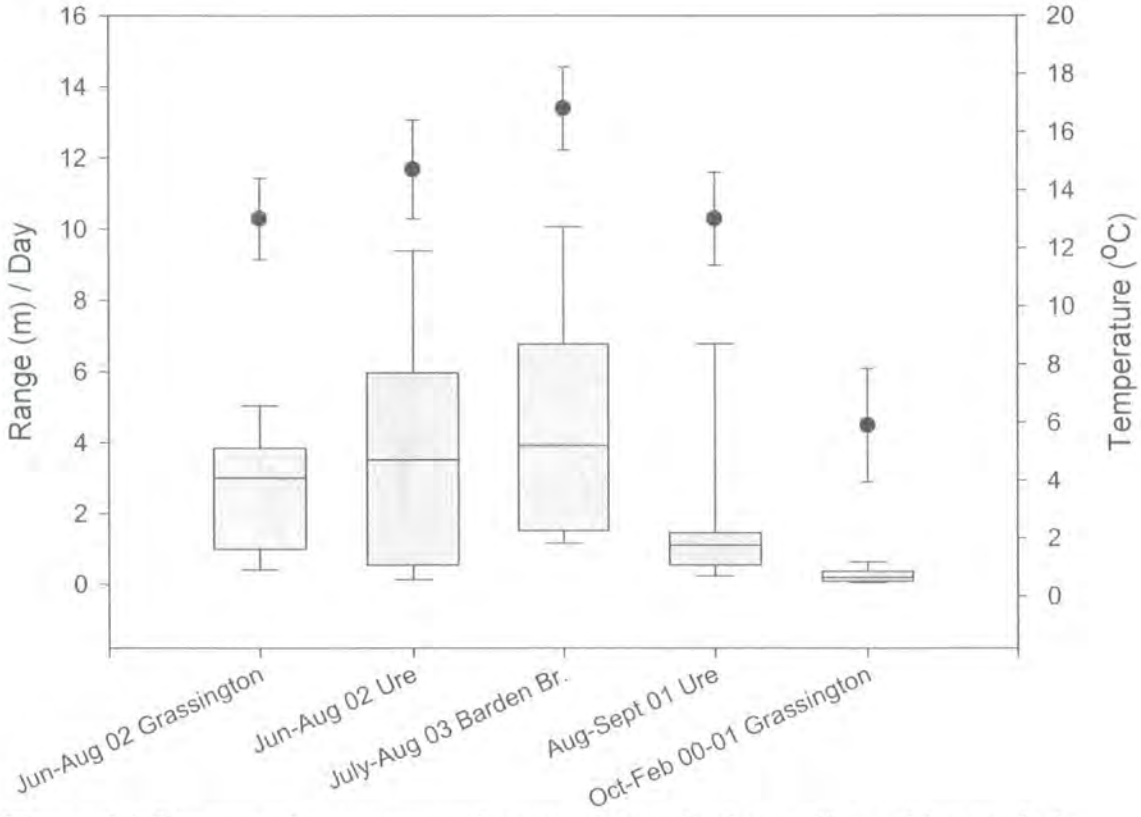


Figure 6.4 Comparative ranges and temperature during radiotracking periods. Box plots represent range per day tracked, the 10th, 25th, 50th, 75th and 90th percentiles are shown. Circles represent mean water temperature (±SD) during tracking period.

During tracking in autumn-winter 2000/01 (Grassington site) there was a large reduction in movement of crayfish, particularly from mid-December onwards (Figure 6.5). Prior to this, the amount of movement during the tracking period was relatively constant but still lower than during track periods in summer and early autumn. After mid-December, virtually no movement of crayfish was recorded and those movements

that were recorded were relatively small. There was a significant difference in the range per day of radiotagged crayfish recorded before 16 December compared to range per day after 16 December (Wilcoxon matched pairs; $T = 11$, n = 17, $P = 0.002$; Figure 6.6). The reduction in movement occurred at the same time as a rapid and substantial decline in water temperature (Figure 6.5). Temperature before and after 15 December 2000 was significantly different (*t*-test, t = 92.4, $P<0.001$). A mean (± SD) temperature of 7.9 ± 1.2 °C was recorded from 16 October to 15 December 2000 compared to a mean (± SD) of 4.2 ± 1.3 °C in the period from 16 December to 10 February.

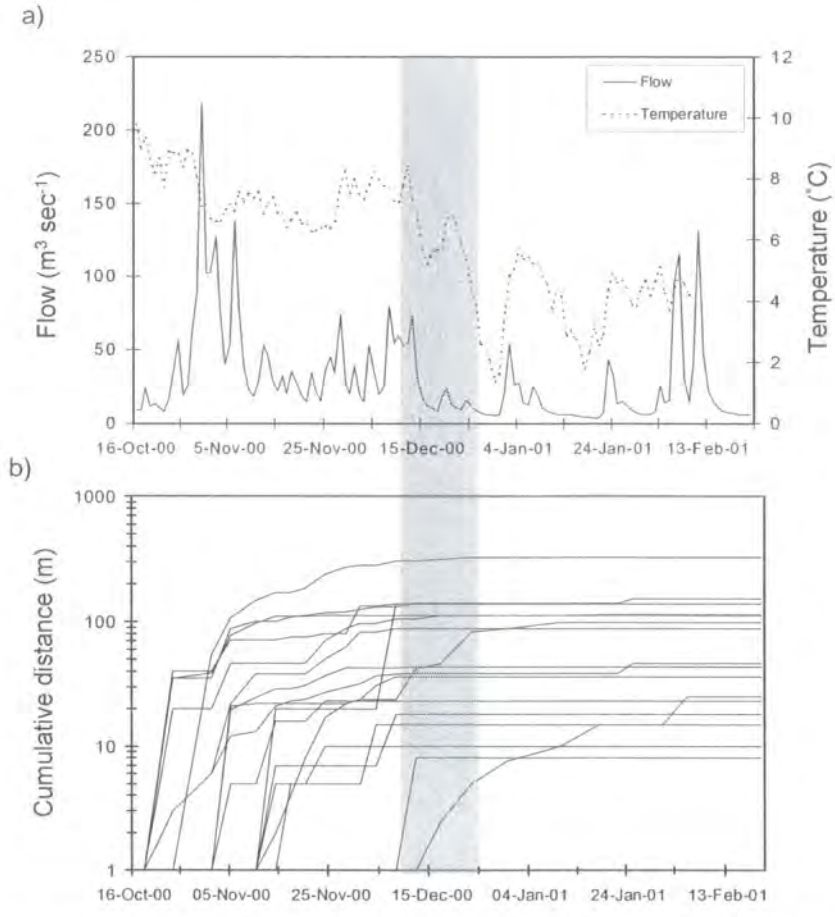


Figure 6.5 a) Mean daily flow (16 October 2000 – 22 February 2001) and mean daily water temperature (16 October 2000 – 10 February 2001) in the upper River Wharfe. b) Cumulative linear distance moved by 18 radio-tracked signal crayfish. All 0 readings have been transformed to 1. Grey bar indicates period in which decline in water temperature corresponded with decline in large scale movements of crayfish.

Analysing the movement of all radiotagged signal crayfish (n=79), there was no apparent effect of size or sex on the amount of movement recorded. General Linear Models were constructed (Genstat, version 6.0, VSN International Ltd, U.K.) with a negative binomial error function. Range day^{-1}was used as the response and size, sex and tracking session as predictors into the model. Full factorial models were initially

constructed then least significant factors removed. Only tracking session was significant ($P < 0.05$), neither size (Figure 6.7) nor sex were significantly related to the range day^{-1}.

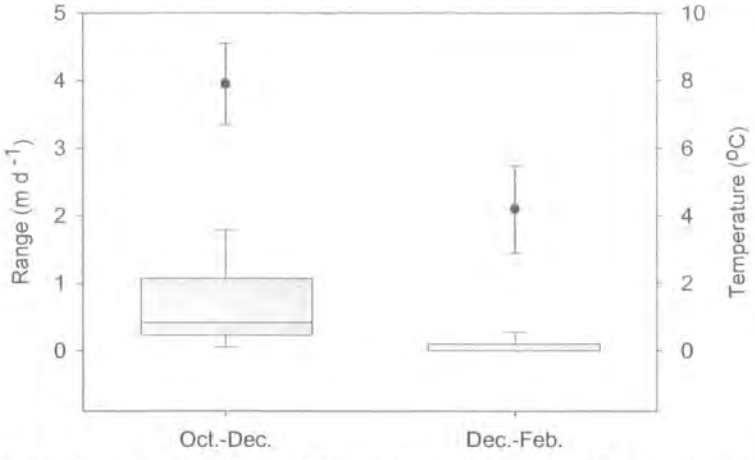


Figure 6.6 Range per day of 18 radiotagged signal crayfish from 16 October to 15 December and 16 December to 10 February. Box plots represent range per day tracked, the 10th, 25th, 50th, 75th and 90th percentiles are shown. Circles represent mean temperature (±SD) during tracking period.

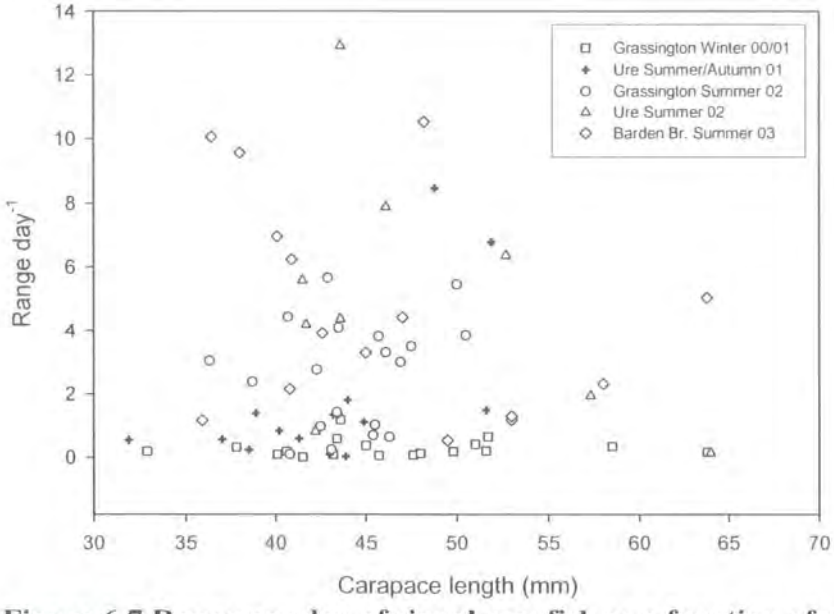


Figure 6.7 Range per day of signal crayfish as a function of size for each tracking session.

6.3.1.3 Dispersal

The upstream and downstream range of a crayfish is defined as the maximum distance moved upstream and downstream from the release location. This was used to provide a measurement of the dispersal potential of the tagged crayfish. The frequency distribution of upstream and downstream ranges of all crayfish are given in Figure 6.8a. Using the data from Figure 6.8a the inverse cumulative proportion of individuals ranging over certain distances upstream and downstream were separately fitted to a

negative-exponential function where the probability of an individual (I) having a range greater than (R (m)) is given by:

$$I = e^{-kR}$$

where k is a species-specific dispersal constant describing the shape of the exponential curve. Ln I was regressed upon upstream ranges ($R^2 = 0.898$, $F_{1,12} = 115.47$, $P < 0.001$) (Figure 6.8b). The gradient of the line then gave the value of k:

$$\ln I = -0.00949 \text{ (SE} = 0.001) R$$

The same procedure was carried out for downstream ranges ($R^2 = 0.924$, $F_{1,17} = 205.94$, $P < 0.001$)

$$\ln I = -0.00774 \text{ (SE} = 0.001) R$$

There was no significant difference between the two regression lines ($t_{29} = 1.238$, $P > 0.05$).

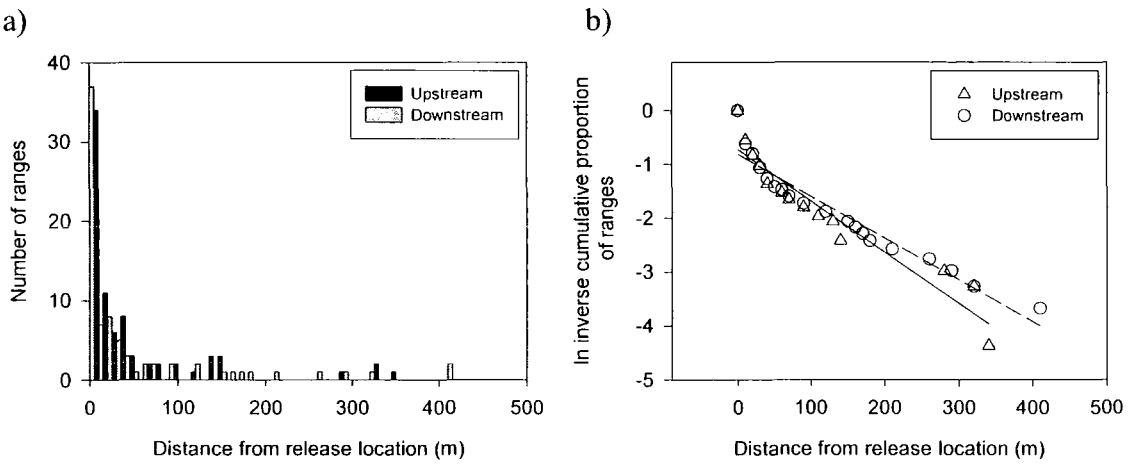


Figure 6.8 a) Frequency distribution of upstream and downstream ranges of radiotracked signal crayfish. Values of maximum distance upstream and downstream of all radiotracked crayfish (n = 79) shown. b) Semi ln plot of inverse cumulative proportions of paired upstream and downstream ranges of radiotracked signal crayfish (n = 79). The solid line shows the fitted exponential function of upstream ranges and the dashed line the exponential function of the downstream ranges.

6.3.1.4 Environmental Factors

When all crayfish in all tracking periods were combined (treating early and late winter 2000/01 tracking periods separately; Section 6.3.1.2), there was a significant positive correlation between mean water temperature and range per day tracked (Spearman Rank, $r_s = 0.664$, $P < 0.001$) (Figure 6.9).

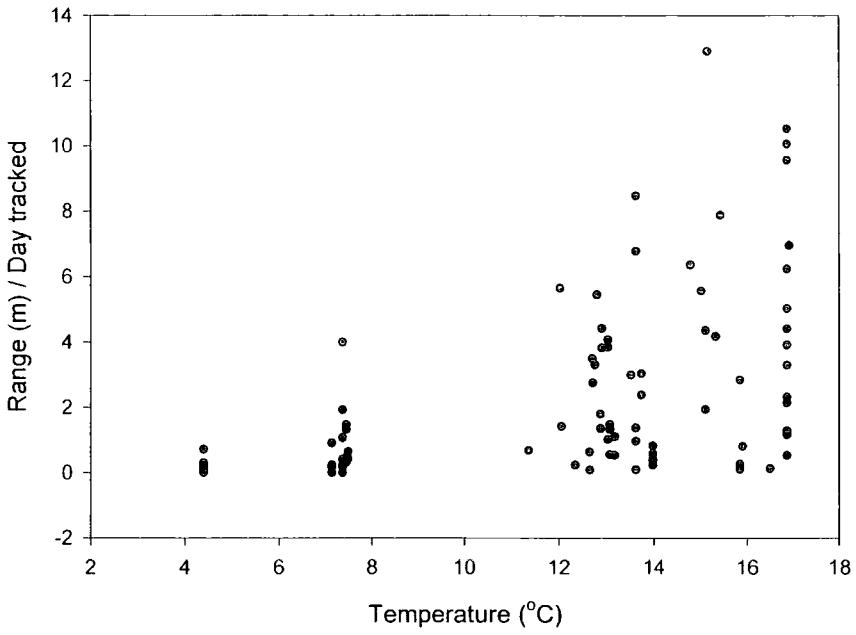


Figure 6.9 Plot of range per day tracked of 79 radiotagged signal crayfish and mean water temperature during period crayfish tracked for. Spearman Rank correlation, $r_s = 0.664$, $P < 0.001$.

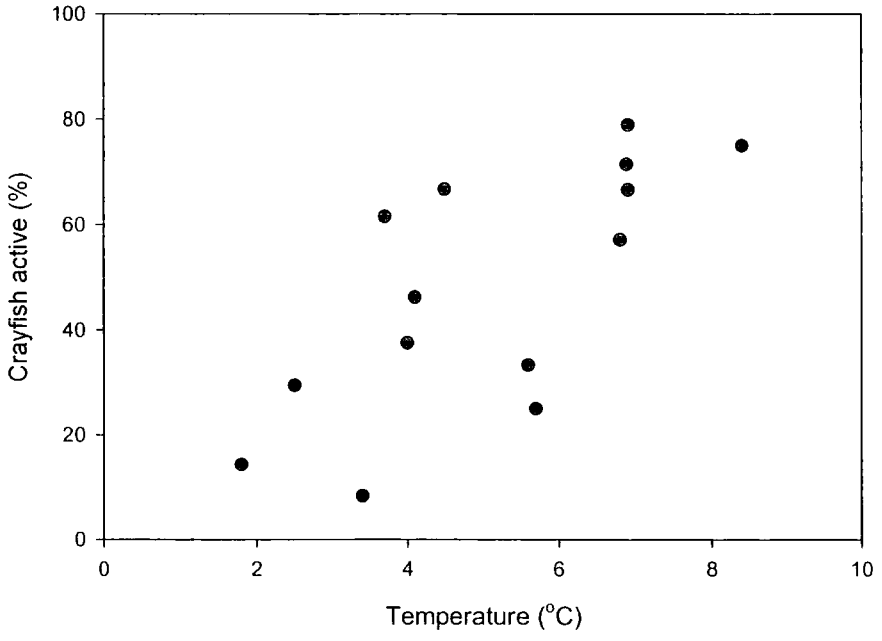


Figure 6.10 Relationship between the percentage of radio-tagged signal crayfish locally active at night and water temperature during autumn and winter 2000/01 ($r_s = 0.755$, $P = 0.002$)

Analysis of the relationship between water temperature (range 1.8 – 8.4 °C) and the percentage of crayfish that were locally active (Grassington site winter 2000/01 tracking session) showed a highly significant positive correlation (Spearman Rank, $r_s = 0.755$, $P = 0.002$). The percentage of crayfish recorded as active was lower at reduced temperatures, although even at very low temperatures (1-4°C) a proportion of crayfish were recorded as active (Figure 6.10).

The proportion of crayfish moving between tracking sessions (2 days) was calculated for the Ure and Grassington 2002 tracking sessions combined and the mean temperature and flow of the two rivers calculated. The flow of the two rivers was highly correlated ($r_s = 0.948$, $P < 0.001$) as was temperature ($r_s = 0.746$, $P < 0.001$). Both displayed very similar patterns (Appendix 4), although during the summer period the Ure was an average of 1.7 °C warmer. As water temperature and flow were correlated (River Ure $r_s = -0.424$, $P = 0.001$, River Wharfe $r_s = -0.650$, $P < 0.001$) partial rank correlations were used to correlate water temperature and flow with proportion of crayfish moving. Fixing the effect of temperature, Kendall's test of partial rank correlation between the proportion (arcsine transformed) of crayfish moving and flow was negative and significant ($\tau_{\text{movement, flow | temperature}} = -0.261$, $P < 0.05$). The partial correlation of movement and temperature, fixing the effect of flow, was not significant ($\tau_{\text{movement, temperature | flow}} = 0.126$, $P > 0.05$). During periods of high flow there was an apparent reduction in the number of crayfish moving (Figure 6.11).

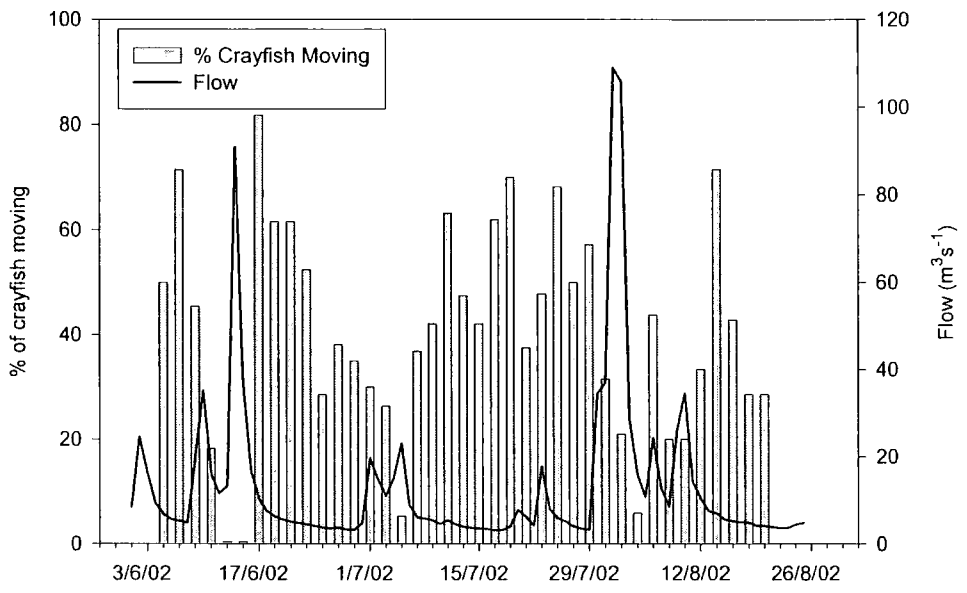


Figure 6.11 Plot of proportion of radiotagged signal crayfish moving and river discharge. Data for proportion of crayfish moving are combined from Grassington and Ure during summer 2002. Discharge data are from Wharfe, information on Ure discharge is not given because of very high correlation ($R_s = 0.948$, $P < 0.001$) with Wharfe.

During all tracking sessions there were periods of high flow (Appendix 4) although discharge was most variable during late autumn/winter 2000/01 tracking and summer 2002 tracking. There was no evidence from any of the tracking sessions that any radiotagged crayfish were swept significant distances downstream by the high flows. There were no large movements > 20 m during periods of high flow during any of the tracking periods.

6.3.2 Comparative spatial behaviour of syntopic signal and white-clawed crayfish

6.3.2.1 Comparative Movement

There was considerable variation in the distance moved by syntopic white-clawed and signal crayfish over summer 2003 (Figure 6.12). There was a general pattern of greater distances moved by signal crayfish compared to white-clawed crayfish. The maximum distance moved from release location by a white-clawed crayfish was 90 m compared to a maximum of 342 m moved by a signal crayfish.

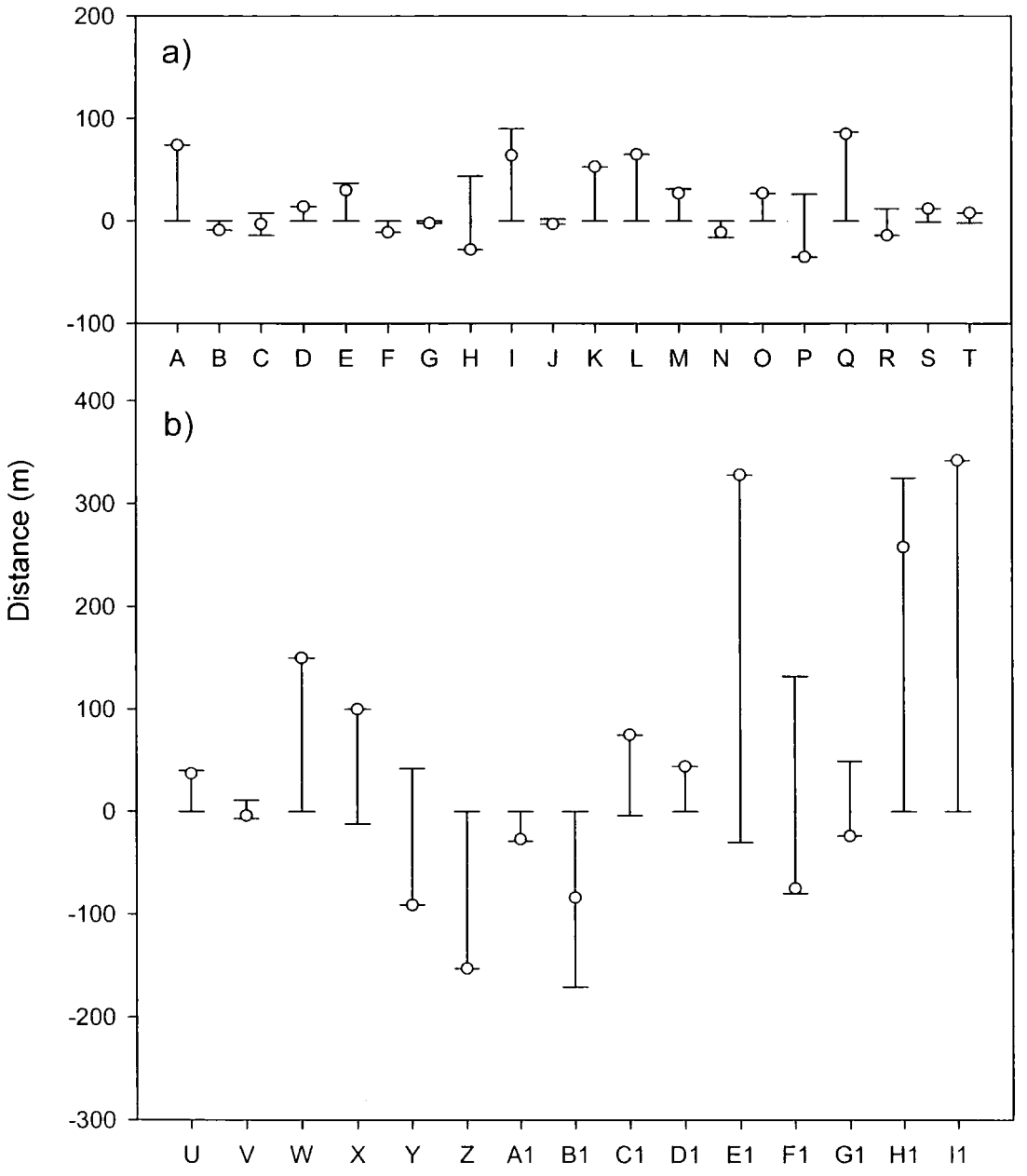


Figure 6.12 The upstream and downstream range of movement of radiotagged a) white-clawed crayfish and b) signal crayfish tracked in the River Wharfe at Barden Bridge, July-August 2003. Circles represent final position and attached bars represent maximum distance moved upstream (+) and downstream (-). The release location of crayfish is represented by 0 m on the vertical axis.

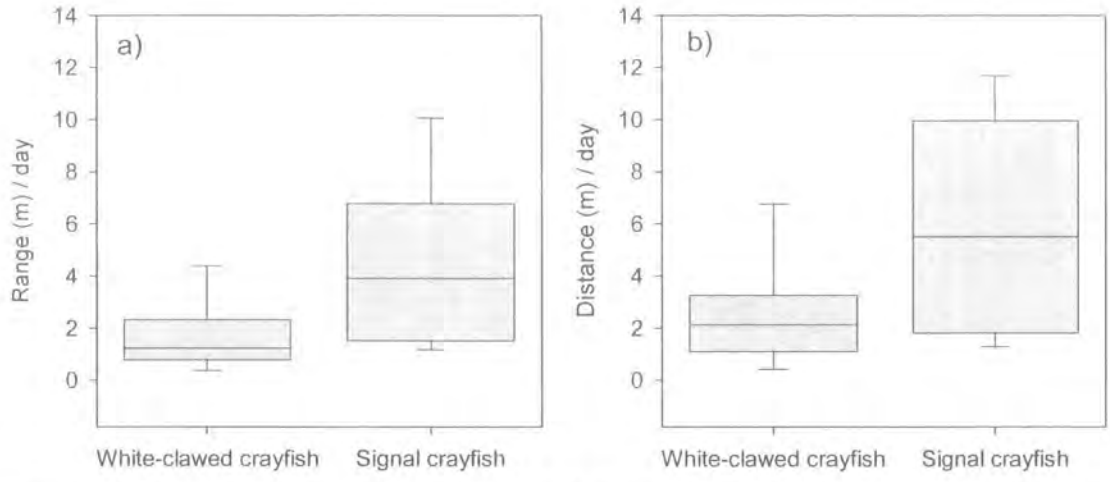


Figure 6.13 Comparative a) ranges and b) distance moved of white-clawed and signal crayfish. Box plots represent range per day tracked and distance moved per day tracked, the 10th, 25th, 50th, 75th and 90th percentiles are shown.

There were significant differences between white-clawed and signal crayfish in both the range per day tracked (Mann-Whitney U-test, $U = 65$, $P = 0.005$) and daily distance moved ($U = 80.5$, $P = 0.021$). The range and distances moved by signal crayfish were greater than those moved by white-clawed crayfish (Figure 6.13).

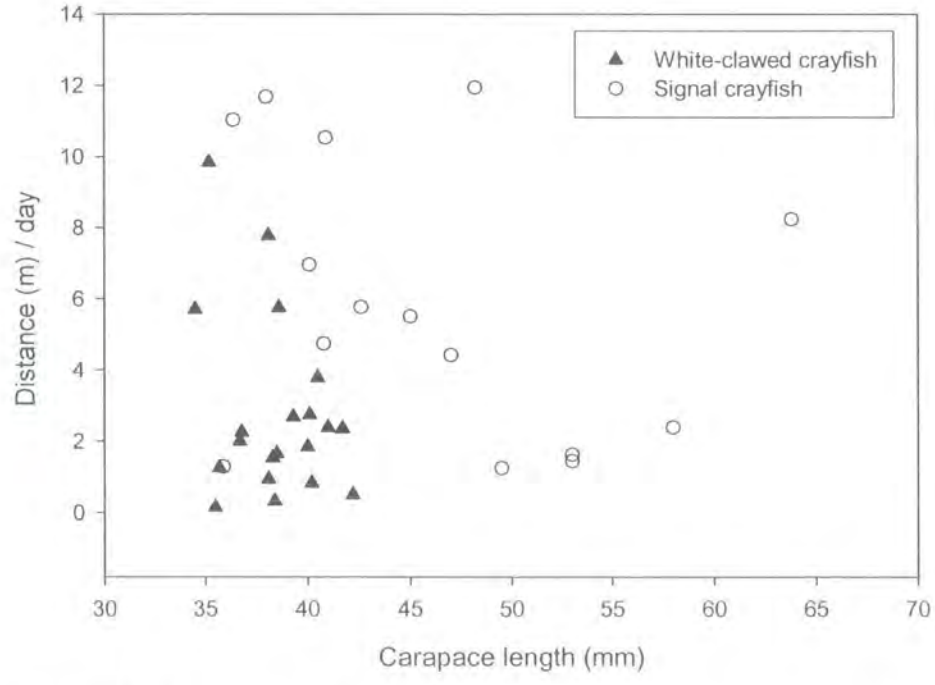


Figure 6.14 Distance per day and carapace length of signal and white-clawed crayfish tracked during summer 2003.

There was no significant relationship between the size of crayfish and distance per day tracked (Spearman rank correlation, Signal crayfish, $r_s = -0.281$, $P > 0.05$, White-

clawed crayfish, $r_s = -0.071$, $P > 0.05$; Figure 6.14). However the numbers of each species tagged was low. The size of signal crayfish tagged (mean 46.15 S.D. = 8.17) was significantly larger than the size of white-clawed crayfish tagged (mean 38.47 S.D. = 2.21; t-test, $t = 4.03$, d.f. = 33, $P<0.001$). This reflects the size structure of the population of white-claws and signal crayfish at the study site and the crayfish that could be captured for tagging. The size structure of the population of crayfish at Barden Bridge as recorded through hand searching is shown in Figure 6.15. Signal crayfish were numerically dominant by a ratio of approximately 2:1. Although the sizes of radiotagged crayfish varied considerably all crayfish tagged were mature adults.

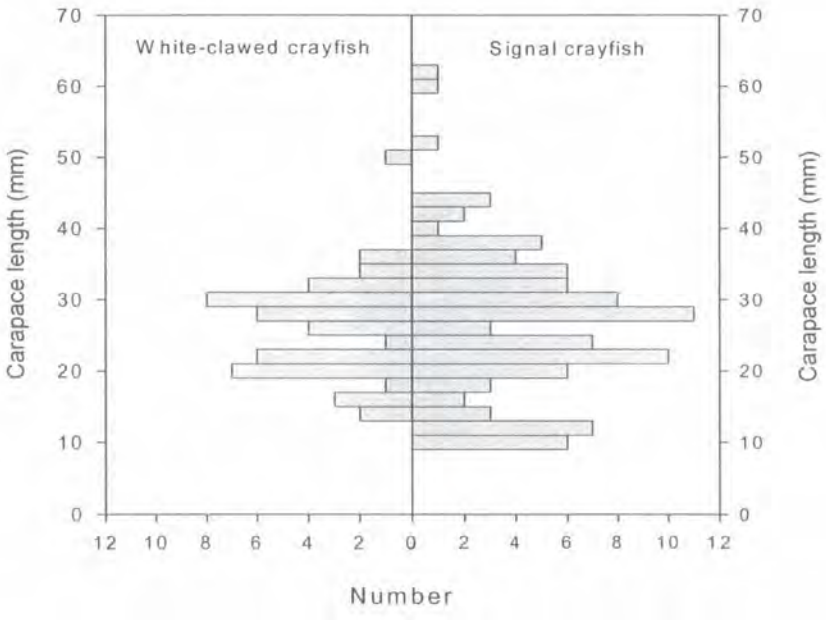


Figure 6.15 Size frequency distribution of white-clawed and signal crayfish at Barden Bridge, River Wharfe

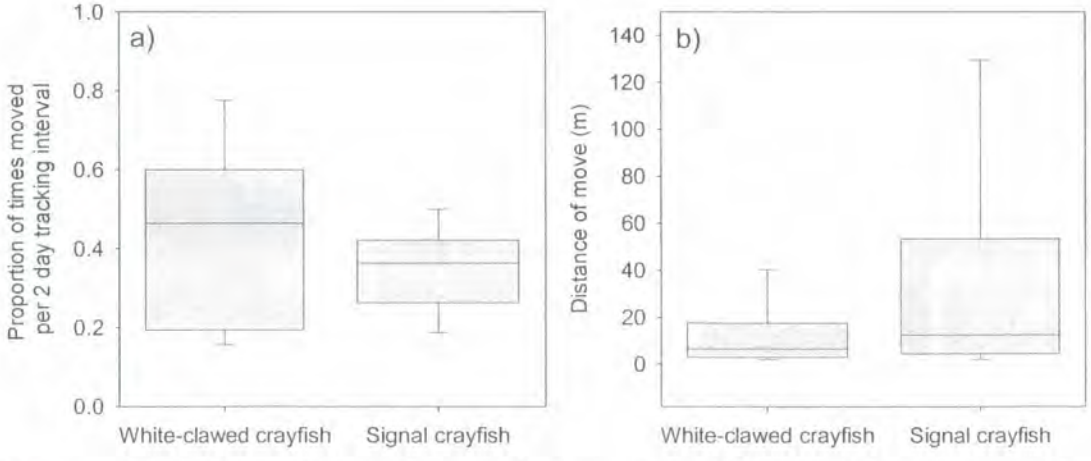


Figure 6.16 a) Proportion of times radiotagged crayfish moved between tracking sessions (2 day interval) b) Distance of movements made by radiotagged crayfish. Box plots show the 10th, 25th, 50th, 75th and 90th percentiles.

There appeared to be a tendency for white-clawed crayfish to move more frequently than signal crayfish (Proportion of time moving: White-clawed crayfish, mean = 0.45, S.D. = 0.24, Signal crayfish mean = 0.34, S.D. 0.11; Figure 6.16). Whilst not significantly different it approached significance (Data arcsine transformed t = -2.04, P = 0.052). The analysis may lack power due to the small numbers of animals tracked. Although white-clawed crayfish appeared to move more frequently, the distance moved by signal crayfish was greater than movements made by white-clawed crayfish (Mann-Whitney U test, U = 45, P < 0.001). No movements between tracking sessions (every 2 days) greater than 70 m were made by white-clawed crayfish, whilst over 15% of movements made by signal crayfish were greater than 70 m with maximum distance of 341 m moved by a signal crayfish in two days (Figure 6.17).

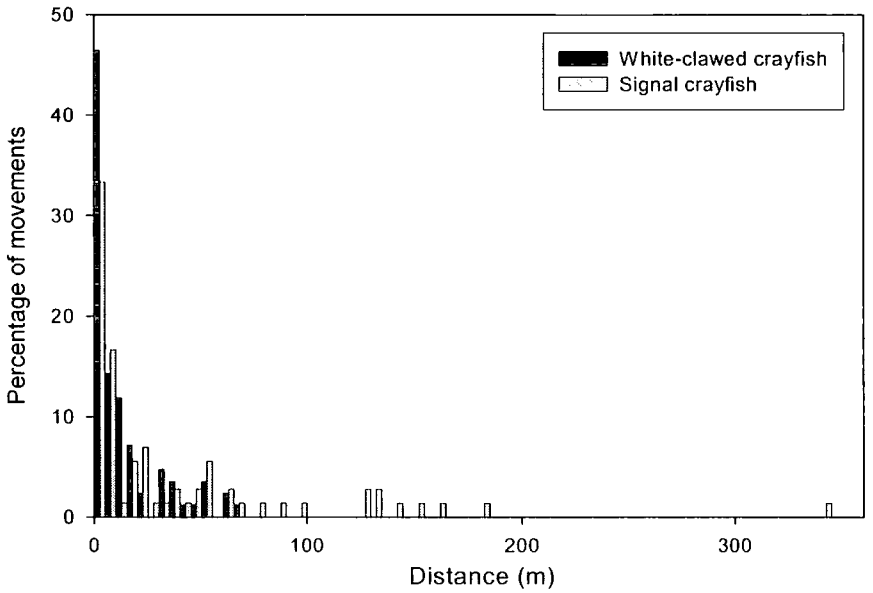


Figure 6.17 Frequency distribution of all movements made by signal and white-clawed crayfish between tracking sessions (every two days). Crayfish which remain in the same location between tracking sessions are not considered to have moved and are not included in figure.

6.3.2.2 Microhabitat Use

Microhabitat use was determined from 83 white-clawed and 78 signal crayfish unique locations. Both white-clawed and signal crayfish were only recorded at locations at which either boulder or large cobble substrate or a combination of the two was present. The PCA that was performed on the microhabitat observations (n=161) for positions at which crayfish were located, produced two component axes that explained 70.0 % of the total variance in the dataset. Principle component 1 (PC1) was a combination of

depth, flow, shade and % cobble, whilst principle component 2 (PC2) was a combination of percentage cover of boulder and substrate index (Table 6.2).

Table 6.2 Percentage of variance explained, eigenvalues and component loadings for the principle component analysis of microhabitat use of white-clawed and signal crayfish. Component loadings > 0.50 are included.

Variable	Principle Component 1	Principle Component 2
Percentage of variance explained	39.37	30.62
Eigenvalue	2.362	1.837
Depth	0.715	---
Water velocity	0.718	---
Shade	-0.634	---
Substrate Index	---	0.848
Boulder	---	-0.881
Cobble	0.815	---

The biplot of microhabitat use with all records included showed a high overlap of microhabitats used by signal and white-clawed crayfish (Figure 6.18a). The maximum convex polygon (MCP) of habitat used by white-clawed crayfish overlapped the MCP of signal crayfish by 85.4% and the MCP of habitat used by signal crayfish overlapped the white-clawed crayfish MCP by 79.7%. Although there was high degree of overlap in the range of microhabitats used, the white-clawed and signal crayfish records appeared to have dissimilar clustered distributions (Figure 6.18a). White-clawed records appeared to be clustered to the left of signal crayfish records.

Because multiple measurements collected on the same individual are not independent and individual replication was limited, to allow the habitat use of white-clawed and signal crayfish to be statistically tested the mean habitat characteristics (PC1 & PC 2) of each radiotracked crayfish from all the locations at which it had been located were calculated. The mean microhabitat characteristics of each crayfish were used to compare white-clawed and signal crayfish (Figure 6.18b). There was a significant difference between signal crayfish and white-clawed crayfish microhabitat use in PC1 when mean positions from each radiotagged crayfish are considered (t = -2.989, d.f. = 33 P = 0.005) but not for PC2 (t = 1.509, d.f. = 33 P = 0.141). Signal crayfish had higher PC1 scores than white-clawed crayfish indicating that they tended to use deeper, higher water velocity, areas with greater percentage cover of large cobble substrate and less shade than those areas used by white-clawed crayfish. Examination of Figure 6.19 supports

this; it primarily appears to be differences in depth, velocity and % large cobble in which signal crayfish differ from white-clawed crayfish rather than shade.

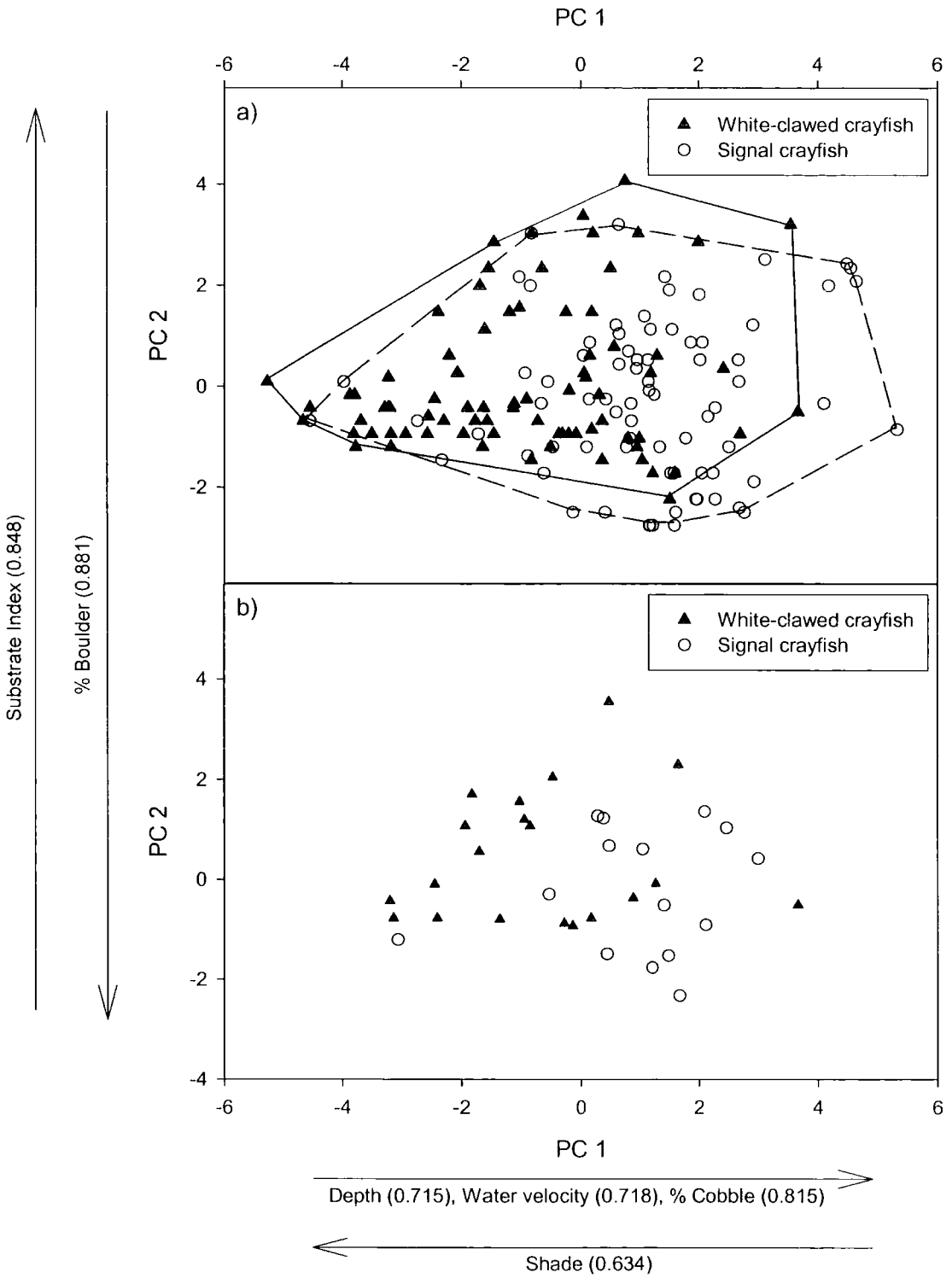


Figure 6.18 Interspecific overlap in habitat use of white-clawed and signal crayfish on biplot of the first and second principle components. a) all locations of radiotagged crayfish shown with maximum convex polygons, dashed line signal crayfish, solid line white-clawed crayfish. b) mean positions of each individual radiotagged crayfish. Signal crayfish n = 15, white-clawed crayfish n = 20.

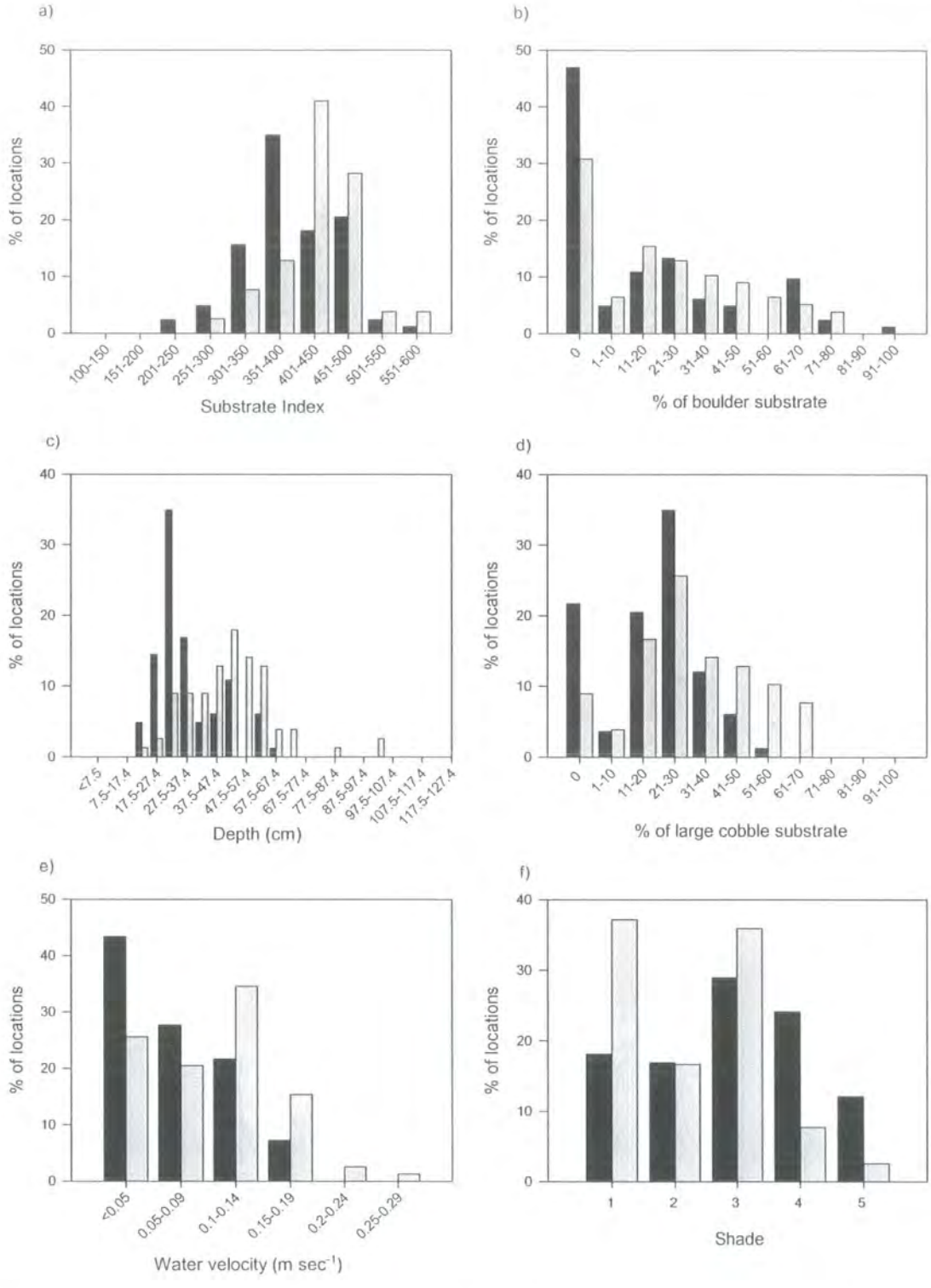


Figure 6.19 Proportion of habitats a) substrate index, b) % boulder, c) depth, d) % large cobble, e) velocity and f) shade used by white-clawed crayfish (black bars) and signal crayfish (grey bars). For calculation of substrate index see section 6.2.6.

6.4 Discussion

Radiotelemetry proved a useful tool for studying the movement of crayfish. It provided finer scale information on the movements of crayfish than can be achieved by mark-recapture techniques. In addition mark-recapture techniques are difficult to use in low-density populations and in autumn and winter when it is difficult to capture sizeable numbers of crayfish. Radiotelemetry has two main limitations. Firstly the relatively high cost of transmitters which restricted the numbers of crayfish which could be radiotagged in each session. Secondly it was limited to relatively large adult crayfish; other techniques (see chapter 3 & 4) must be utilised for studying movement in smaller age classes.

6.4.1 Movement of signal crayfish

The pattern of movement of individual crayfish is similar to that recorded in previous studies on other crayfish species (Gherardi et al. 1998, Schütze et al. 1999, Robinson et al. 2000, McCreesh 2000). Crayfish remained at one refuge for several days to weeks and then made a movement to a different refuge. Once a crayfish had moved from one daytime refuge to another there was no evidence of subsequent return to a previously occupied refuge. The occupation of a single refuge for several days or weeks does suggest that signal crayfish may maintain an 'ephemeral home range' (Robinson et al. 2000) during this stationary phase. The lack of return to any previously occupied refuges and increasing range size with duration tracked suggests that home ranges are not maintained at least in the longer term.

The pattern of maximum movement occurring during summer with reduced movements during autumn and winter, was as might be expected in an aquatic ectotherm responding to changes in water temperature. Previous studies have shown that there is a strong correlation of the activity of crayfish with water temperature (Flint & Goldman 1975, Lozán 2000, Barbaresi & Gherardi 2001). In this study it is shown that movements also appear to be correlated with temperature. The results suggest that in temperate climates maximum dispersal and expansion of populations will occur during midsummer when water temperatures reach a maximum. Both size and sex did not appear to influence the amount of movement recorded. The lack of a relationship between size and movement may reflect the relatively small size range of radiotagged crayfish, as all tagged animals were relatively large mature adults. The pattern from mark-recapture studies involving a greater range of sizes of signal crayfish is unclear. Light (2003) reported that larger

crayfish move greater distances whilst Guan & Wiles (1997) reported no difference in movements with size. Very large movements of males in reproductive condition have been described in red swamp crayfish *Procambarus clarkii* (Gherardi & Barbaresi 2000). Although the sample sizes in this study were small, there was no apparent difference in the movement patterns of males and females. This included the period when mating occurred (September). Mark-recapture studies have also not demonstrated a sex difference in movements of signal crayfish in river (Guan & Wiles 1997b) and lake (Kirjavainen & Westman 1999) populations. However, in a high gradient stream, Light (2003) found larger female signal crayfish tended to move upstream early in the summer and move downstream later in the summer, but found there was no particular trend for male crayfish.

Although most crayfish remained relatively close to the release location a few individuals did make longer movements. It is these crayfish that make more substantial movements that are likely to be important for the range expansion of crayfish populations. There was no apparent difference in the upstream and downstream ranges of signal crayfish. When a negative exponential model was fitted to the data, although the gradient of the upstream ranges was steeper there was no significant difference between the two models suggesting that the upstream and downstream dispersal recorded over this study did not differ greatly.

Within the late autumn/winter tracking session two distinct temporal periods in the spatial behaviour of crayfish were observed. In the period up to mid-December, crayfish were actively moving between refuge sites, although distances moved were relatively small. From mid-December onwards the degree of movement was greatly reduced. The period from mid-December onwards may equate to the 'winter torpor' reported by Brewis & Bowler (1982) in white-clawed crayfish. This reduction in movement occurred at the same time as a drop in the water temperature, which may have been responsible for the reduction in movements. Whilst large-scale movements almost ceased from mid-December onwards, patterns in local activity were less clear. Local activity was strongly correlated with water temperature, and showed no distinction before and after mid-December.

Crayfish are generally considered to become inactive in temperate countries during winter due to low temperatures (Abrahamsson 1981, Riggert et al. 1999). White-clawed

crayfish have been reported to go into torpor for 30 weeks over winter in a population in northern England (Brewis & Bowler 1982). The results from overwinter radiotracking suggest that signal crayfish may become inactive in terms of large-scale movements, as would be reflected in trap catches but at very local scales they remain somewhat active. This local activity may allow crayfish to continue feeding as described by Guan & Wiles (1998) who found signal crayfish feeding during winter at temperatures of 4-6°C. Localised feeding activity would be reliant on sufficient food being available at or near the refuge. Local activity of radio-tagged signal crayfish, possibly related to feeding activity, would appear to reflect a linear temperature-mediated metabolic response over a temperature range of 1-8°C. Whereas larger-scale movements between refuges appear to be mediated through behavioural inhibition of movement following the onset of winter conditions. The decline in activity described in this study corresponds well with that described by Lozán (2000) in signal crayfish held in the laboratory over the temperature range 4 – 20°C. The decline in large-scale movements may have the effect of reducing the exposure of crayfish, with limited metabolic capacity for locomotion at low temperatures, to floods or predation.

Both the Wharfe and Ure have fluctuating discharge patterns; the rivers respond rapidly to rainfall. High discharges and their associated high water velocities have been reported to cause downstream displacement (Momot 1966, Parkyn 2000, Robinson et al. 2000), mortality of crayfish (Robinson et al. 2000, Royo et al. 2002) and significant spring spates have been linked to declines in density (Light 2003). The information from this study suggests that high flows do not have a significant impact on survival or cause downstream movement of signal crayfish. The results from all periods of tracking suggest that during periods of high discharge adult crayfish are able to remain in refuges, protected from the high flows. Passive dispersal of adult signal crayfish downstream during high flows would not appear to occur frequently and does not form a major factor in their dispersal.

The densities of crayfish at the Ure and Wharfe sites differed greatly. However, there was no significant difference in the amount of movement recorded at the two sites. Refuges and food may be a limiting factor in crayfish populations and competition can be severe (Lodge & Hill 1994). It was hypothesized that the higher densities of crayfish at the Wharfe site may result in greater competition for refuges and food and hence lead to greater movement. As size is one of the major factors affecting dominance

(Vorburger & Ribi 1999) the tagging of only large adult crayfish may have possibly been why this effect was not observed in the results. The effect of competition may be greater on smaller, less dominant age classes. It also possible that although densities on the Wharfe were higher, refuges and food were not limiting and other factors were more important in determining the levels of movement recorded.

No radiotagged crayfish were recorded being predated. Potential predators of adult crayfish at the field sites include brown trout, grey heron and American mink. Although mink and grey heron were present at field sites neither were abundant and mink were subject to control efforts. Whilst brown trout are abundant at all field sites it is likely that they are gap size limited and have limited ability to feed on adult crayfish. The lack of predation of adult radiotagged crayfish, low occurrence of field signs indicating predation of adult crayfish (D. Bubb pers. obs.) and apparent low densities of potential predators suggest that predation of adult crayfish seems not to be a significant factor in population regulation.

6.4.2 Comparative spatial behaviour of white-clawed and signal crayfish

Differences in the spatial behaviour of white-clawed and signal crayfish were found in this study. Signal crayfish showed greater dispersal and movement away from the release location than white-clawed crayfish. Our results appear to support the proposed characteristics of invasive species being more vagile (Erlich 1989). The increased dispersal of signal crayfish was primarily caused by signal crayfish moving greater distances between refuges and not by a higher frequency of moving. Although the result was not quite significant at the 5% level white-clawed crayfish appeared to show a tendency to move more frequently than signal crayfish, however the movements made by white-clawed crayfish between refuges were shorter. The motivation and cause of movements undertaken by crayfish were not investigated, however the greater distances moved by signal crayfish may contribute to their ability to disperse and colonise new areas. This has the potential to give signal crayfish a competitive advantage over white-clawed crayfish in their ability to utilise patchy resources and move between suitable microhabitat patches. It is possible that the higher frequency of movement of white-clawed crayfish between refuges may be linked to displacement from their refuges by the apparently dominant signal crayfish (Holdich et al. 1995).

Both signal crayfish and white-clawed crayfish were only found in locations that contained large cobble and boulder substrate. This is likely to reflect the requirement of both species for a stable refuge. Though both white-clawed and signal crayfish are able to construct burrows (Huxley 1880, Guan 1994), at the Barden Bridge site they appeared to utilise only natural refuges beneath large cobble and boulder. Refuges are a critical resource for crayfish survival (Gherardi 2002). Their availability is considered by Hobbs (1976) to be the 'principle resource bottleneck' in crayfish populations. Refuges appear to play an important role in protection from environmental extremes such as flooding and also from predators (Lodge & Hill 1994).

The characteristics of the microhabitat used by signal and white-clawed crayfish, as shown by maximum convex polygons, were similar with a high degree of overlap. The high level of overlap suggests that the potential for competitive interactions exists, although measuring overlap in spatial resources does not demonstrate the existence of interspecific competition. Although the range of microhabitats used were similar, there were differences in the microhabitat predominantly used by the two species. Compared to signal crayfish white-clawed crayfish appeared to use shallower, slower velocity areas with lower proportion of large cobble substrate. It is possible that these differences are indicative of a degree of resource partitioning occurring between the two species in the River Wharfe. Resource partitioning has been suggested to facilitate species coexistence in crayfish in a few instances; although it appears more common for introduced species to competitively exclude the native species (Lodge & Hill 1994, Söderbäck 1995, Hill & Lodge 1999). In Tasmania where the introduced Australian crayfish *Cherax destructor* coexists in a stream with the endemic *Astacopsis franklinii* microhabitat resource partitioning has been suggested to enable both species to survive, *C. destructor* is confined to open, slow-flowing sections whilst *A. franklinii* is found in shaded, rocky, fast-flowing sections (Elvey et al. 1996). However in most instances displacement of native crayfish species occurs after the introduction of non native species. The differentiation of microhabitat use between white-clawed and signal crayfish in the River Wharfe appears insufficient to facilitate long term coexistance of the two species (Chapter 2). An alternative explanation of the observed differences in microhabitat use is that white-clawed crayfish may be being displaced from their preferred habitat by competitively dominant signal crayfish. The use of shallower areas has been reported to increase the risk of predation from terrestrial predators and for this reason may be avoided by larger crayfish (Englund & Krupa 2000).

The mechanisms behind species replacements are often ambiguous and it appears that several may operate simultaneously (Söderbäck 1995, Hill & Lodge 1999). Competitive exclusion, involving a variety of mechanisms has often been suggested to explain observed replacements (Gherardi 2002), although other mechanisms such as differential predation or reproductive interference may also contribute (Butler & Stein 1985, Söderbäck 1995). The replacement of white-clawed crayfish by signal crayfish in the absence of crayfish plague has not been investigated. This study has suggested that the habitat use at least by adults is similar with relatively small differences and both species have similar life histories and diets (Chapter 1). Considering these similarities, interspecific competition could play an important role in the observed species replacement. Signal crayfish are generally considered to be more aggressive than white-clawed crayfish and in mesocosms the survival of white-clawed crayfish was lower in mixed populations apparently due to predation by signal crayfish (Holdich et al. 1995). It may be possible that the aggressive dominance of signal crayfish combined with higher growth rate, higher fecundity and interspecific predation (Chapter 1, Holdich et al. 1995) results in signal crayfish competitively excluding white-clawed crayfish when they are syntopic. However, this has not been investigated and requires further field and laboratory based research.

This study did not address nocturnal habitat use by white-clawed and signal crayfish and only relates to the microhabitat characteristics of daytime refuges. Although nocturnal foraging by crayfish is relatively unstudied especially in signal crayfish, the residency of crayfish at the same refuge for several days and the relatively short distances which white-clawed crayfish have been reported to move from refuges whilst foraging (Robinson 1997, Ghereadi et al. 2001), suggests that the area used whilst foraging at night may be restricted to close to the refuge, and the refuge habitat used may be similar to the wider habitat use. Ideally, integrated nocturnal and diurnal radiotracking would have been carried out to allow an assessment of both the refuge and foraging microhabitats used by crayfish. Initially it was intended to conduct radiotracking at night but safety considerations and difficulties in tracking at night without disturbing the crayfish prevented this.

CHAPTER 7. GENERAL DISCUSSION

The aim of this thesis has been to investigate within-catchment expansion of signal crayfish populations and the spatial ecology and movement of signal and white-clawed crayfish in upland rivers. In this chapter the key conclusions of the study are drawn together and the significance of the work to the field of crayfish ecology and its wider implications are discussed. In addition, suggestions for the direction which future work should take are made.

The populations of non-indigenous signal crayfish in the rivers Wharfe and Ure are established and continuing to increase in the extent of river that is occupied (Chapter 2). The rate of expansion varied between the two rivers, the comparatively young population on the River Ure is currently expanding at a much slower rate than the more extensive, established population on the River Wharfe. The rate of expansion of the Wharfe population appears to be gradually increasing. Range expansion of invasive organisms commonly proceeds in three successive stages: establishment, expansion and saturation phase (Shigesada & Kawasaki 1999). The populations of signal crayfish studied appear to be within the expansion phase. Within the expansion phase the relationship between time and range can be broadly classified into three types i) range expands linearly with time, ii) slow initial spread is followed by linear expansion at a higher rate, iii) the rate of spread continually increases with time (Shigesada & Kawasaki 1999). The expansion of signal crayfish populations appears to fit with type iii), initial slow expansion as observed on the River Ure and higher and increasing rates of expansion as observed on the River Wharfe. Further expansion of the signal crayfish populations in the Wharfe and Ure is expected although the rate of expansion is likely to be influenced by the characteristics of the invaded environment. There is little information on the impact that the changing characteristics (substrate, depth, flow, velocity, gradient) of rivers both upstream and downstream will have on the expanding signal crayfish population.

The information gained from radiotracking adult signal crayfish (Chapter 6) within the River Wharfe suggests that movement of adults has the potential to be responsible for the observed rates of population expansion. The average rate of population expansion on the Wharfe (1997-2003) was 2.06 km y^{-1} (5.6 m d^{-1}) recorded in a downstream direction. The maximum rate of downstream range expansion recorded by a signal

crayfish was 12.91 m d^{-1}. Although this level of movement occurred during summer, it would require range expansion of 12.91 m d^{-1} during the five and a half summer months only to equate to yearly movements of 2.06 km. It was hypothesised that larger adult signal crayfish would make the most substantial movements and be the primary cause of upstream active dispersal. In signal crayfish in both the radiotagging study (Chapter 6) and external PIT study (Chapter 4) there was no relationship between size and sex and the amount of movement recorded. Whilst the radiotagging study was restricted to relatively large animals the external PIT study included a wide range of sizes of signal crayfish from aged 1+ to large adults, although it was only conducted over a relatively short period. These results are in agreement with Guan & Wiles (1997b) who also found no difference in movement of signal crayfish with size and sex. The results suggest that all components of the population (aged $\geq$1+) potentially contribute to dispersal. Although the utilisation of external PIT tags allowed the movement of crayfish aged 1+ to be recorded this still does not include the smallest age class. Obtaining information on the movement of 0+ age class is problematic. It seems unlikely that they are capable of making substantial active movements but the potential exists that aged 0+ crayfish could be passively transported downstream.

Though the extent and rates of expansion differ between the two rivers, both populations show a bias towards downstream colonisation. The distance colonised downstream was over three times the distance colonised upstream. The passive downstream drift of many macro-invertebrates contributes to their species dispersal ability (Bilton et al. 2001). In this thesis it was initially considered that passive dispersal of crayfish might be important. Previous studies had suggested that high flows might be a significant source of mortality and passive dispersal downstream (Parkyn 2000, Robinson et al. 2000, Royo et al. 2002). However high flows appeared to have little impact on adult signal crayfish. During periods of high discharge, signal crayfish moved little and presumably remained in refuges; this strategy apparently limits their exposure to the potential adverse impacts of being swept downstream (Chapter 6). The possibility remains that the passive downstream movements of juvenile crayfish and smaller age classes during periods of high discharge may form a component of downstream dispersal of crayfish populations. An alternative explanation for the observed bias towards downstream expansion of populations may be a reduced ability of crayfish to make movements upstream through areas of riffles and falls. The higher gradient of upland rivers is associated with an increased number of riffles and falls, which whilst

they may not form a complete barrier to movements of crayfish, may have a reduced permeability to upstream movements. The movement of adult radiotracked crayfish did not demonstrate any bias towards downstream movements with movements equally distributed upstream and downstream (Chapter 6), however the movement of signal crayfish in the main River Wharfe in an upstream direction studied with external PIT tags (Chapter 4) was apparently limited by the presence of a waterfall.

In-stream barriers both natural (Chapter 4) and artificial (Chapter 5) appear to have the potential to impact on the movement and dispersal of crayfish. Whilst there is widespread recognition of the impact of barriers on fish populations and communities and the ability of fishes to ascend obstructions (e.g. Jungwirth et al. 1998, Lucas & Baras 2001), there is little or no information on the ability of crayfish to traverse potential barriers. Barriers appear to have some impact on other invasive freshwater crustaceans. The presence of a weir has been reported to slow the upstream expansion of a population of the non-indigenous amphipod *Gammarus pulex* (Kelly et al. 2003) and the upstream migration of juvenile mitten crabs *Eriocheir sinensis* appears to be slowed but not prevented by in-stream barriers. Juvenile mitten crabs congregate downstream of obstructions and attempt to bypass them by climbing over the barrier or climbing the banks and moving over land (Anon. 2002). The spread and expansion of signal crayfish populations could potentially be impeded by significant within stream structures. The maintenance of structures with substantial vertical drop and high water velocity may offer a short to medium-term conservation measure to reduce the natural colonisation of signal crayfish populations in an upstream direction. The converse situation applies when considering the conservation and management of white-clawed crayfish populations. Connectivity throughout the catchment and between populations of white-clawed crayfish is likely to be beneficial and may be required to allow population expansion and colonisation. Thus removal of barriers or mitigation measures to allow free movement of white-clawed crayfish should be encouraged.

The expansion of the signal crayfish population in the River Wharfe is causing the progressive loss of white-clawed crayfish populations where they come in direct contact. Complete loss of white-clawed crayfish appears to occur about 7 years after the first signal crayfish have been recorded. The mechanism(s) leading to loss of white-clawed crayfish was not investigated but this study found limited differences in the microhabitat utilised by the two species, suggesting that the potential exists for direct

competition between the two species and this may contribute to the observed replacement. Whilst the two species broadly used similar microhabitats signal crayfish showed greater dispersal and movement than white-clawed crayfish. Dispersal ability has been suggested to be a key element of a species invasiveness (Ehrlich 1986). Although many studies have addressed how dispersal influences the pattern of spatial spread of invading organisms (Hengeveld 1989, Shigesada & Kawasaki 1997) and suggested that dispersal ability is a key factor determining invasion success (Ehrlich 1986, Sakai et al. 2001), few studies have tested whether invasive species are better dispersers than the species they displace (Rehage & Sih in press). Most efforts in describing the characteristics of invasive species have concentrated on life-history traits and abiotic tolerances (Kolar & Lodge 2002). This study suggests that dispersal, a rarely examined factor may be an important characteristic and predictor of invasiveness, and appears to contribute substantially to the ability of signal crayfish to colonise rivers relatively rapidly. The increased dispersal and movement of signal crayfish may also offer a competitive advantage over white-clawed crayfish in their ability to utilise patchy resources and move between suitable habitat patches thus contributing to the observed replacement.

Dispersal and movement was highly variable between individual crayfish within all studies (Chapters 4,5,6). High intraspecific variation in dispersal distances or rates has been reported for a variety of other taxa (e.g. Bradford & Taylor 1997, Fraser et al. 2001) and appears common. In crayfish the majority of movements or dispersal were over comparatively short distances, but there were individuals that dispersed significant distances (Chapters 4,5,6, Robinson 1997). Maximum dispersal from release location of individual crayfish of 375 m, 918 m and 417 m were recorded in Chapter 4, 5 and 6 respectively. Although long distance movements were relatively uncommon it is individuals that make long movements that are most influential in the range expansion and colonisation of new areas.

For most studies (Chapters 5 and 6) a negative exponential function was fitted to the empirical frequency distribution of distances, and in Chapter 4 a negative binomial distribution was fitted. These functions have frequently been used to describe frequency distribution of dispersal distances in a wide range of aquatic and terrestrial organisms (e.g. Tonkyn & Plissner 1991, Hill et al. 1996, Bagutte 2003, Telfer et al. 2003), although they have not previously been applied to the dispersal of crayfish.

A large amount of variation exists in the homing behaviour and site fidelity of crustacean decapods (for review see Vannini & Cannicci 1995), from species that appear to wander at random to others which maintain a well defined home range. In general burrows and shelters appear to form the primary homing goal for most crustaceans (Vannini & Cannicci 1995) and this seems to apply to at least some crayfish species (Robinson 1997, Gherardi et al. 1998). In all investigations of the spatial behaviour of crayfish (Chapters 4,5,6) a common pattern of movement was observed. Crayfish would remain at one refuge for several days to weeks (static phase) and then make a movement to a different refuge (active phase). This pattern was consistent throughout all periods of the studies although during summer when crayfish were more active the static phase was generally shorter. If it is presumed that signal crayfish are homing to their daytime refuge after nocturnal foraging, the behaviour of signal crayfish appears to fit with the suggestion of Robinson et al. (2000) that crayfish maintain an 'home range'. During the static phase crayfish make short excursions in the locality of the refuge primarily for foraging (Robinson 1997, Gherardi et al. 2001). The area traversed by crayfish during these localised excursions represents the 'home range' of the crayfish. Crayfish often moved significant distances suddenly to a new refuge and the process of local home range use is repeated. The maintenance of a home range over longer time span does not appear to occur, crayfish were never recorded returning to a previously occupied refuge once a different refuge has been occupied. Vannini & Cannicci (1995), reviewing the movement patterns of decapods, suggest that in species that live on hard substratum, switching between refuges is common, whilst decapods living on soft substrate which construct burrows, refuge fidelity is higher. Refuge switching in crayfish within the upland rivers studied where crayfish are primarily found in natural refuges within hard substrate was relatively frequent. The behaviour of signal crayfish in habitats where they frequently construct and inhabit burrows (e.g. River Great Ouse; Guan 1994) would offer the opportunity to examine if they show stronger site fidelity to burrows than natural refuges.

7.1 Future directions for research

In this study the expansion and colonisation of signal crayfish populations was only considered in two upland rivers. Comparison of the rates and pattern of spread in these upland rivers with other rivers is difficult as there is little published information available from other river systems. The information which is available is limited to the distribution at a single point in time (Holdich et al. 1995, Guan & Wiles 1999) thus does

not give any information on temporal changes in the rates of colonisation. Information on the rate of spread of signal crayfish from rivers of varying characteristics (flow, gradient, substrate, prevalence of potential barriers) is important if a clearer understanding of the factors affecting the expansion of signal crayfish populations is to be achieved. Spatial modelling of the spread of signal crayfish integrated within a geographical information system and utilising techniques such as network analysis (Johnston 1998) could potentially lead to the ability to make predictions of the rate of expansion of signal crayfish populations within catchments and identify patterns in how catchments are invaded. This is essential if predictions are to be made regarding the timescale of the threat that signal crayfish populations pose to white-clawed crayfish within the same catchment.

An important component of the spread and expansion of signal crayfish populations is the colonisation of tributaries and low order headwater streams. The limited information gathered during this study suggested that the colonisation of small tributaries may occur at a slower rate than upstream in the main river. This is however based on the colonisation of a single tributary and further research and information is required on the ability, extent and timescale over which signal crayfish colonise small tributaries. The invasion of these small tributaries by signal crayfish is of particular importance for conservation of white-clawed crayfish populations as many of the remaining populations of white-clawed crayfish have been recorded in these habitats.

Chapters 5 and 6 suggested that in-stream barriers may have an impact on the expansion and movement of crayfish yet our understanding on the extent and severity of this is limited. Further information is required on the ability of signal and white-clawed crayfish to traverse potential barriers in an upstream direction, both directly and by bypassing the barrier over land or by marginal habitat. This should include high-velocity rapids and waterfalls, as well as anthropogenic structures such as weirs of varying height and shape and fish ways.

This study and a substantial amount of previous research has been focused on the impact of signal crayfish on white-clawed crayfish (Holdich et al. 1995). Very little research has considered the impact of signal crayfish on the wider ecosystem especially in upland rivers. With no practical control measures available signal crayfish are likely to become a permanent component of the ecosystems in which they have been

introduced. By virtue of their higher growth rates, size and density the impact of signal crayfish may be greater than that of white-clawed crayfish populations that they often replace. Preliminary research as part of this study (Appendix 1) and in other rivers (Guan & Wiles 1997a) has suggested that signal crayfish may be having a negative effect on benthic fish communities. Signal crayfish are now attaining high densities in the River Wharfe and many other rivers (Holdich et al. 1995, Guan & Wiles 1999) and may interact with and negatively affect populations of fish in a variety of ways. Possible interactions may involve, direct predation of signal crayfish on fish, exclusion of fish from refuges occupied by crayfish and interference with fish breeding and consumption of fish eggs. It is unclear if the effects of signal crayfish and white-clawed crayfish on benthic fishes are similar or if the increased effect of signal crayfish is a reflection of the higher densities which this species tends to attain or differences in behaviour e.g. aggressiveness. Future research to investigate the impact of signal crayfish on fish communities would allow an increased understanding of the threat that signal crayfish present.

Locations of crayfish recorded during this study represent daytime refuge sites; whilst they are indicative of long-term movements they do not provide information on the localised foraging behaviour of crayfish. The foraging behaviour and extent of localised movements of crayfish has received little attention. Crayfish were frequently recorded residing at the same refuge for an extended period of time, during which time they are believed to forage and make localised movements in the vicinity of the refuge (Robinson 1997). These movements represent a relatively unknown component of their spatial behaviour. The habitat use of crayfish recorded during this study only relates to refuge habitat, research on the foraging behaviour of crayfish would provide information on the broader scale habitat use of crayfish. This would be of relevance for both conservation of white-clawed crayfish in terms of the habitat requirements and for assessing the potential impact of signal crayfish and aiding further insights into the mechanisms of interaction between syntopic crayfish species.

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APPENDIX 1
DENSITIES OF CRAYFISH AND BENTHIC FISH

Introduction

Studies have shown that when abundant, crayfish can have strong effects on aquatic food webs both by direct and indirect trophic effects (see Nyström 2002, Chapter 1). Signal crayfish have been reported to have a negative impact on benthic fish abundance in a lowland river (Guan & Wiles 1997a). Guan & Wiles (1997a) reported an inverse correlation between the abundance of benthic fish and signal crayfish and laboratory experiments suggesting that signal crayfish may compete with bullheads *Cottus gobio* and stoneloach *Noemacheilus barbatulus* for refuges and may also directly directly on the fish. As part of distribution surveys of crayfish populations in the River Wharfe during summer 2002, the relationship between crayfish and benthic fish densities was assessed. Time constraints only enabled a limited number of sites to be surveyed and the results of these are presented here.

Methods

The comparative abundance of benthic fish and crayfish was assessed at nine sites distributed across the River Wharfe (see Table 1 for details of sites). Seven of the sites were distributed within the area occupied by signal crayfish, one of these within the area where both signal crayfish and white-clawed crayfish are present. The remaining two sites were upstream (where no crayfish were present) and downstream (where only white-clawed crayfish were present) of the signal crayfish population.

Depending on time constraints each site between 25 and 40 quadrats (0.49 m^2) were taken from each site using a modified Surber sampler. To prevent crayfish and fish from escaping during surveying the front and both sides of the sampler were enclosed with nets, the back was connected to a 0.5 m long net bag. At each site areas of less than 0.6 m deep, low flow and consisting of relatively unembedded substrate that were dominated by large cobble and boulder substrate were selected. Within these areas the sampler was randomly placed, stones beneath the frame were removed and the base of the sampler pushed into the substrate. All potential refuges within the sampler were searched and any crayfish and fish within the sampler were recorded. Attempts were made to catch all crayfish observed; captured crayfish were identified to species, sexed and the carapace length measured.

Results

Bullhead was the dominant (>95%) species of benthic fish at all sites with small numbers of stone loach also recorded. Due to the numerical dominance of bullhead subsequent analysis only considers this species.

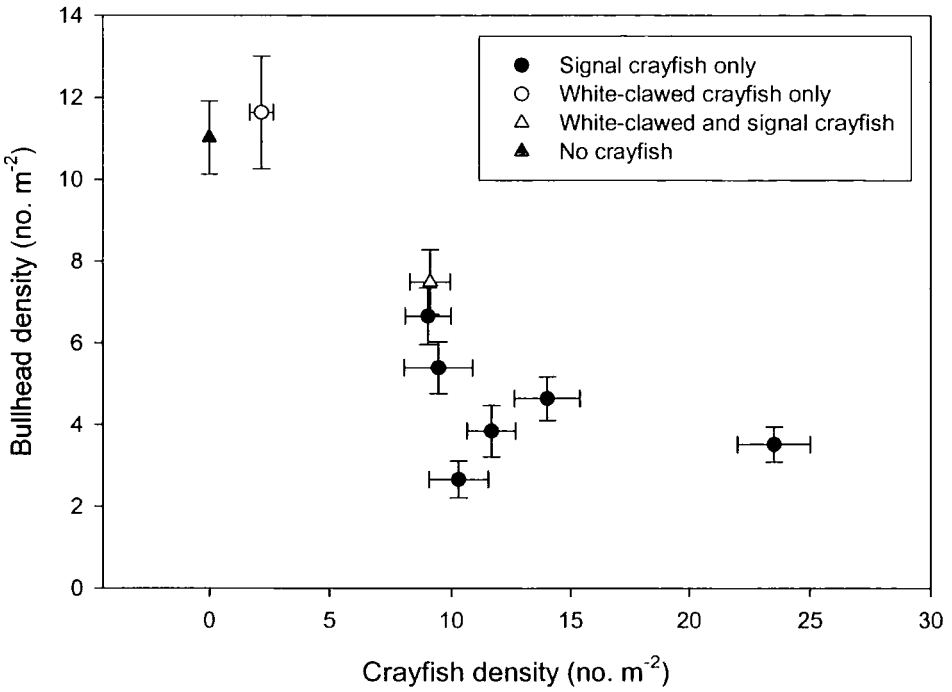


Figure 1. Crayfish and bullhead density at 9 sites on River Wharfe surveyed during summer 2002. Error bars represent standard error.

The density of crayfish and bullheads varied considerably between sites (Table 1, Figure 1). The abundance of crayfish and benthic fish was significantly and inversely correlated (Spearman rank correlation of mean abundance at each site, r_s = -0.85, d.f. = 7, P = 0.009), with bullheads most abundant when there was low density of white-clawed crayfish (Site 4) or no crayfish present (Site 28).

Discussion

The preliminary results presented here suggest that crayfish within the River Wharfe may be having a negative impact on the bullhead population. The results appear to agree with the reported correlation of benthic fish and signal crayfish on the lowland River Great Ouse (Guan & Wiles 1997a). It is possible that the more aggressive signal crayfish may have a stronger impact on benthic fish than the white-clawed crayfish. In addition, the density and biomass of signal crayfish is generally higher. The results are too limited to enable comparisons between signal and white-clawed crayfish and the density of benthic fish to be made and further research into the relative impact of the

two species is needed. The potential mechanisms by which crayfish may impact on benthic fish include direct predation, competition for refuges, interference with breeding and consumption of eggs. The prevalence and importance of these in field populations is unknown and requires further investigation.

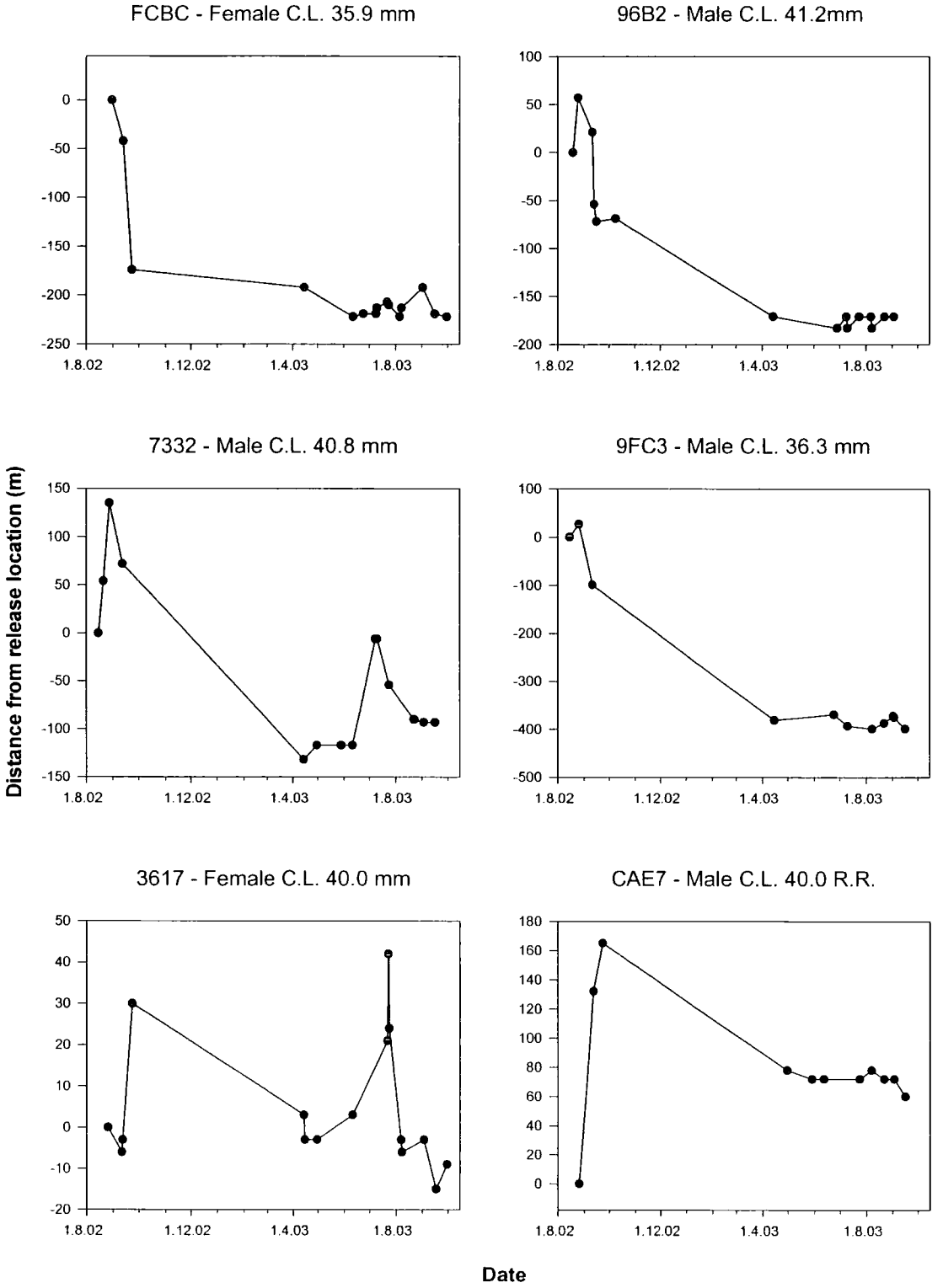
Table 1. Details of survey sites and density of crayfish and bullhead recorded during surveys of River Wharfe, summer 2002.

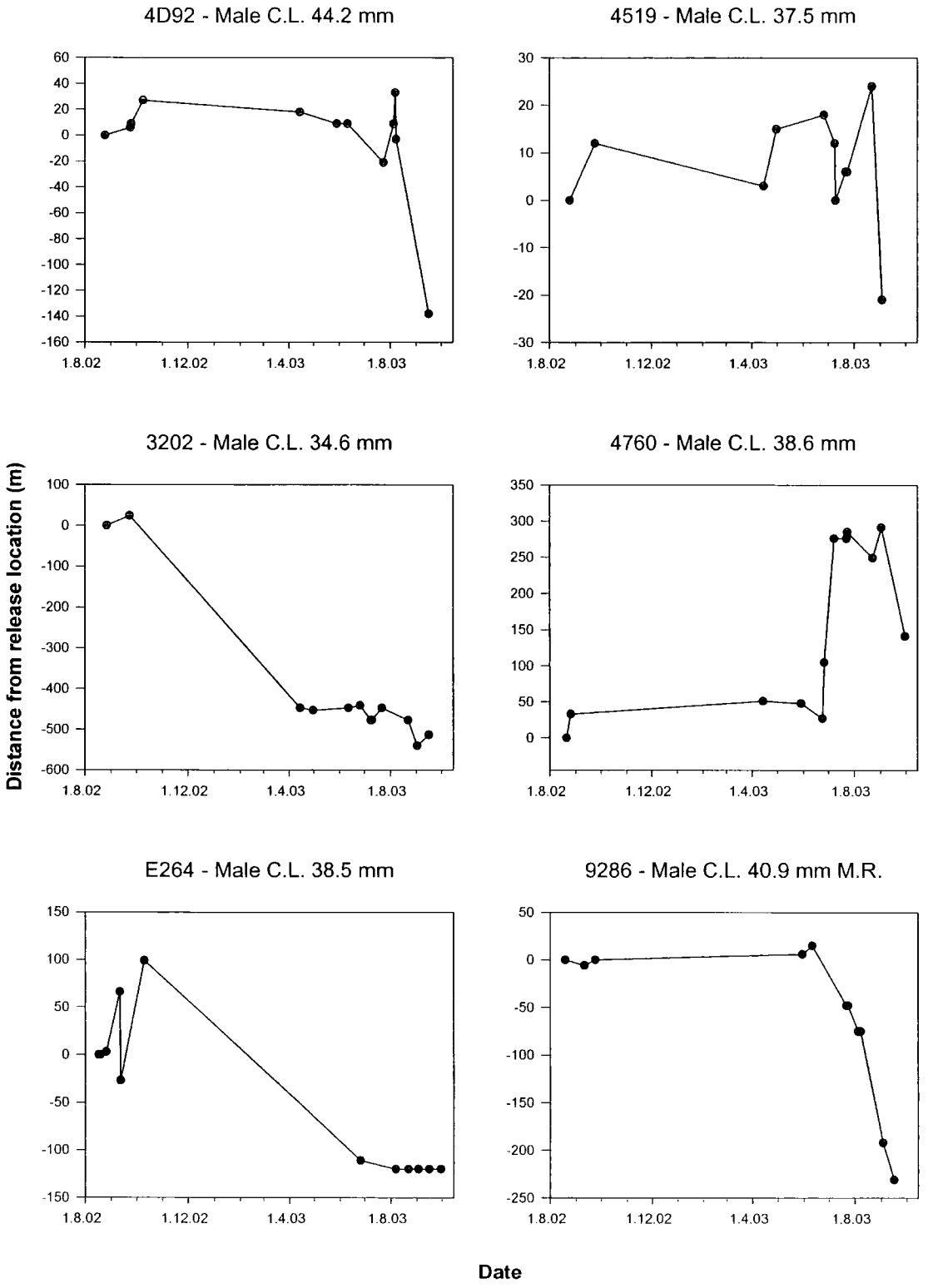
Location	Date	Grid ref.	Site*	Number of quadrats	Crayfish species present	Crayfish density (number m^{-2}) (S.D.)	Bullhead density (number m^{-2}) (S.D.)
Bolton Bridge	5/9/02	SE 071526	4	30	White-clawed	2.18 (2.67)	11.63 (7.55)
Appletreewick	29/8/02	SE 047601	7	30	White-clawed (33) and Signal (78)	9.12 (4.51)	7.49 (4.33)
Burnsall	22/9/02	SE 033616	9	25	Signal	9.47 (7.06)	5.39 (3.16)
Lythe House	20/9/02	SE 012628	10	25	Signal	23.51 (7.53)	3.51 (2.16)
Grassington	30/7 – 19/8/02	SD 997639	12	40	Signal	10.31 (7.76)	2.65 (2.86)
White Beck	3/9/02	SD 979668	14	30	Signal	14.02 (7.61)	4.63 (2.94)
US Conistone	16/9/02	SD 977680	15	25	Signal	11.67 (5.06)	3.84 (3.14)
DS Confluence	21/9/02	SD 977693	16	30	Signal	9.04 (5.22)	6.65 (3.82)
Skirfare Br.	2/9/02	SD 971692	28	30	None	0	11.02 (4.90)

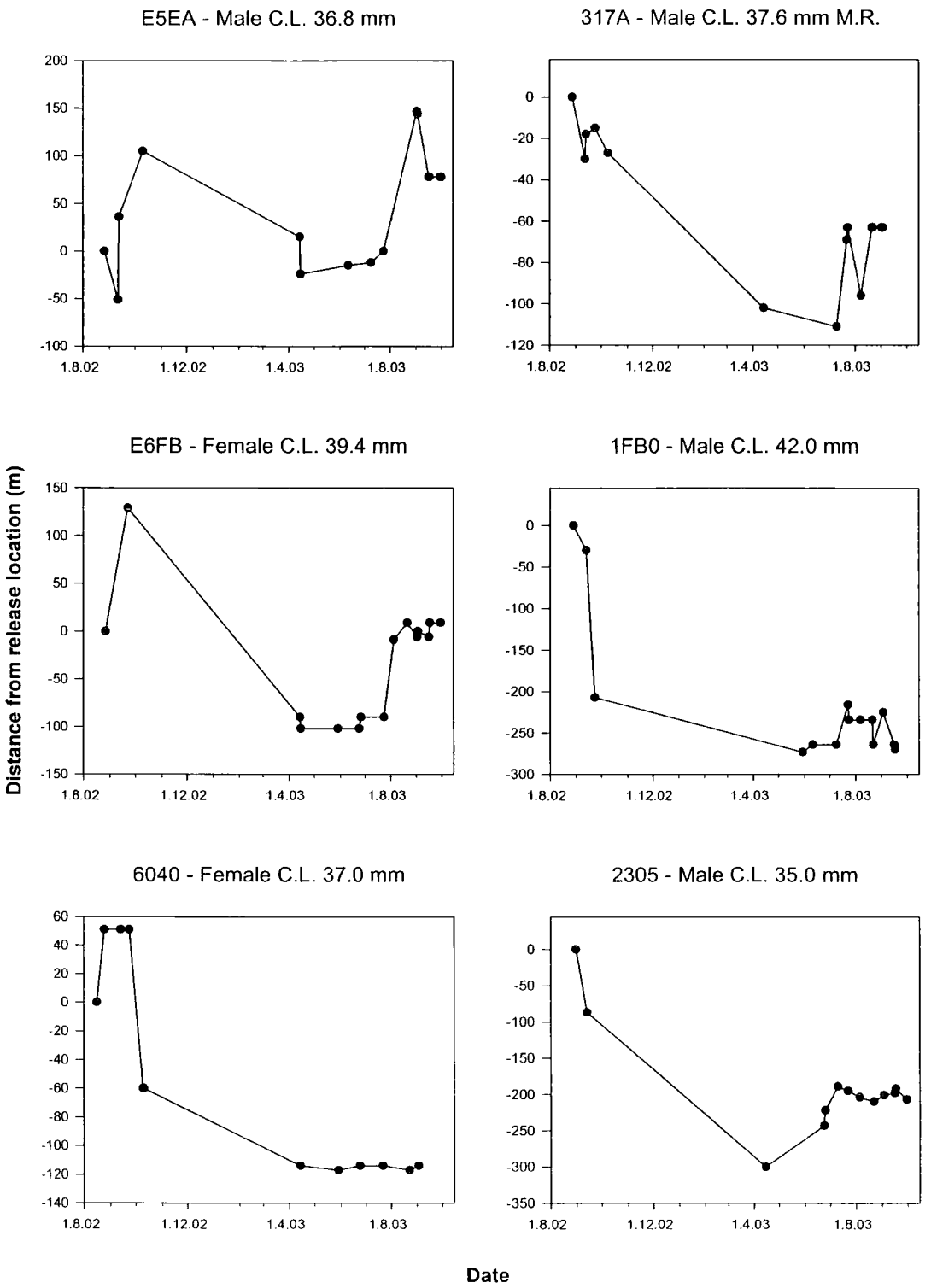
*see Chapter 2, Figure 2.2 for map showing position of sites.

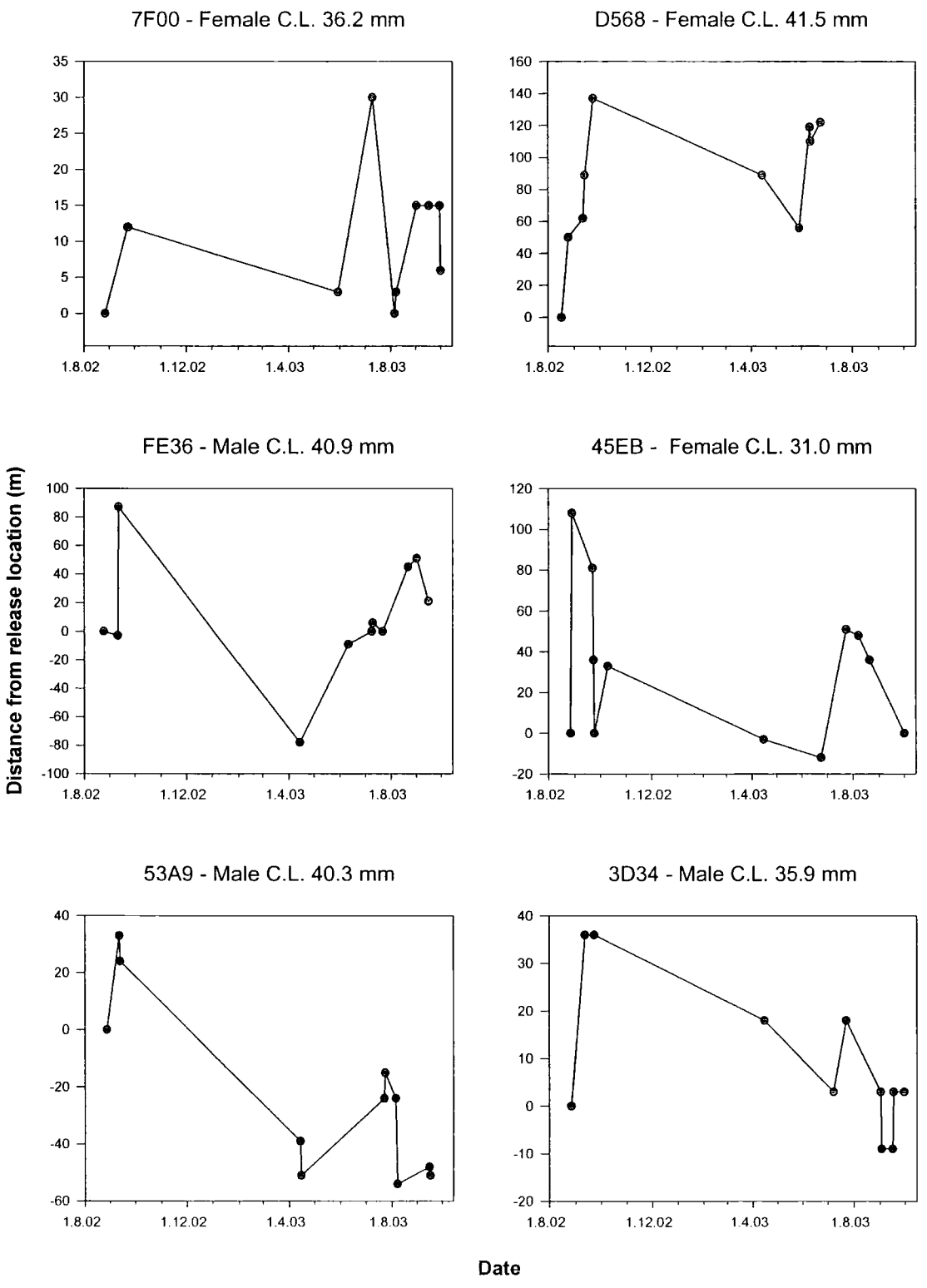
APPENDIX 2.
MOVEMENTS OF INTERNALLY PIT TAGGED WHITE-CLAWED CRAYFISH IN ELLER BECK (CHAPTER 5)

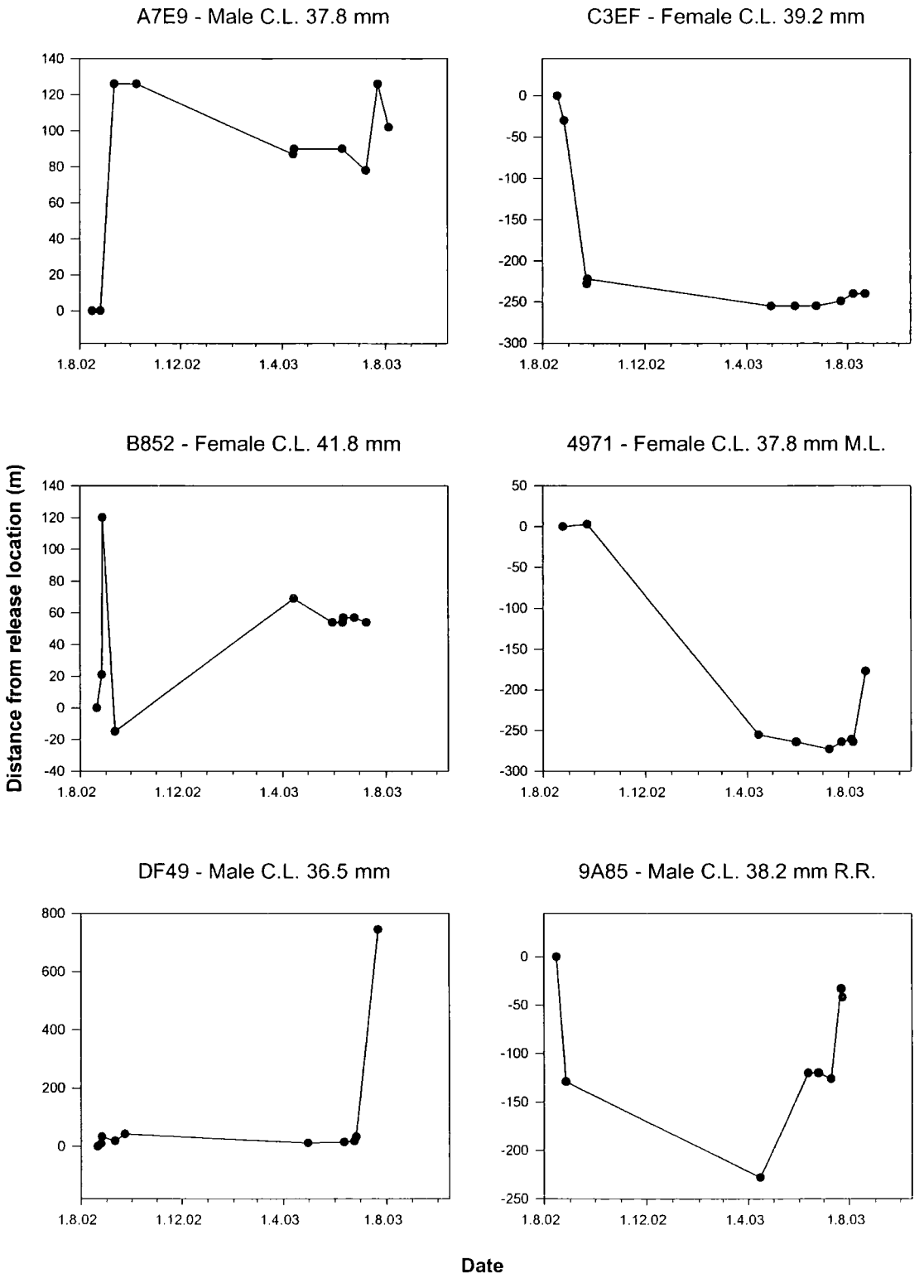
Crayfish that were tagged in August 2002 and were relocated 8 or more times are shown. Y axis refers to distance of crayfish from release location, + ve values represent upstream movements and –ve values represent downstream movements. Note varying scale on Y axis. CL – carapace length; ML missing left chela; MR missing right chela; RL regenerating left chela; RR regenerating right chela.

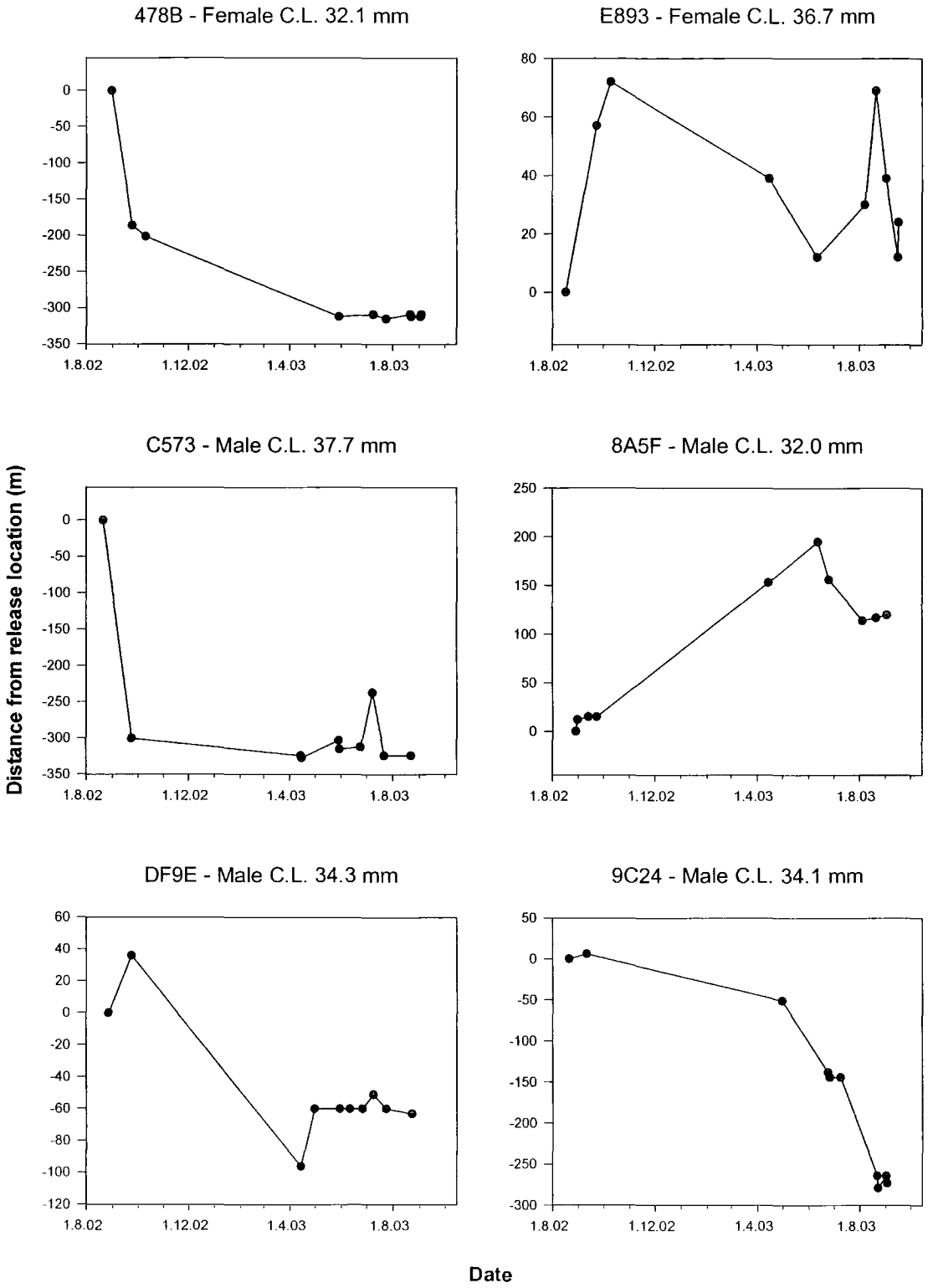


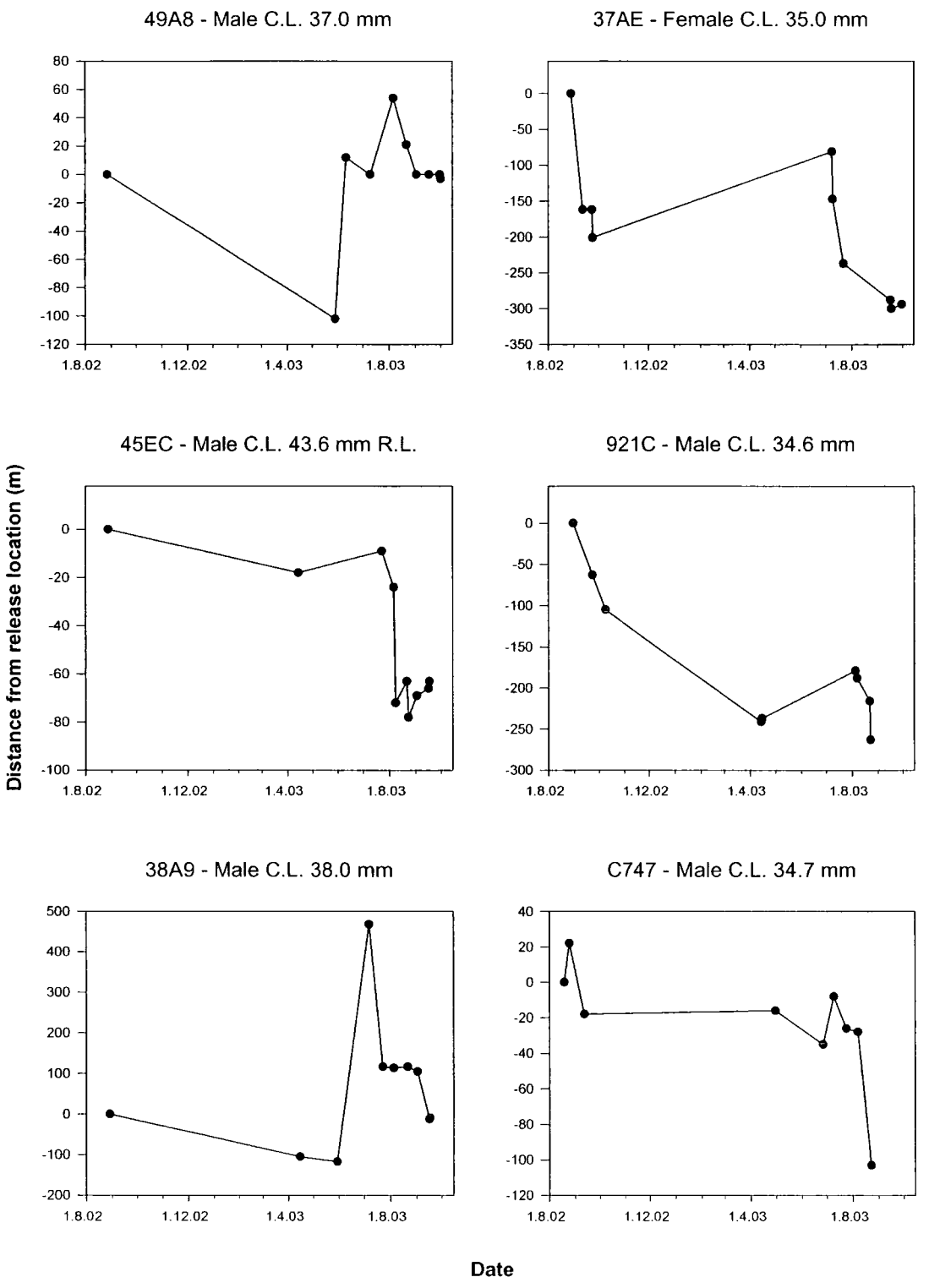

4D92 - Male C.L. 44.2 mm
4519 - Male C.L. 37.5 mm
3202 - Male C.L. 34.6 mm
4760 - Male C.L. 38.6 mm
E264 - Male C.L. 38.5 mm
9286 - Male C.L. 40.9 mm M.R.
Distance from release location (m)
Date
1.8.02
1.12.02
1.4.03
1.8.03

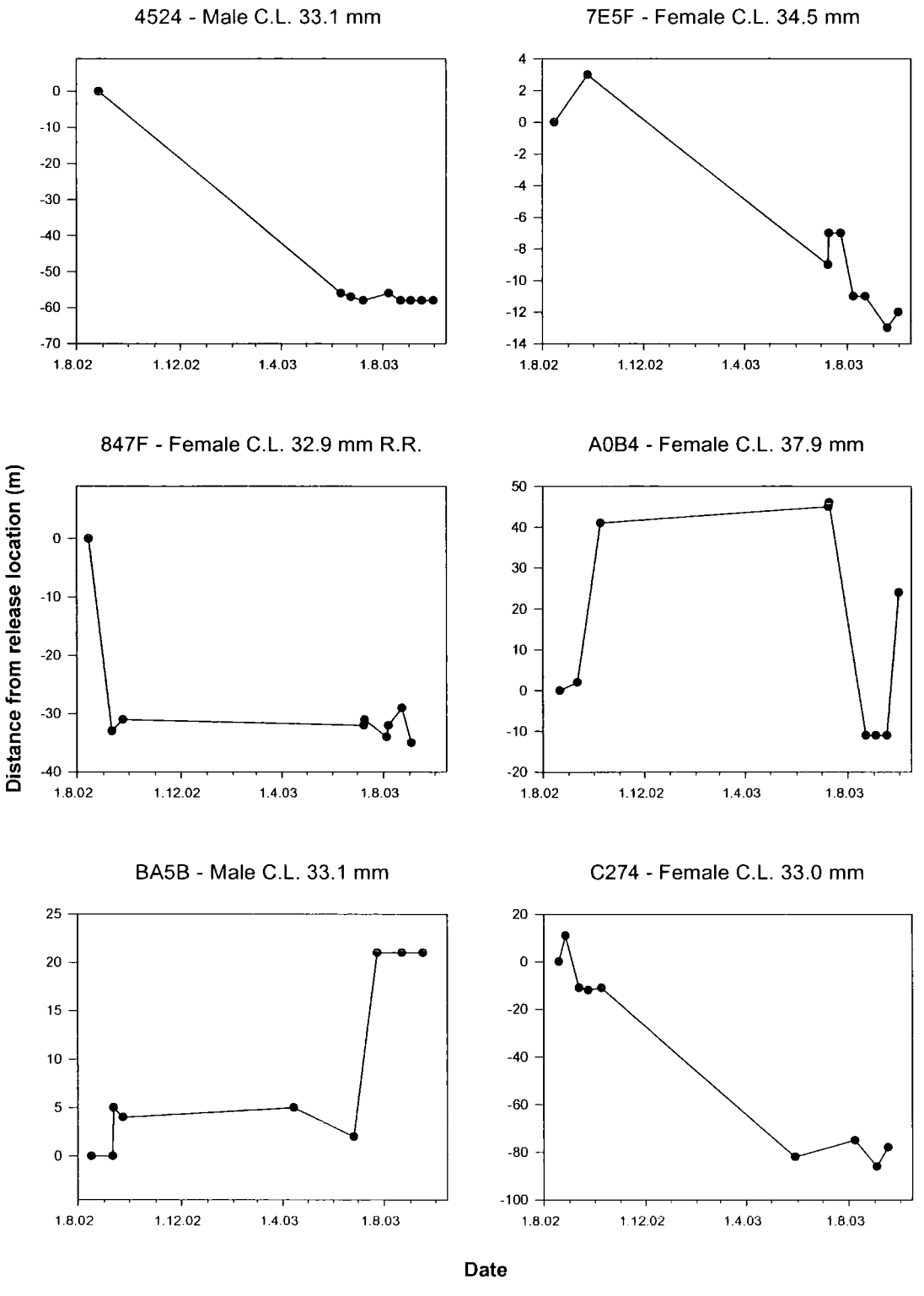

E5EA - Male C.L. 36.8 mm
317A - Male C.L. 37.6 mm M.R.
E6FB - Female C.L. 39.4 mm
1FB0 - Male C.L. 42.0 mm
6040 - Female C.L. 37.0 mm
2305 - Male C.L. 35.0 mm
Distance from release location (m)
Date
1.8.02
1.12.02
1.4.03
1.8.03

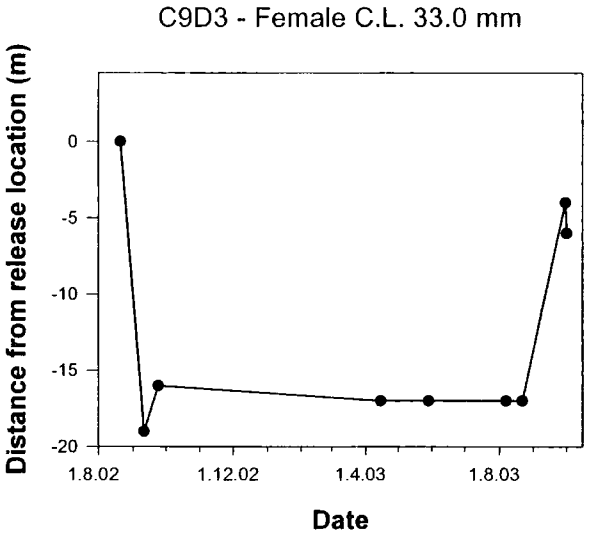

7F00 - Female C.L. 36.2 mm
D568 - Female C.L. 41.5 mm
FE36 - Male C.L. 40.9 mm
45EB - Female C.L. 31.0 mm
53A9 - Male C.L. 40.3 mm
3D34 - Male C.L. 35.9 mm
Distance from release location (m)
Date
1.8.02
1.12.02
1.4.03
1.8.03


A7E9 - Male C.L. 37.8 mm
C3EF - Female C.L. 39.2 mm
B852 - Female C.L. 41.8 mm
4971 - Female C.L. 37.8 mm M.L.
DF49 - Male C.L. 36.5 mm
9A85 - Male C.L. 38.2 mm R.R.
Distance from release location (m)
Date
1.8.02
1.12.02
1.4.03
1.8.03


478B - Female C.L. 32.1 mm
E893 - Female C.L. 36.7 mm
C573 - Male C.L. 37.7 mm
8A5F - Male C.L. 32.0 mm
DF9E - Male C.L. 34.3 mm
9C24 - Male C.L. 34.1 mm
Distance from release location (m)
Date
1.8.02
1.12.02
1.4.03
1.8.03


49A8 - Male C.L. 37.0 mm
37AE - Female C.L. 35.0 mm
45EC - Male C.L. 43.6 mm R.L.
921C - Male C.L. 34.6 mm
38A9 - Male C.L. 38.0 mm
C747 - Male C.L. 34.7 mm
Distance from release location (m)
Date
1.8.02
1.12.02
1.4.03
1.8.03


4524 - Male C.L. 33.1 mm
7E5F - Female C.L. 34.5 mm
847F - Female C.L. 32.9 mm R.R.
A0B4 - Female C.L. 37.9 mm
BA5B - Male C.L. 33.1 mm
C274 - Female C.L. 33.0 mm
Distance from release location (m)
Date
1.8.02
1.12.02
1.4.03
1.8.03


C9D3 - Female C.L. 33.0 mm
Distance from release location (m)
0
-5
-10
-15
-20
1.8.02
1.12.02
1.4.03
1.8.03
Date

APPENDIX 3.
DETAILS OF ALL CRAYFISH SUCCESSFULLY RADIOTAGGED AND TRACKED (CHAPTER 6).

Tracking Session	Crayfish	Species	Sex	CL (mm)	Weight (g)	Date Tagged	Track Duration (days)	D.S. (m)	U.S. (m)	Final (m)	Range (m)	Range (m) /Day	Total Distance (m)
Grassington - Winter 2000/01	A	*Pacifastacus leniusculus*	F	32.9	32.9	16.10.00	128	0	24.5	18.5	25	0.19	43.5
Grassington - Winter 2000/01	B	*Pacifastacus leniusculus*	F	40.1	26.9	20.10.00	124	0	10	10	10	0.08	25
Grassington - Winter 2000/01	C	*Pacifastacus leniusculus*	F	43.4	25.7	20.10.00	124	-54	18	0	72	0.58	328
Grassington - Winter 2000/01	D	*Pacifastacus leniusculus*	F	43.6	28	10.11.00	102	-100	20	-100	120	1.18	140
Grassington - Winter 2000/01	F	*Pacifastacus leniusculus*	F	45	29.6	20.10.00	124	-6	40	40	46	0.37	112
Grassington - Winter 2000/01	G	*Pacifastacus leniusculus*	F-b	40.6	22.8	10.11.00	102	-18	0	-18	18	0.18	18
Grassington - Winter 2000/01	H	*Pacifastacus leniusculus*	F-b	45.7	29	10.11.00	102	-5	0	0	5	0.05	10
Grassington - Winter 2000/01	I	*Pacifastacus leniusculus*	F-b	47.6	34.4	17.10.00	127	-4	5	0	9	0.07	36
Grassington - Winter 2000/01	J	*Pacifastacus leniusculus*	F-b	49.8	45.2	17.10.00	127	0	23	23	23	0.18	23
Grassington - Winter 2000/01	K	*Pacifastacus leniusculus*	M	37.8	21.7	17.10.00	127	-39	0	-20	39	0.31	152
Grassington - Winter 2000/01	L	*Pacifastacus leniusculus*	M	41.5	20	17.10.00	127	0	0	0	0	0.00	0
Grassington - Winter 2000/01	M	*Pacifastacus leniusculus*	M	43.2	22	10.11.00	102	-8	0	-8	8	0.08	8
Grassington - Winter 2000/01	N	*Pacifastacus leniusculus*	M	48	32	24.10.00	124	-15	0	-15	15	0.12	15
Grassington - Winter 2000/01	O	*Pacifastacus leniusculus*	M	51	50.8	16.10.00	128	-35	18	14	53	0.41	114
Grassington - Winter 2000/01	Q	*Pacifastacus leniusculus*	M	51.6	41.7	20.10.00	124	0	25	10	25	0.20	88
Grassington - Winter 2000/01	R	*Pacifastacus leniusculus*	M	51.7	52.5	20.10.00	124	-80	0	-20	80	0.65	140
Grassington - Winter 2000/01	S	*Pacifastacus leniusculus*	M	58.5	88.3	20.10.00	124	-42	0	-21	42	0.34	99
Grassington - Winter 2000/01	T	*Pacifastacus leniusculus*	M	63.8	112.2	20.10.00	124	0	20	10	20	0.16	46
Ure - Summer/Autumn 2001	A	*Pacifastacus leniusculus*	F	40.2	29.6	10.08.01	46	-30	8	-30	38	0.83	83
Ure - Summer/Autumn 2001	B	*Pacifastacus leniusculus*	F	43.9	31.9	10.08.01	46	-1	0	0	1	0.02	13
Ure - Summer/Autumn 2001	C	*Pacifastacus leniusculus*	F	38.5	35.8	13.08.01	43	-5	5	5	10	0.23	29
Ure - Summer/Autumn 2001	D	*Pacifastacus leniusculus*	F	41.3	28.3	13.08.01	43	-25	0	-6	25	0.58	96
Ure - Summer/Autumn 2001	E	*Pacifastacus leniusculus*	F	48.8	27.2	24.08.01	32	-262	9	-262	271	8.47	284
Ure - Summer/Autumn 2001	F	*Pacifastacus leniusculus*	F	43	27.2	24.08.01	32	-3	0	-3	3	0.09	10
Ure - Summer/Autumn 2001	G	*Pacifastacus leniusculus*	M	38.9	25	24.08.01	32	-15	29	3	44	1.38	152

Tracking Session	Crayfish	Species	Sex	CL (mm)	Weight (g)	Date Tagged	Track Duration (days)	D.S. (m)	U.S. (m)	Final (m)	Range (m)	Range (m) /Day	Total Distance (m)
Ure - Summer/Autumn 2001	H	*Pacifastacus leniusculus*	F	51.9	32.5	24.08.01	32	-217	0	-217	217	6.78	226
Ure - Summer/Autumn 2001	I	*Pacifastacus leniusculus*	M	44.9	26.6	28.08.01	28	-15	16	16	31	1.11	112
Ure - Summer/Autumn 2001	J	*Pacifastacus leniusculus*	M	31.9	39.5	28.08.01	28	0	15	10	15	0.54	33
Ure - Summer/Autumn 2001	K	*Pacifastacus leniusculus*	F	51.6	39	29.08.01	27	-4	36	-4	40	1.48	111
Ure - Summer/Autumn 2001	L	*Pacifastacus leniusculus*	F	43.2	50.9	29.08.01	27	-35	1	-35	36	1.33	99
Ure - Summer/Autumn 2001	M	*Pacifastacus leniusculus*	F	37	49.1	29.08.01	27	-8	7	5	15	0.56	44
Ure - Summer/Autumn 2001	N	*Pacifastacus leniusculus*	F	44	23.8	31.08.01	25	-15	30	25	45	1.80	90
Ure - Summer/Autumn 2001	O	*Pacifastacus leniusculus*	F	43.5	26.2	31.08.01	25	-24	10	-2	34	1.36	77
Grassington - Summer 2002	A	*Pacifastacus leniusculus*	F-b	40.8	24.4	05.06.02	68	-3	3	2	6	0.09	20
Grassington - Summer 2002	B	*Pacifastacus leniusculus*	F	42.3	21.2	05.06.02	70	-190	3	-188	193	2.76	222
Grassington - Summer 2002	C	*Pacifastacus leniusculus*	F	42.9	25.4	07.06.02	20	0	113	57	113	5.65	84.5
Grassington - Summer 2002	D	*Pacifastacus leniusculus*	F	43.1	22.2	03.06.02	50	0	12	9	12	0.24	12.5
Grassington - Summer 2002	E	*Pacifastacus leniusculus*	F	45.5	28.5	17.06.02	58	-41	18	-41	59	1.02	255
Grassington - Summer 2002	F	*Pacifastacus leniusculus*	F-b	45.7	32.1	07.06.02	74	0	283	283	283	3.82	523
Grassington - Summer 2002	G	*Pacifastacus leniusculus*	F-b	46.3	31.5	03.06.02	72	-41	5	-17	46	0.64	115
Grassington - Summer 2002	H	*Pacifastacus leniusculus*	F-b	47.5	36.1	07.06.02	60	-64	146	-64	210	3.50	694
Grassington - Summer 2002	I	*Pacifastacus leniusculus*	F-b	50	43.3	03.06.02	78	-417	8	-387	425	5.45	537
Grassington - Summer 2002	J	*Pacifastacus leniusculus*	F	50.5	35.1	17.06.02	48	-122	63	63	185	3.85	449
Grassington - Summer 2002	K	*Pacifastacus leniusculus*	M	36.3	19.3	25.07.02	26	-5	74	2	79	3.04	162
Grassington - Summer 2002	L	*Pacifastacus leniusculus*	M	38.7	18.3	25.07.02	26	-35	27	-7	62	2.38	52
Grassington - Summer 2002	M	*Pacifastacus leniusculus*	M	40.7	22.8	07.06.02	74	-327	0	-320	327	4.42	790
Grassington - Summer 2002	N	*Pacifastacus leniusculus*	M	42.5	24.4	17.07.02	34	0	33	28	33	0.97	82
Grassington - Summer 2002	O	*Pacifastacus leniusculus*	M (MR)	43.4	26.1	05.06.02	26	-1	36	36	37	1.42	38
Grassington - Summer 2002	P	*Pacifastacus leniusculus*	M	43.5	25.6	19.06.02	40	-28	135	-28	163	4.08	149
Grassington - Summer 2002	Q	*Pacifastacus leniusculus*	M	45.4	33.5	03.06.02	16	-11	0	-7	11	0.69	8.5
Grassington - Summer 2002	R	*Pacifastacus leniusculus*	M	46.1	33.6	21.06.02	26	-21	65	61	86	3.31	113
Grassington - Summer 2002	S	*Pacifastacus leniusculus*	M	46.9	28.5	19.07.02	32	-1	95	92	96	3.00	106
Ure - Summer 2002	A	*Pacifastacus leniusculus*	F	41.5	32.6	21.06.02	30	-167	0	-167	167	5.57	213
Ure - Summer 2002	B	*Pacifastacus leniusculus*	F	41.7	21.2	25.06.02	34	0	142	15	142	4.18	349
Ure - Summer 2002	C	*Pacifastacus leniusculus*	F	42.2	23.9	18.07.02	27	-2	20	20	22	0.81	34

Tracking Session	Crayfish	Species	Sex	CL (mm)	Weight (g)	Date Tagged	Track Duration (days)	D.S. (m)	U.S. (m)	Final (m)	Range (m)	Range (m) /Day	Total Distance (m)
Ure - Summer 2002	D	*Pacifastacus leniusculus*	F	43.6	25	21.06.02	36	-124	33	33	157	4.36	347
Ure - Summer 2002	E	*Pacifastacus leniusculus*	F	43.6	23.4	25.06.02	32	-413	0	-307	413	12.91	519
Ure - Summer 2002	F	*Pacifastacus leniusculus*	F	57.3	56.2	21.06.02	36	-35	35	30	70	1.94	126
Ure - Summer 2002	G	*Pacifastacus leniusculus*	F	*	*	19.07.02	26	-3	0	0	3	0.12	6
Ure - Summer 2002	H	*Pacifastacus leniusculus*	M	46.1	21.3	21.06.02	42	-299	32	-295	331	7.88	387
Ure - Summer 2002	I	*Pacifastacus leniusculus*	M	52.7	36.3	25.06.02	22	0	140	120	140	6.36	160
Ure - Summer 2002	J	*Pacifastacus leniusculus*	M	64	72.2	18.07.02	15	1	1	0	2	0.13	4
Ure - Summer 2002	K	*Pacifastacus leniusculus*	M	*	*	19.07.02	26	-63	11	9	74	2.85	139
Ure - Summer 2002	L	*Pacifastacus leniusculus*	M	*	*	19.07.02	26	-4	3	0	7	0.27	18
Barden Bridge - Summer 2003	A	*Austropotamobius pallipes*	F	40.1	15.2	23.07.03	27	0	74	74	74	2.74	76
Barden Bridge - Summer 2003	B	*Austropotamobius pallipes*	F	38.4	15.9	22.07.03	28	-9	0	-9	9	0.32	9
Barden Bridge - Summer 2003	C	*Austropotamobius pallipes*	F	38.3	15.6	22.07.03	28	-14	8	-3	22	0.79	34
Barden Bridge - Summer 2003	D	*Austropotamobius pallipes*	F	38.1	19.6	23.07.03	15	0	14	14	14	0.93	14
Barden Bridge - Summer 2003	E	*Austropotamobius pallipes*	F	38.1	15.7	23.07.03	27	0	37	30	37	1.37	210
Barden Bridge - Summer 2003	F	*Austropotamobius pallipes*	F	35.7	13.7	07.08.03	12	-11	0	-11	11	0.92	14
Barden Bridge - Summer 2003	G	*Austropotamobius pallipes*	F	35.5	13.2	16.07.03	34	-2	0	-2	2	0.06	5
Barden Bridge - Summer 2003	H	*Austropotamobius pallipes*	F (RB)	35.2	11.9	07.08.03	12	-28	44	-28	72	6.00	124
Barden Bridge - Summer 2003	I	*Austropotamobius pallipes*	F	34.5	13.6	23.07.03	27	0	90	64	90	3.33	154
Barden Bridge - Summer 2003	J	*Austropotamobius pallipes*	M (ML)	42.2	21.2	07.08.03	12	-3	2	-3	5	0.42	6
Barden Bridge - Summer 2003	K	*Austropotamobius pallipes*	M	41.7	24.9	16.07.03	34	0	53	53	53	1.56	80
Barden Bridge - Summer 2003	L	*Austropotamobius pallipes*	M	41	22.4	16.07.03	34	0	65	65	65	1.91	81
Barden Bridge - Summer 2003	M	*Austropotamobius pallipes*	M	40.5	20.8	16.07.03	10	0	31.4	27	31	3.14	38
Barden Bridge - Summer 2003	N	*Austropotamobius pallipes*	M	40.2	19.6	16.07.03	34	-16	0	-11	16	0.47	23
Barden Bridge - Summer 2003	O	*Austropotamobius pallipes*	M	40	21	25.07.03	25	0	27	27	27	1.08	48
Barden Bridge - Summer 2003	P	*Austropotamobius pallipes*	M	39.3	19.4	16.07.03	34	-35	26	-35	61	1.79	76
Barden Bridge - Summer 2003	Q	*Austropotamobius pallipes*	M	38.6	18.1	16.07.03	16	0	87	85	87	5.43	90
Barden Bridge - Summer 2003	R	*Austropotamobius pallipes*	M	38.5	18.1	16.07.03	34	-14	12	-14	26	0.76	54
Barden Bridge - Summer 2003	S	*Austropotamobius pallipes*	M	36.8	16.2	07.08.03	12	-1	12	12	13	1.08	27
Barden Bridge - Summer 2003	T	*Austropotamobius pallipes*	M	36.7	16.8	16.07.03	6	-2	8	8	10	1.67	12
Barden Bridge - Summer 2003	U	*Pacifastacus leniusculus*	F	53	45.7	16.07.03	34	0	40	37	40	1.18	58

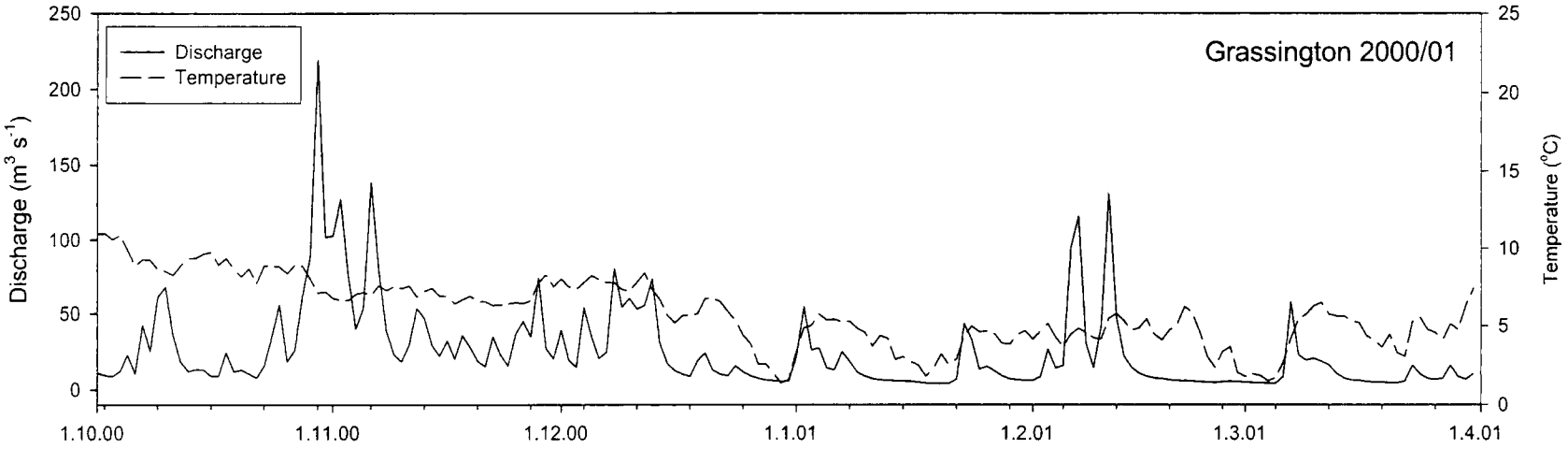
Tracking Session	Crayfish	Species	Sex	CL (mm)	Weight (g)	Date Tagged	Track Duration (days)	D.S. (m)	U.S. (m)	Final (m)	Range (m)	Range (m) /Day	Total Distance (m)
Barden Bridge - Summer 2003	V	*Pacifastacus leniusculus*	F	49.5	37.3	16.07.03	34	-7	11	-4	18	0.53	42
Barden Bridge - Summer 2003	W	*Pacifastacus leniusculus*	F	47	32.7	16.07.03	34	0	150	150	150	4.41	150
Barden Bridge - Summer 2003	X	*Pacifastacus leniusculus*	F	45	27.5	16.07.03	34	-12	100	100	112	3.29	189
Barden Bridge - Summer 2003	Y	*Pacifastacus leniusculus*	F	42.6	21.9	16.07.03	34	-91	42	-91	133	3.91	196
Barden Bridge - Summer 2003	Z	*Pacifastacus leniusculus*	F	40.1	50.2	28.07.03	22	-153	0	-153	153	6.95	153
Barden Bridge - Summer 2003	A1	*Pacifastacus leniusculus*	F	35.9	13	25.07.03	25	-29	0	-27	29	1.16	32
Barden Bridge - Summer 2003	B1	*Pacifastacus leniusculus*	M	63.8	110	16.07.03	34	-171	0	-84	171	5.03	280
Barden Bridge - Summer 2003	C1	*Pacifastacus leniusculus*	M	58	53.2	16.07.03	34	-4	75	75	79	2.32	81
Barden Bridge - Summer 2003	D1	*Pacifastacus leniusculus*	M	53	47.8	16.07.03	34	0	44	44	44	1.29	51
Barden Bridge - Summer 2003	E1	*Pacifastacus leniusculus*	M	48.2	32.5	16.07.03	34	-30	328	328	358	10.53	429
Barden Bridge - Summer 2003	F1	*Pacifastacus leniusculus*	M	40.9	19.4	16.07.03	34	-80	132	-75	212	6.24	340
Barden Bridge - Summer 2003	G1	*Pacifastacus leniusculus*	M	40.8	19.9	16.07.03	34	-24	49	-24	73	2.15	161
Barden Bridge - Summer 2003	H1	*Pacifastacus leniusculus*	M	38	15.4	16.07.03	34	0	325	258	325	9.56	405
Barden Bridge - Summer 2003	I1	*Pacifastacus leniusculus*	M	36.4	15.6	16.07.03	34	0	342	342	342	10.06	406

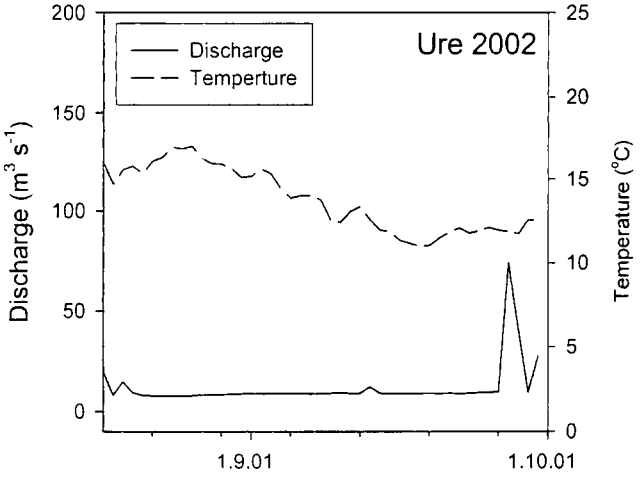
F-b – berried female, MR – missing right chelae, ML – missing left chelae, RR - regenerating right chelae, RL - regenerating left chelae, RB - regenerating both chelae. D.S. – Maximum recorded linear distance downstream from release location, U.S. – Maximum recorded distance upstream from release location. Range – difference between maximum distance upstream and maximum distance downstream, Final – Distance from release location of final recorded position.

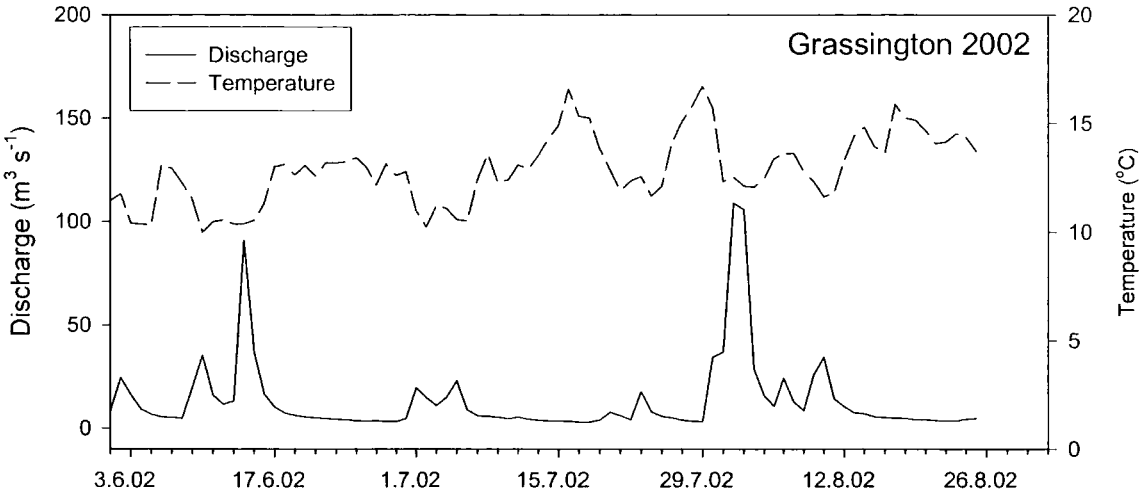
APPENDIX 4

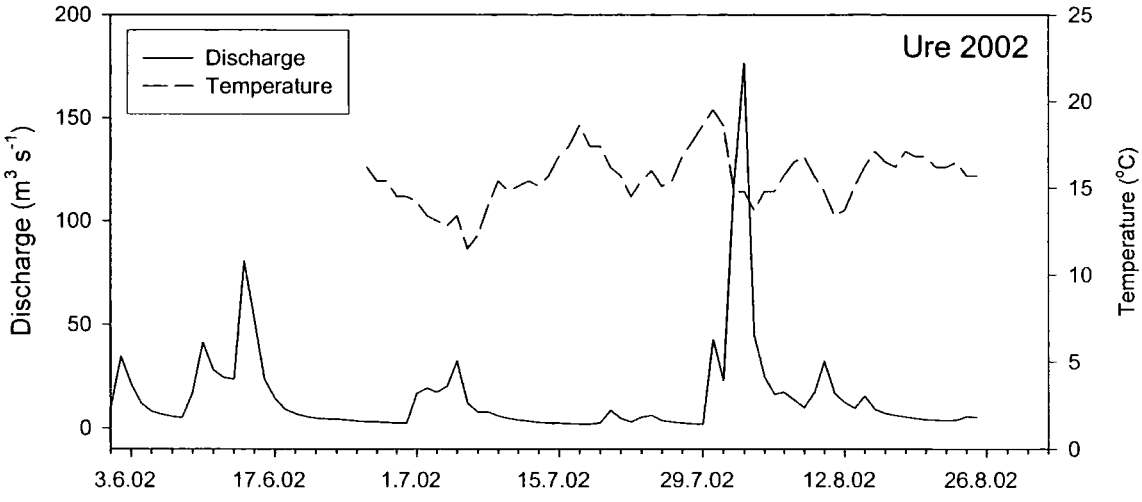
DISCHARGE AND WATER TEMPERATURE FOR ALL PERIODS OF RADIOTRACKING (CHAPTER 6)

Discharge measured at Addingham Gauging Weir (River Wharfe) and Kilgram Gauging Weir (River Ure). Water temperature is mean daily water temperature at study sites calculated from hourly measurements, measured hourly with Tinytalk temperature loggers.






Grassington 2002
Discharge
Temperature
Discharge (m3 s-1)
Temperature (°C)
200
150
100
50
0
20
15
10
5
0
3.6.02
17.6.02
1.7.02
15.7.02
29.7.02
12.8.02
26.8.02


Ure 2002
Discharge
Temperature
Discharge (m3 s-1)
Temperature (°C)
200
150
100
50
0
25
20
15
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5
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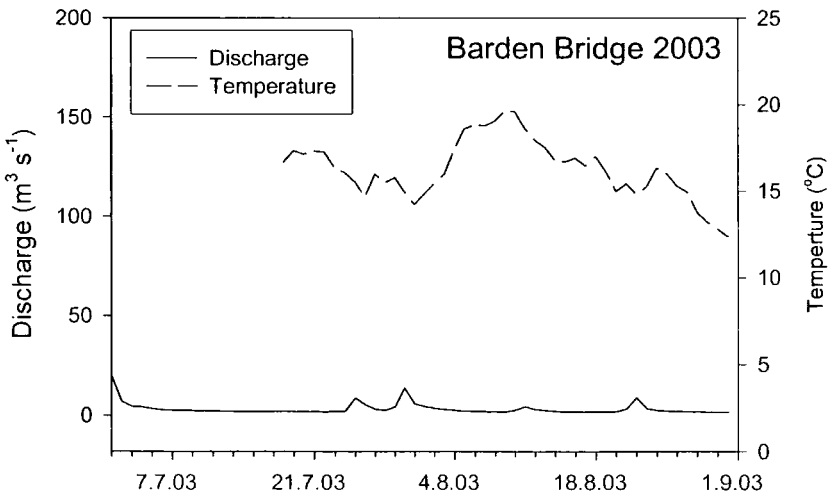
3.6.02
17.6.02
1.7.02
15.7.02
29.7.02
12.8.02
26.8.02


Barden Bridge 2003
Discharge
Temperature
Discharge (m3 s-1)
Temperture (°C)
200
150
100
50
0
25
20
15
10
5
0
7.7.03
21.7.03
4.8.03
18.8.03
1.9.03

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The potential use of PIT telemetry for identifying and tracking crayfish in their natural environment

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Key words: passive integrated transponder, *Pacifastacus leniusculus*, Crustacea, streams, tagging, telemetry

Abstract

A method for tracking crayfish and other benthic animals in rivers and streams, based on passive integrated transponder (PIT) technology, using a portable detector was investigated. The effect of implanting crayfish with PIT tags and the efficiency of the PIT tag detector system at locating tags is described. In a laboratory study 30 signal crayfish *Pacifastacus leniusculus* (>33.7 mm carapace length) were internally implanted with PIT tags (12-mm long×2.1-mm diameter) and 30 crayfish matched for size and sex were kept as controls and maintained for 6 months. Tagging had no significant effect on survival, moulting or growth of crayfish, and tag retention was 100%. The reader unit consists of an antenna coil mounted on a pole and designed to be moved over the streambed to search for tagged crayfish. Efficiency testing indicated that more than 80% of tags were identified and located when hidden within different stream microhabitats.

Introduction

Crayfish are large mobile invertebrates capable of making substantial active movements (Gherardi & Barbaresi, 2000). This enhances their ability to utilise patchy resources and also to colonise new areas and so information on their spatial behaviour is of importance in understanding their habitat requirements and behaviour. Whilst radio telemetry and mark-recapture studies have been used to study movements of freshwater crayfishes (Robinson et al., 2000), both methods have limitations. The size of even the smallest radio transmitters limits their use to external attachment on large crayfish, and cost usually precludes tracking a large number of individuals. A major problem with external marking or tagging methods for arthropods is that the tag or mark may be lost at moult, or it becomes difficult to discriminate within a few moults in the case of branding or hole-punching (e.g. Abrahamsson, 1965; Guan, 1997). For large juvenile and adult crayfish this may prohibit individual recognition for periods of longer than 12 months, depending on age and sex (Guan, 1997). Tags may also interfere with the moulting process in arthropods (Hurley, 1990), and tagging or marking methods that require recapture of the animal risk substantial disturbance to behaviour. A suitable long-term tagging method for individual identification of crayfish and other decapods therefore needs to be based on a system using implanted tags, with a low rate of rejection at moult. Ideally the tags should be externally readable with minimal disturbance to the animal.

Passive integrated transponder (PIT) tags are physiologically neutral, with modest physical size, permitting internal implantation in relatively small animals, this provides the advantage in crayfish that potentially they are not lost at moult. They are sealed electronic modules that when energised from an external antenna, return information programmed into them, typically a unique identification number. PIT

tags are detected at some distance from the receiver which offers the possibility of detecting and identifying tagged organisms in the natural environment without subsequent capture or handling (Prentice et al., 1990; Castro-Santos et al., 1996; Lucas et al., 1999). They have a theoretically indefinite life span and allow repeated non-destructive sampling. Portable detectors for searching rivers and streams for tagged fish have recently been developed (Roussel et al., 2000; Morhardt et al., 2000).

Here we describe a technique for implanting PIT tags into crayfish and report on the effects that tagging has on captive animals. We also report initial results of the efficiency of a modified portable PIT tag reader designed for searching the stream bed for tagged crayfish.

Methods

The experiment was designed to: (i) investigate the effects of tagging on survival, moulting and growth of captive signal crayfish *Pacifastacus leniusculus* (Dana), (ii) field test the efficiency of a portable PIT detector in a variety of stream microhabitats.

Effects of tagging on crayfish

Signal crayfish were captured in the River Wharfe, northern England during November 2000. Crayfish were acclimated to laboratory conditions for at least 20 days before tagging. The carapace length (CL), from the rostral apex to the posterior median edge of the cephalothorax, was measured to the nearest 0.1 mm and crayfish were assigned to pairs matched for sex and size. Sixty crayfish were used (CL 33.7–61.4 mm), 34 males and 26 females. On the basis of preliminary assessment and past work (Wiles & Guan, 1993), we considered that crayfish smaller than 25-mm CL were not taggable with 12-mm PIT tags due to physical size limitations.

One individual from each pair was tagged (using Trovan ID 100, nominally 12×2.1 mm PIT tags, 0.10 g in air) whilst the other acted as a control. Tagging was carried out by holding the animal around the cephalothorax with the ventral surface uppermost and making an incision, using the tip of a sterile large gauge (diameter 2.5-mm) hypodermic needle, c. 3 mm wide and deep through the cuticle and underlying tissue at the base of the fifth pereopod (fourth walking leg). The tag was inserted through the incision, by gently pushing the tag anteriorally so that it came to rest underneath the digestive gland (hepatopancreas) and above the segmental musculature.

Crayfish were kept in individual tanks (50 cm×30 cm×30 cm), filled with de-chlorinated tap water, and provided with sections of plastic drainpipe for shelter. Water was changed at regular intervals (4–6 days). Crayfish were maintained at 15 °C, a temperature at which they exhibit substantial feeding activity, with a light regime of 12 h:12 h LD. Two months after tagging, to encourage crayfish to moult, the light regime was changed to 16 h:8 h LD over a 4-week period, with light increased by an hour each week. Crayfish were fed *ad libitum* with slices of carrot and potato and weekly with pellets of amphibian food (protein 48%). Tanks were checked daily for mortality, tag loss and shed exoskeletons. Moulting date was recorded and the new CL was measured once the new exoskeleton had hardened. The experiment lasted for 6 months (182 days). Crayfish were tagged on 11 December 2000 and the experiment terminated on 11 June 2001.

PIT tag reader design

The reader design (UKID System, Preston, UK) was based on a modified Trovan LID 500 (Trovan Ltd., Douglas, UK) portable reader. It is a full-duplex system operating at 125 kHz. It consists of a coil antenna (diameter 180-mm), mounted on a pole (length 1.5-m), to facilitate searching of the stream bed, connected to a decoding electronics module. When detected the transponder ID number is displayed on a 2 line×16 character LCD, the transponder ID number is also saved (with a time/date stamp) and can be downloaded to a PC. The reader unit weighs 800 g and the search antenna and pole 1900 g, total weight of the system 2700 g. The system is powered by an integral 1500 mA/h NiMH battery pack which provides approximately 7 h of continuous use.

Trovan ID100 PIT tags (12-mm long×2.1-mm diameter) were used in the laboratory experiment for assessing effects of tagging on crayfish, and UKID122GL PIT tags (12-mm long×2.1-mm diameter) were used in the field testing. Both tags had similar detection ranges measured using the method of Morhardt et al. (2000). The detection range varied with the orientation of the tag to the antenna and ranges of up to 150 mm were recorded when the tag was vertical (long axis of the tag perpendicular to the flat surface of the search head, measured as the distance from tag to antenna). Range was reduced by

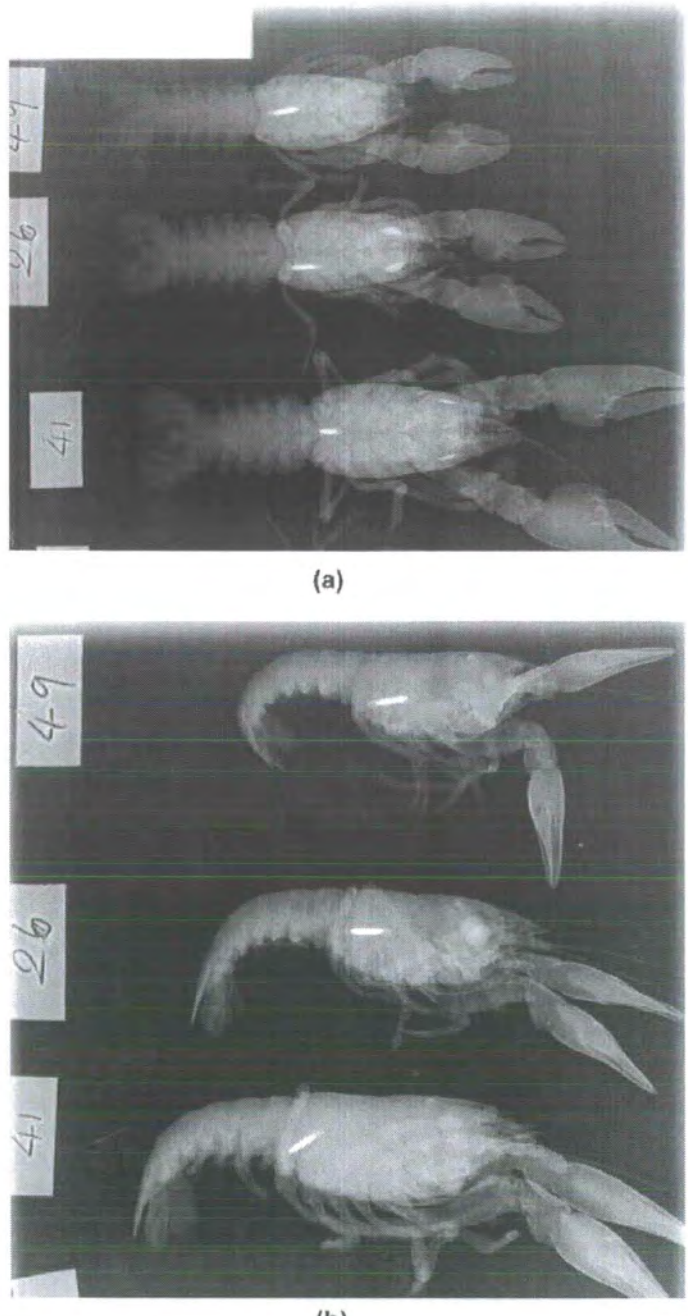

Figure 1. X-radiographs of three PIT tagged *Pacifastacus leniusculus*. Crayfish had been tagged for 6 months and undergone one moult before X-radiographs were taken. (A) dorsal view (B) lateral view. Tag measures 12 mm in length.

approximately 40% when the long axis of the tag was parallel to the flat surface of the search head. Range loss with tags in water or within the substrate was not apparent or was negligible.

Efficiency testing

An assessment was made of the ability of the reader unit to detect and locate tags in the field. Within a small river (depth <1 m) an area of approximately 60 m^2 was surveyed, consisting of equal areas of small cobble (20 m^2), medium cobble (20 m^2) and large cobble (20 m^2). Within each microhabitat 25 PIT tags were placed beneath rocks in similar positions to where crayfish are normally found. The mean depth (MD) and mean maximal axis (MMA) of the rocks beneath which the tags were placed in each of the microhabitats were: small cobble (MD 26.6 mm, MMA 68.2 mm) medium cobble (MD 48.2 mm, MMA 130.4 mm) large cobble (MD 78.8 mm, MMA 178.6 mm). In addition, tags were placed in burrows within a 30-m long stretch of bank. Burrows of lengths 5, 10 and 15 cm were made and tags were positioned 2.5 cm from the end of the burrow. Thus, tags were positioned at depths of 2.5, 7.5 and 12.5 cm within the burrows. Twenty tags were placed in each of these burrow lengths. The area in which the tags were hidden was blind-searched by an operator unfamiliar with the site. When searching, the operator walked in an upstream direction, moving the antenna across the search area, just above the streambed, and across the submerged bank.

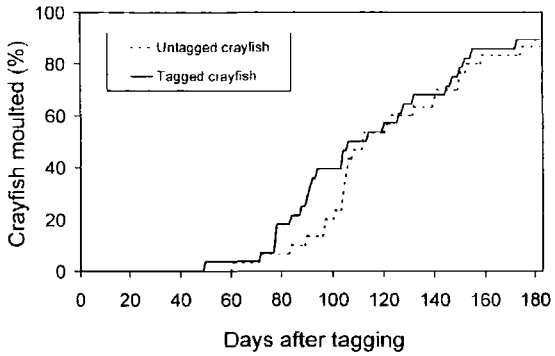

Figure 2. Timing of first moult during the experimental period for tagged and untagged *Pacifastacus leniusculus* held under laboratory conditions. Data are for all crayfish that survived to the end of the experiment (28 tagged, 29 untagged).

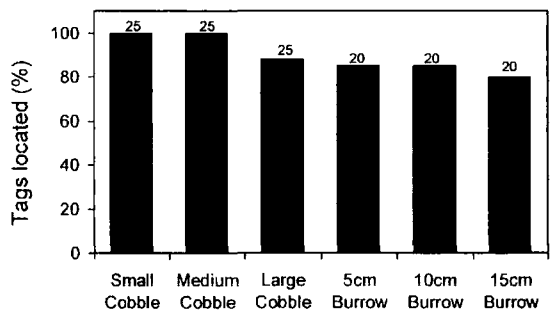

Figure 3. Efficiency of PIT tag detection depending on microhabitat. Tags within burrows were placed 2.5 cm from the extremity of the burrow to mimic a 5-cm long crayfish at the end of the burrow with the tag implanted in its body cavity. Each bar superscript denotes the number of tags placed within each microhabitat.

Results

Survival and tag retention

Although histological studies were not carried out, the injection site appeared to heal within 2 weeks, but in some cases could be identified by slight pigmentation. Following moult there was no sign of the incision site. The position of tags was verified by X-radiography of three tagged crayfish (Fig. 1), these showed little movement of the tag from the injection site.

Both control and tagged groups exhibited high survival during the 182 days of the experiment, Two tagged crayfish and one control animal died over this period, resulting in percentage survival of 93.3% of tagged crayfish, and 96.7% of the control group. There was no significant difference in mortality between tagged and control groups (Fisher exact test, $P > 0.05$). One mortality in the tagged group appeared to have been caused by the tagging procedure. Immediately after tagging the crayfish became comparatively unresponsive and it died within 24 h of tagging. It appears that, in this case, the ventral nerve cord, which lies close to the ventral surface, may have been damaged. During the remainder of the experiment two crayfish died, one from each group. Reasons for mortality are unknown, but both cases occurred in the immediate pre-moult phase.

Over the duration of the experiment, tag retention was 100%. All tags remained operational throughout the experiment and the tag identification number could be read by passing the reader unit over the tagged crayfish.

Table 1. Per moult increment (MI), and percentage moult increment (% MI) of *Pacifastacus leniusculus* tagged with PIT tags and untagged controls retained under laboratory conditions. Data comprises 23 pairs of crayfish matched for size and sex in which both crayfish moulted

	Initial CL, mm ($\bar{x}$ ± SD)	Post-moult CL, mm ($\bar{x}$ ± SD)	MI, mm ($\bar{x}$ ± SD)	% MI, mm ($\bar{x}$ ± SD)
Tagged (n = 23)	42.19±4.61	45.99±5.03	3.80±1.18	9.04±2.92
Males (n = 12)	42.61±5.56	46.66±5.88	4.04±0.91	9.55±2.21
Females (n = 11)	41.72±3.50	45.26±4.07	3.54±1.42	8.47±3.57
Controls (n = 23)	42.13±4.23	46.32±4.75	4.19±1.08	10.08±2.97
Males (n = 12)	42.51±5.94	46.80±5.71	4.29±0.90	10.35±2.81
Females (n = 11)	41.71±3.15	45.79±3.64	4.08±1.28	9.78±3.25

Moult

All crayfish that moulted did so successfully without any apparent complications. During the course of the study 51 crayfish moulted (25 tagged, 26 controls), including three crayfish (1 tagged, 2 controls) that moulted twice. In pairs in which both crayfish moulted, the timing of first moult in tagged ($\bar{x}$ = 109 days post tagging) and control animals ($\bar{x}$ = 114 days post tagging) did not differ significantly (paired t-test, t = 0.77, $P > 0.05$) (Fig. 2). The moult increment (MI) and% moult increment (% MI) of tagged and untagged crayfish was not significantly different in males, females and both sexes combined (2-Factor ANOVA; MI F = 0.866, $P > 0.05$; % MI F = 0.781, $P > 0.05$). The growth of tagged crayfish was slightly reduced, by about 10% compared to untagged controls, although this difference (Table 1) was not significant.

Field detection of tags

The position of tags could be determined to within a 10-cm radius. In all microhabitats, including burrows, a high percentage (≥80%) of tags were detected and located (Fig. 3). There was no significant difference in the number of tags located within the different cobble classes (Fisher exact test, $P > 0.05$) or the different burrow depths (Fisher exact test, $P > 0.05$). Comparison of cobble classes combined with burrow classes combined, indicated that significantly more tags were located within the cobble classes than burrow classes (Fisher exact test, P = 0.018).

Discussion

In comparison with other techniques for marking crayfish, PIT tagging has several benefits. It permits repeated non-destructive sampling of individuals, has a theoretically indefinite life span, negligible tagging mortality, high tag retention, and no apparent long term effects on growth and survival of tagged animals. PIT tagging has also been used successfully in the laboratory without ill effect on prawns tagged in the abdominal musculature (Cacaci et al., 1999). Information on possible effects of tagging on copulation and egg production would be useful, although the current study suggests that tagging does not unduly affect adult crayfish. The laboratory trials support the preliminary findings of Wiles & Guan (1993) that PIT tagging does not adversely affect growth or survival. Growth and moulting of tagged crayfish appeared normal with no significant difference between the growth of tagged and control crayfish. This contrasts with a reduction in growth of 15.4–18.3% when marking crayfish externally by punching and clipping holes in uropods, telson and pleura (Guan, 1997).

The survival of both tagged and control crayfish was high. The death of one crayfish immediately after tagging suggests the insertion of PIT tags may cause a low level of acute tagging mortality. Care needs to be taken to ensure that the tag is not inserted too close to the median line, along which the ventral nerve cord runs. Wiles & Guan (1993) reported a high level of tagging mortality in small crayfish (<25 mm CL) when using 13-mm×2-mm tags, but in large crayfish they did not report any tagging mortality. Where possible, for tagging in the field, we recommend retaining crayfish individually (to avoid

aggressive behaviour) for several hours at ambient water temperatures and checking for normal mobility and posture before release.

The field trials of the reader unit suggest that the system is efficient at searching for tags and the majority of crayfish that are within range of the antenna will be located and identified. The detection efficiency was lower in the burrow microhabitat classes compared to cobble microhabitats, possibly as it was found harder to position the antenna coil close to the substrate on vertical banks in comparison with the horizontal streambed. The main limitation of the system is the relatively short distance from which tags can be detected. In environments in which large boulders and root masses are common it may be difficult to position the antenna close enough to tagged crayfish to detect them. Similarly the depth of crayfish burrows may be influential in determining if crayfish are detected. This may result in some size bias in the burrowing crayfish that are recorded, as larger crayfish tend to make deeper burrows (Guan, 1997). *Pacifastacus leniusculus* are capable of burrowing to depths of over 30-cm, which could potentially place tagged crayfish out of the detection range. Larger half-duplex tags have substantially longer ranges (Roussel et al., 2000; Morhardt et al., 2000) but these tags would be too large for implantation into most freshwater crayfish species, although they could be used for larger decapod species. Use of a larger search head and antenna coil could enable faster searching of a given area, although for use of a fully enclosed coil as used in this study, increased size would result in greater resistance to flow and reduced ability to search around rocks and other likely refuges. This could be solved by using an 'open coil' design such as that of Roussel et al. (2000) in which the antenna coil is protected by plastic piping and which could be placed over rocks of smaller radius than the coil.

We believe that this PIT tag detector system represents a valuable addition to conventional mark-recapture and radio telemetry methods for studying the spatial ecology of crayfish, and potentially also for other large invertebrates occurring in shallow water or on land, and for small benthic fishes such as sculpins (Cottidae) (Bruyndoncx et al., 2002). The system allows a large number of animals to be marked and has the potential to address numerous questions relating to behaviour, movements and habitat use. The accuracy of the system in locating crayfish (<10 cm) permits fine scale movements and microhabitat use to be assessed without the need to disturb crayfish and habitat.

Acknowledgements

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Winter movements and activity of signal crayfish *Pacifastacus leniusculus* in an upland river, determined by radio telemetry

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Key words: Pacifastacus leniusculus, home range, overwintering, telemetry, behaviour, invasive species

Abstract

Radio-telemetry was used to study the late autumn and winter movements of twenty adult signal crayfish *Pacifastacus leniusculus* (32.9–63.8 mm carapace length) an introduced exotic crayfish species, in the upland River Wharfe, northern England. The distances moved during the study varied greatly between individuals (0–328 m). Movements were generally sporadic; crayfish would remain in one position for several weeks and make occasional movements to new locations. Total distances travelled, linear range and ranging area did not differ significantly between males and females. The distance travelled in upstream and downstream directions did not differ significantly and there was no correlation between distance travelled and crayfish size. Several high flow events occurred during the study, but these did not cause any mortality or apparent displacement of crayfish downstream, suggesting that this is not a significant factor in downstream dispersal or mortality of adults of this invasive crayfish species in winter. A marked reduction in large-scale movements occurred in mid-December which coincided with a decline in water temperature. There was a less distinct pattern in local activity which was strongly correlated with water temperature and varied before and after mid-December.

Introduction

In an ecological context, information about animal movements and activity is important in contributing to an understanding of habitat requirements, patterns of resource utilisation and the potential for interspecific interaction (Sutherland, 1996). Crayfish are large mobile invertebrates capable of making substantial active movements against water flows. This enhances their ability to utilise patchy resources and also to colonise new areas (Gherardi & Barbaresi, 2000). In rivers and streams, the ability to make active movements upstream may be important for recolonising areas that have been disturbed and depopulated (Lucas et al., 1998). Upstream movements of the crayfish *Orconectes nais* (Faxon) to depopulated areas have been recorded following floods (Momot, 1966). Equally, high flows may displace aquatic animals, including crayfish, resulting in flood-related mortality (Robinson et al., 2000) or, if such mortality is low, enhancing downstream dispersal. Active and passive movements may also be important in expanding the geographical range of introduced crayfish species.

The signal crayfish *Pacifastacus leniusculus* (Dana) is native to North America but has been widely introduced outside its natural range by man and now has a global distribution. It was introduced to Europe for aquacultural purposes from the 1960s onwards and, through escapes and deliberate introductions, is now established in the wild in most northern European countries (Lowery & Holdich, 1988; Holdich, 1999). Its presence has been responsible partially for the decline of native crayfish species in Europe, primarily through the transmission of crayfish plague to which European species are highly susceptible (Alderman et al., 1990), but also through interactions and replacement of native species (Holdich & Domaniewski, 1995; Söderbäck, 1995). *Pacifastacus leniusculus* is

highly invasive, with feral populations from escapes quickly becoming established and expanding.

An understanding of the spatial and temporal patterns of movements and activity of crayfish is relevant in predicting their expansion and colonisation ability. Investigations of the spatial behaviour of crayfish have predominantly been concerned with movements during the summer months when growth and mating occurs. Movements of *P. leniusculus* have been studied by mark-recapture techniques (Abrahamsson, 1981; Guan & Wiles, 1997; Kirjavainen & Westman, 1999). Several studies on other crayfish species have shown radio-telemetry to be a highly effective technique for studying the movements of adult crayfish in riverine systems (Schütze et al., 1999; Bohl, 1999; Robinson et al., 2000; Gherardi & Barbaresi, 2000). In this study we used radio-telemetry to investigate the movements and activity of *P. leniusculus* during late autumn and winter, and the effects that low temperatures and high flows may have on their behaviour, including the possibility of downstream dispersal and/or mortality of adults.

Methods

Study site

This study was centred upon a 1.2-km section of the upper River Wharfe, northern England (54° 04′ N 2° 00′ W), an eroding upland river (altitude 170 m). For most of the study area the river is approximately 30-m wide. In the study area the right-hand valley slope is generally steep and wooded, whilst the left hand valley slope tends to be less steep and consists mostly of grazed grassland. The channel shape is quite uniform and the distribution of flow across the river channel is relatively even. Within the river, the substratum varies from large boulders on exposed bedrock to silt. In several areas the bank is eroding and there are vertical muddy banks, some of which have been reinforced by facing them with large rocks, between which there are large crevices. The study site includes areas of riffle, glide and deeper water and is partially regulated by two weirs. The upper Wharfe flows for much of its length over limestone and as a result is rich in dissolved calcium carbonate (in the range 130–160 mg l^{-1}) and has a pH in the range 7.4–8.5. It has a 10-year mean daily flow of 18.5 m s^{-3} during winter (September–March). The upper valley's hydrology is dominated by surface water flow, as a result the river responds rapidly to rainfall.

Capture and tagging

Signal crayfish were captured using a technique similar to that of Thomas & Ingle (1971). Stones were moved aside from the bed of the river by hand and any large crayfish that were concealed beneath were collected. Twenty (10 male and 10 female) signal crayfish were tagged between 16 October and 10 November 2000. The carapace length (CL) of crayfish, from the rostral apex to the posterior median edge of the cephalothorax, was measured to the nearest 0.1 mm using vernier callipers. The wet mass of crayfish was recorded to the nearest 0.1 g using an electronic balance, crayfish were dried prior to weighing to remove excess water. Mean (± SD) CLs were 43.2 ± 4.7 mm for females and 49.8 ± 7.8 mm for males, and mean (± SD) wet mass was 29.9 ± 6.4 g for females and 47.6 ± 30.5 g for males (Table 1).

Radio transmitters (type PIP, powered by an Ag 392 battery; Biotrack, Wareham, UK) were used to track crayfish. Tags measured 17 × 8 × 6 mm, with a whip antenna length of c. 10 cm and were potted in dental acrylic. In order to maximise tag life, pulse length was limited to 15 ms, with a pulse period of 2.0 s, giving a predicted minimum life of 2.9 months, although achieved life was in excess of 4 months for 70% of tags. Frequencies between 173.700 and 173.910 MHz, with minimum spacing of 10 kHz were used to identify individual crayfish. The tag, slightly concave in shape on its lower surface, was attached to a chela with a combination of cyanoacrylate adhesive and dental acrylic. The chela was dried, then cyanoacrylate adhesive applied to attach the tag in position, and dental acrylic was used to fill crevices round the tag and provide a strong, robust means of attachment (based on Robinson et al., 2000). Care was taken to ensure that the joints on the chela were free from glue, and that full mobility of the chela was retained. Tagged crayfish were retained for ≈30 min until the acrylic was set. Care was taken to replace the crayfish as close as possible (<0.5 m) to the original location from which they were captured.

Tags were attached to the chela rather than cephalothorax, because it was felt that attachment to the cephalothorax would increase body depth and could influence the mobility of crayfish in refuges. Total tag mass was not more than 1.8 g, which represented 1.4–8.3% of body mass. This is a similar tag mass: body

Table 1. Details of radio-tagged crayfish (b, berried (egg-carrying) female)

Crayfish	Sex	Carapace length (mm)	Wet weight (g)	Date tagged	Duration of tracking (days)
A	F	32.9	32.9	16.10.00	128
B	F	40.1	26.9	20.10.00	124
C	F	43.4	25.7	20.10.00	124
D	F	43.6	28.0	10.11.00	102
E	F	43.7	24.9	17.10.00	13*
F	F	45.0	29.6	20.10.00	124
G	F-b	40.6	22.8	10.11.00	102
H	F-b	45.7	29.0	10.11.00	102
I	F-b	47.6	34.4	17.10.00	127
J	F-b	49.8	45.2	17.10.00	127
K	M	37.8	21.7	17.10.00	127
L	M	41.5	20.0	17.10.00	127
M	M	43.2	22.0	10.11.00	102
N	M	48.0	32.0	24.10.00	124
O	M	51.0	50.8	16.10.00	128
P	M	51.1	35.4	16.10.00	14*
Q	M	51.6	41.7	20.10.00	124
R	M	51.7	52.5	20.10.00	124
S	M	58.5	88.3	20.10.00	124
T	M	63.8	112.2	20.10.00	124

* Tag lost by crayfish.

mass ratio as in other telemetry studies of crayfish (Bohl, 1999; Schütze et al., 1999; Robinson et al., 2000; Gherardi & Barbaresi, 2000; McCreesh, 2000), none of which reported interference with behaviour or survival.

Tracking

Crayfish were tracked using a modified Yaesu FT290R receiver (Argus Electronics, Great Yarmouth, UK) and a collapsible three-element Yagi antenna. Crayfish were tracked during daylight hours once or twice a week, and 25 positional fixes were taken of all tagged animals between 16 October 2000 and 20 February 2001. These locations, therefore, represent daytime refuge sites but are indicative of long-term movements. On approximately 35% of occasions tracking continued into darkness, when the behaviour of several radio-tagged crayfish was followed. Although localised movements (usually <20 m) were observed in the early part of the study, there was no evidence that daytime monitoring of locations within refuges gave a false picture of 'long-distance' movements patterns.

Tagged crayfish could be recorded at a distance of 50–100 m with the Yagi antenna held at head height. By using a 0.1-m length of coaxial cable to reduce the gain on the signal, the linear location of the crayfish could be determined to within c. 2 m. By removing the antennna altogether, and reducing gain still further, location could be determined to c. 0.3 m, but on some occasions, due to water levels or tag location this was not possible. Signal strength from crayfish in riverbank burrows or crevices was lower than those under rocks on the river bed or in the open, and the positions of these were located to within c. 0.3 m using the 0.1 m coaxial antenna. The accuracy of the location was verified on several occasions. When crayfish were located their position was recorded with reference to riverside features which had been marked on a scale map of the area. Their position upstream or downstream of the release location was calculated. The position of the crayfish from the bank was also assessed when radio-tracking. The river was split into thirds and the location was recorded as either left bank, right bank or central channel.

The movements of crayfish and other animals in running waters are often described in terms of linear range in upstream and downstream directions from the release location (Black, 1963; Gherardi et al., 1998; Bohl, 1999). In order to compare between environments i.e. rivers of different widths, the ranging area of crayfish may be more useful. Previous studies have multiplied the linear range by the width of the river to give a ranging area (Guan & Wiles, 1997). We calculated the ranging area from the linear range and the amount of movement across the river. Linear range was multiplied by the distance crayfish moved across the river (crayfish which remained at one side $\times 10$ m, crayfish which moved into central channel $\times 20$ m and crayfish which moved from one side to the other $\times 30$ m).

Whilst crayfish are active to a limited extent during the day they are primarily nocturnal (Abrahamsson, 1981; Lozán, 2000; Robinson et al., 2000). Therefore in order to compare local activity, on a standardised basis, over the full period of study measurements were made over 4 h beginning 30 min after sunset. Local activity levels were monitored during 10-min time periods using changes in signal strength as an index of activity (Lucas & Batley, 1996; Robinson et al., 2000). Crayfish were classified as active (1+ changes) or inactive (0 changes) based on the number of variations in signal strength recorded. Changes in transmitter antenna orientation relative to the receiver antenna that occur due to movements of the whole animal or of the chelae, are responsible for observed variations in signal strength (Robinson et al., 2000). Thus these measurements reflect behaviour patterns such as feeding and aggressive interactions as well as locomotion. Tests with non-moving tags and resting crayfish during the day, further validated the applicability of these night-time local activity measurements. Local activity of between 7 and 18 individual tagged crayfish was monitored in each session (mean number of crayfish monitored per sesion 14.2). The percentage of crayfish that were active was calculated and compared with temperature.

Environmental measurements

Water temperature at the study site, was measured at 60 min intervals continuously throughout the study using Tinytalk temperature loggers (Orion Components, Chichester, U.K.). The flow in the upper Wharfe was recorded at Addingham Gauging Station, the nearest continuous gauging station to Grassington, 18-km downstream of the study site. Although this site was a significant distance downstream of the study area, there are no major tributaries between Grassington and Addingham and the pattern and magnitude of discharge are similar (D. Bubb unpubl. data). Daily flow data from Addingham are therefore felt to be appropriate for relating to the spatial behaviour of crayfish.

Results

Tag retention and survival

The radio-transmitters on two crayfish (E & P) are believed to have become detached from the crayfish (Table 1). Both transmitters travelled long distances downstream (>1 km) within two weeks of attachment and no activity was recorded after this large movement. In the case of E the transmitter was recovered, showing apparent failure at the point of attachment to chela. It was not possible to search for P as it was in deep water. The results from crayfish E and P are not considered in further analyses. No tags were lost through moulting which, in this population, occurs outwith the time period of the experiment (D. Bubb pers. obs.). All transmitters remained operational until the study was terminated. Survival of crayfish during the study period was high, and with the possible exception of P, all crayfish survived, based on observation of some tagged crayfish and recording of local activity and movements for all. Tag attachment did not appear to adversely affect survival or behaviour, crayfish were observed to take cover under rocks and boulders, within tree roots and in cavities and burrows within the bank.

Movements

Robinson et al. (2000) reported an apparent post-release 'fright response' in radio-tagged white-clawed crayfish *Austropotamobius pallipes* (Lereboullet), with the greatest movements in the 2 days following release. There was no evidence in this study of a similar response. The distance moved by crayfish during the first week did not differ significantly from that during the second week after tagging (Wilcoxon matched pairs test, $T = 28_{n=12}$, $P > 0.05$).

There was considerable variation in the distance moved by individual crayfish (Table 2). The maximum cumulative distance moved by any one crayfish was

Table 2. Cumulative distance moved by 18 radio-tracked *Pacifastacus leniusculus* (9 males, 9 females) in the River Wharfe during autumn and winter 2000/2001

	Median cumulative distance moved, m (25%,75% quartile)		
	All directions	Upstream	Downstream
All crayfish	44.5 (18.0, 114.0)	25.5 (5.0, 60.0)	18.0 (8.0, 60.0)
Males	99.0 (30.5, 129.5)	39.0 (0.0, 62.0)	45.0 (12.0, 72.5)
Females	36.0 (20.5, 126.0)	20.0 (11, 53.3)	18.0 (6.3, 78.0)

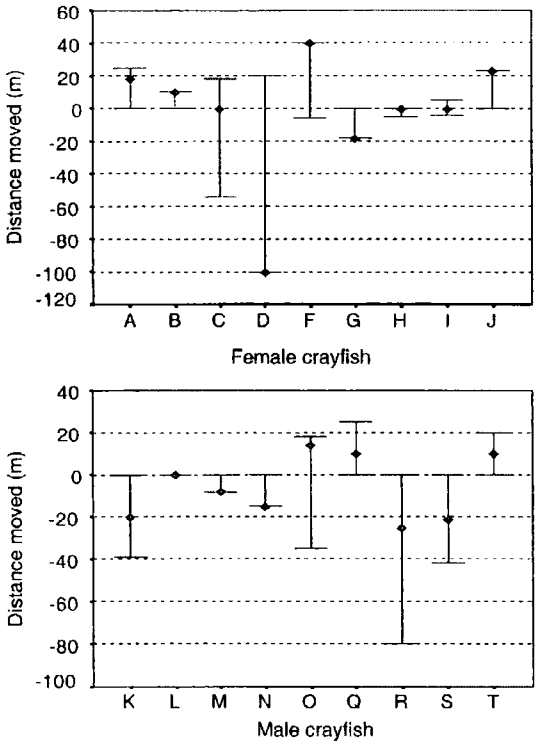

Figure 1. The upstream and downstream range of movement of 18 radio-tracked *Pacifastacus leniusculus* during autumn and winter 2000/01. Diamonds show the final position (20 February 2001) and attached bars represent maximum distance moved upstream (+) and downstream (−) by that individual. The release location of crayfish is represented by 0 m on the vertical axis.

328 m (crayfish C) and the minimum 0 m (crayfish L). Although males appeared to show an overall tendency for downstream movement (Fig. 1), the cumulative distance moved by crayfish in an upstream and downstream direction over the study period did not differ significantly for both sexes combined, males only or females only (Wilcoxon matched pairs tests; all crayfish, $T = 45_{n=14}$, $P > 0.05$; males only, $T = 9_{n=8}$, $P > 0.05$; females only, $T = 7.5_{n=6}$, $P > 0.05$). The distance moved by females and males was similar and did not differ significantly (Mann–Whitney $U = 39$, $P > 0.05$). Inspection of the data suggest that berried (egg-bearing) females moved less (median = 20.5 m, 25% quartile = 14 m, 75% quartile = 29.5 m) than other crayfish (median = 99.5 m, 25% quartile = 25 m, 75% quartile = 140 m). Whilst the difference was not significant (Mann–Whitney, $U = 12$, $P > 0.05$) this may be attributable to the small sample size of berried females ($n = 4$). Movements of crayfish were generally sporadic, crayfish would remain in one position for several weeks and make occasional movements to new locations.

Range

There was considerable variation in the linear range of radio-tracked crayfish (Fig. 1). The maximum range was 120 m (crayfish D) and the minimum 0 m (crayfish L). The linear range did not differ significantly between male and female crayfish (Mann–Whitney, $U = 41$, $P > 0.05$). The upstream range was less than the downstream range for all crayfish, males only and females only (Table 3), but this difference was not significant (Wilcoxon matched pairs; all crayfish, $T = 46_{n=17}$, $P > 0.05$; males only, $T = 9_{n=8}$, $P > 0.05$; females only, $T = 22_{n=9}$, $P > 0.05$).

In addition to the linear movement described above, several radio-tracked crayfish made movements across the river. Fifty percent of tagged crayfish made movements into the centre of the river (≈10–20 m) and 22% of crayfish moved to the opposite side (≈30 m) of the river to their release site. Using this information, the estimated ranging area for males was less than that of females (Table 3). However there was considerable variation in ranging area between individual crayfish (0–3600 m^2) and the difference between sexes was not significant (Mann–Whitney, $U = 38$, $P > 0.05$). Nor was there any difference between berried and non-berried females (Mann–Whitney, $U = 4.5$, $P > 0.05$) although sample sizes were small.

The size of crayfish did not appear to influence the amount of movement recorded. There was no significant correlation between size and the cumulative distance moved (Spearman Rank, $r_s = 0.16$, $P > 0.05$), linear range (Spearman Rank, $r_s = 0.193$, $P > 0.05$) and ranging area (Spearman Rank, $r_s = 0.121$, $P > 0.05$) with carapace length for all radio-tracked crayfish combined, although the size range

Table 3. Linear range of movements and the estimated ranging area of 18 radio-tracked *Pacifastacus leniusculus* (9 males, 9 females) in the river Wharfe during autumn and winter 2000/2001

	Median linear range, m (25%,75% quartile)			Median ranging area, m^2 (25%,75% quartile)
	All directions	Upstream	Downstream	Total area
All crayfish	23.8 (10.0, 46.0)	7.5 (0.0, 20.0)	7.0 (0.0, 39.0)	470 (180, 780)
Males	25.0 (11.5, 47.5)	0.0 (0.0, 19.0)	15 (0.0, 40.5)	450 (180, 765)
Females	23.0 (9.5, 59.0)	18.0 (2.5, 23.8)	5.0 (0.0, 36.0)	490 (140, 1180)

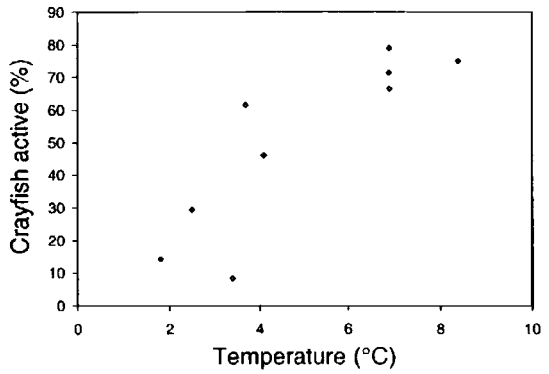

Figure 2. Relationship between the percentage of radio-tagged signal crayfish *Pacifastacus leniusculus* locally active at night and water temperature during autumn and winter 2000/01 ($R_S = 0.900$, $P < 0.01$).

was quite limited (males C.L. 37.8–63.8 mm, females C.L. 32.9–49.8 mm) and all were relatively large.

Activity

Analysis of the relationship between water temperature (range 1.8 – 8.4 °C) and the percentage of crayfish that were active showed a highly significant positive correlation (Spearman Rank, $r_S = 0.900$, $P < 0.01$). The percentage of crayfish recorded as active was lower at reduced temperatures, although even at very low temperatures (1.8–4 °C) a proportion of crayfish were recorded as active (Fig. 2).

Seasonal changes in movements

There was a large reduction in movement of crayfish from mid-December onwards (Fig. 3). Prior to this, the amount of movement during the tracking period was relatively constant. After mid-December, virtually no movement of crayfish was recorded and those movements that were recorded were relatively small. The reduction in movement occurred at the same time as a rapid and substantial decline in water temperature. Temperature before and after 15 December 2000 was significantly different (*t*-test, $t = 92.4$, $P < 0.001$). A mean (± SD) temperature of 7.9 ± 1.2 °C was recorded from 16 October to 15 December 2000 compared to a mean (± SD) of 4.2 ± 1.3 °C in the period from 16 December to 10 February. Despite very high flows throughout late October and early December 2000, as well as numerous other, smaller high-flow events during the study period there was no evidence of any crayfish being swept significant distances downstream by the high flows. It is possible that the transmitters E and P were swept downstream, attached to crayfish, but it is more likely that they became detached and were then swept downstream, since they were motionless in their new positions. There was no evidence that high flows caused any mortality of tagged crayfish.

Discussion

Radio telemetry provided a useful tool for studying the movement of crayfish in autumn and winter. It provided finer scale information on the movements of crayfish than can be achieved by mark-recapture techniques. In addition, the difficulties that are experienced in capturing sizeable numbers of crayfish during late autumn and winter (Abrahamsson, 1981; Matthews & Reynolds, 1995; Riggert et al., 1999) makes the use of mark-recapture to describe winter movements very limited.

The movements of crayfish described in this study were considerably less than those reported previously for *P. leniusculus* (Abrahamsson, 1981; Guan

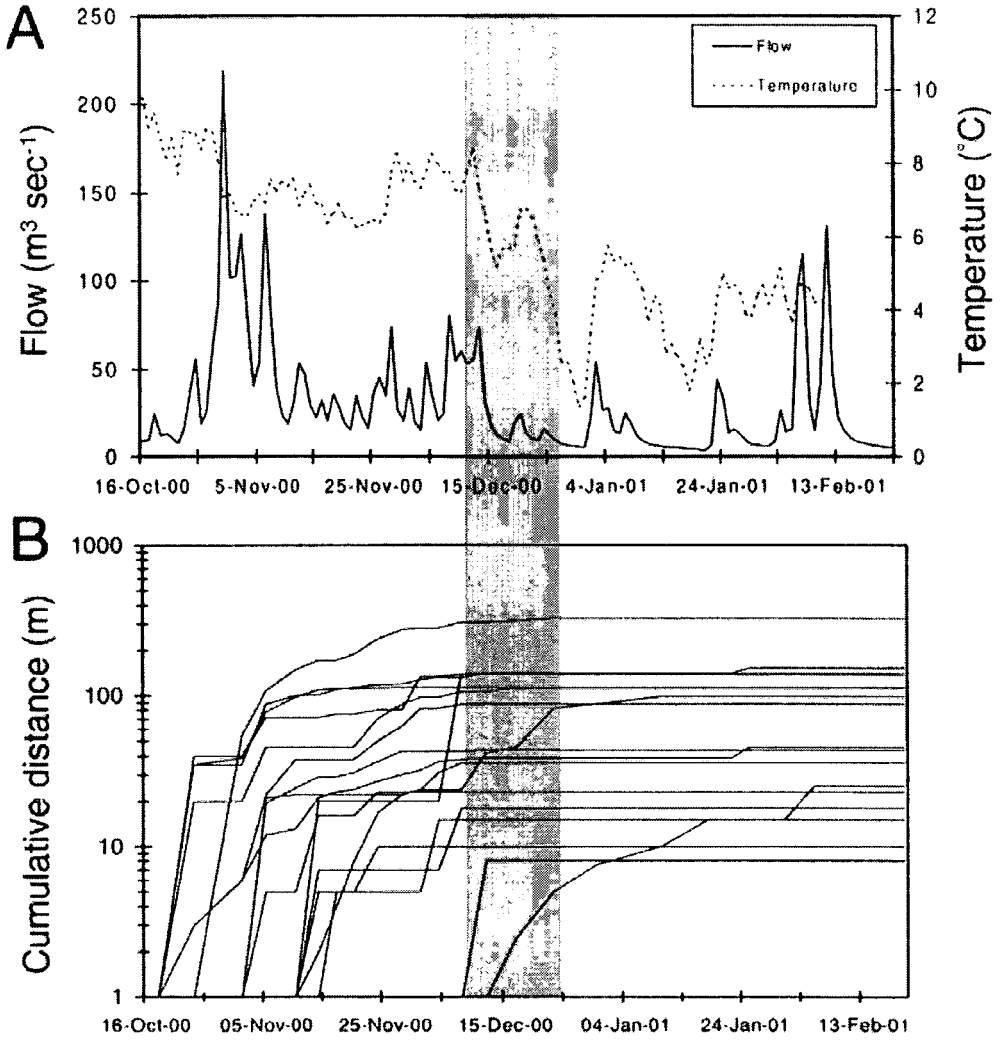

Figure 3. (A) Mean daily flow (16 October 2000–22 February 2001) and mean daily water temperature (16 October 2000–10 February 2001) in the upper River Wharfe. (B) Linear distance moved by 18 radio-tracked signal crayfish *Pacifastacus leniusculus*. All 0 readings have been transformed to 1. Grey bar indicates period in which decline in water temperature corresponded with decline in large scale movements of crayfish.

& Wiles, 1997; Kirjavainen & Westman, 1999) and other crayfish species (*Austropotamobius pallipes* – Robinson et al., 2000; McCreesh, 2000; *Astacus astacus* (Lereboullet) – Bohl, 1999; Schütze et al., 1999; *Procambarus clarkii* (Girard) – Gherardi & Barbaresi, 2000). However, these studies, were either restricted to the summer months or, encompassed an entire year. The lower temperatures experienced during this study may have contributed to a reduced amount of movement since these animals are ectotherms, and further studies at other periods throughout the year are required to define the full movement potential for this species. The activity pattern, of crayfish described in this study, in which movement phases are interspersed with stationary phases, appears to be consistent with that described in several other studies (Gherardi et al., 1998; Schütze et al., 1999; Robinson et al., 2000; McCreesh, 2000). However the lengths of the stationary periods in this study were greater.

Information concerning the movements of *Pacifastacus leniusculus* are of relevance to the expansion in range and colonisation of new areas. Peay & Ro-

gers (1999) estimated the downstream spread of the signal crayfish population in the River Wharfe to be occurring at a rate of 1.2 km year^{-1} (3.29 m day^{-1}) although the upstream colonisation has not been so rapid. The maximum distance moved by a crayfish during this study (328 m) equates to a movement of 2.65 m day^{-1}. Whilst the daily movement of crayfish reported in this study are less than the apparent rates for downstream colonisation of the river, this may be due to the study being conducted during winter when temperature and locomotion are reduced. In addition the movements of adult crayfish, which are capable of active locomotion against the flow, may be of greatest relevance to the upstream colonisation. Certainly it seems that high flows did not cause passive dispersal of adult crayfish as had been hypothesised. Downstream colonisation may be more strongly influenced by the movement of small crayfish, that are limited in their ability to actively move upstream. However, they may be passively transported downstream over considerable distances and could potentially be important in downstream colonisation as occurs for many other 'drifting' macroinvertebrates (Lancaster et al., 1996).

High discharges have been reported to cause downstream displacement (Momot, 1966; Parkyn, 2000) and mortality of crayfish (Robinson et al., 2000). During winter, discharge and river levels are generally high and in this study there were several periods of very high flow (Fig. 3). These appeared to have no effect on survival of crayfish, or have caused downstream displacement contrary to expectations. The effect of the substrate may be important in determining the effect of high flows, if crayfish can move between rocks, stones and other debris they may be able to avoid the effects of high flows.

This study showed two distinct temporal periods in the spatial behaviour of crayfish. In the period up to mid-December, crayfish were actively moving between refuge sites, although distances moved were relatively small. From mid-December onwards the degree of movement was greatly reduced. The period from mid-December onwards may equate to the 'winter torpor' reported by Brewis & Bowler (1982) in *Austropotamobius pallipes*. This reduction in movement occurred at the same time as a drop in the water temperature, which may have been responsible for the reduction in movements. Whilst large scale movements almost ceased from mid-December onwards, patterns in local activity were less clear. Local activity was strongly correlated with water temperature, with no distinction before and after mid-December.

Crayfish are generally considered to become inactive in temperate countries during winter due to low temperatures (Abrahamsson, 1981; Riggert et al., 1999). *Austropotamobius pallipes* has been reported to go into torpor for 30 weeks over winter in a population in northern England (Brewis & Bowler, 1982). Our results suggest that *P. leniusculus* may become inactive in terms of large scale movements, as would be reflected in trap catches but at very local scales they remain somewhat active. This local activity may allow crayfish to continue feeding as described by Guan & Wiles (1998) who found *Pacifastacus leniusculus* feeding during winter at temperatures of 4–6 °C. Localised feeding activity would be reliant on sufficient food being available at or near the refuge. Local activity of radio-tagged *P. leniusculus*, possibly related to feeding activity, would appear to reflect a linear temperature-mediated metabolic response over a temperature range of 1–8 °C whereas larger-scale movements between refuges appear to be mediated through behavioural inhibition of movement following the onset of winter conditions. The decline in local activity described in this study corresponds well with that described by Lozán (2000) in *P. leniusculus* held in the laboratory over the temperature range 4–20 °C. The decline in large scale movements may have the effect of reducing exposure of crayfish, with limited metabolic capacity for locomotion at low temperatures, to floods or predation. Both of these metabolic and behavioural responses could have some bearing on the ability of *P. leniusculus* to outcompete indigenous crayfish species in cold-temperate climates.

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APPLIED ISSUES

Movement and dispersal of the invasive signal crayfish *Pacifastacus leniusculus* in upland rivers

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SUMMARY

1. The American signal crayfish *Pacifastacus leniusculus*, an invasive species widely introduced throughout Europe, is a major threat to native European crayfish species and is causing increasing concern because of its wide impact on aquatic ecosystems.
2. Whilst various control and management methods have been proposed, very little is known about the factors influencing dispersal and movements of signal crayfish.
3. Sixty-four adult signal crayfish (carapace length 31.9–63.8 mm) were radiotagged in upland rivers in northern England, during four periods. Tracking was carried out at two sites, a low-density establishing population and a high-density established population. Tracking was carried out at both sites concurrently during midsummer (June to August 2002), during late summer (August to September 2001) at the low-density population site and during autumn to winter (October to February 2000/01) at the high-density population site.
4. Maximum movement occurred during midsummer. Temperature appeared to be a major factor influencing the timing and extent of movements between tracking periods.
5. The frequency distribution of the maximum distance moved upstream and downstream by radiotagged crayfish showed an inverse power relationship. The median maximal upstream and downstream distances moved were 13.5 m (range 0–283 m) and 15 m (range 0–417 m), respectively. There was a significant difference between the distributions of upstream and downstream ranges, with greater distances moved downstream.
6. All downstream movements made by crayfish appeared to be active movements and not the result of passive movement during periods of high discharge. There was no apparent influence of size, sex or density on the amount of movement recorded.
7. The study provides important information on the spatial and temporal behaviour of introduced crayfish in upland lotic systems. In contrast to lowland rivers, our results suggest that flow or gradient may influence the invasive potential of signal crayfish in an upstream direction in upland rivers.

Keywords: dispersal, invasive species, *Pacifastacus leniusculus*, telemetry

Introduction

The introduction and translocation of non-native aquatic species is widespread, occurring both deliberately and accidentally. In many parts of the world, non-native species are the first or second (after land use change) most important threat to freshwater biodiversity and ecosystem function (Lodge *et al.*, 2000). The impact of non-native species can be severe, altering ecosystems, causing the loss of native species, harming fisheries and having major economic consequences (Vitousek *et al.*, 1996). The distribution of

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many crayfish species has been highly modified during the 20th century (Taylor, 2002), because of the widespread translocations and introductions of non-native crayfish. The introduction of non-native species is at least partially responsible for an estimated one-third to one-half of the world's crayfish species being at risk of serious population decline or extinction (Taylor, 2002). In Europe the impact on native crayfish species has been particularly severe. Europe has only five native species of crayfish, all of which have been affected by the introduction of non-native species, and the native species are now considered to be threatened (Gherardi & Holdich, 1999).

In northern Europe, crayfish are the largest freshwater invertebrates and commonly dominate the biomass of benthic organisms (Momot, 1995). Because of their size, population density, polytrophic links and importance as prey species they are important trophic components of freshwater ecosystems (Lodge & Hill, 1994; Stenroth & Nyström, 2003) and can be considered as key-species in both lentic and lotic habitats (Hogger, 1988; Momot, 1995; Nyström, 2002). Their elimination or introduction can have substantial effects on the aquatic environment (Matthews & Reynolds, 1992; Nyström & Strand, 1996).

Of the non-native crayfish species that have been introduced into northern Europe, the most widespread species is the signal crayfish *Pacifastacus leniusculus* (Dana). Endemic to western North America, the signal crayfish has been introduced into over 20 countries in Europe since the 1960s (Holdich, 2002; Lewis, 2002). It carries crayfish plague (*Aphanomyces astaci* Schikora) to which it is resistant but which is lethal to European crayfish. The effects of crayfish plague combined with its competitive advantage have been partially responsible for the decline of European native crayfish species (Henttonen & Huner, 1999; Holdich, Rogers & Reynolds, 1999). The continued spread of signal crayfish within and between catchments is causing further losses of native stocks (Holdich, Rogers & Reader, 1995) and has the potential for substantial disruption of the river ecosystem (Guan & Wiles, 1997a; Nyström, 1999; Nyström, 2002; Statzner, Peltret & Tomanova, 2003).

Great Britain has only one native crayfish species, the white-clawed crayfish *Austropotamobius pallipes* (Lereboullet). It is regarded as being threatened nationally and, in common with much of Europe, the most substantial remaining populations occur in headwater river systems (Holdich *et al.*, 1995). Upland rivers in Northern England continue to hold significant populations of white-clawed crayfish although in some instances these are threatened by the expansion of populations of signal crayfish (Sibley, Brickland & Bywater, 2002). Little is known about the movement and range expansion of signal crayfish, especially in upland rivers.

Previous studies of movement and colonisation by signal crayfish have been predominantly concerned with populations in lakes and lowland rivers (Abrahamsson, 1981; Guan & Wiles, 1997b; Kirjavainen & Westman, 1999). Their movement behaviour under the more variable and rapidly changing conditions in upland rivers is mostly unreported, although the study of Light (2003) is an important recent exception. Most crayfish species, including signal crayfish, are large and mobile invertebrates capable of substantial active movements against flows. In rivers and streams the ability of crayfish to make active movements may be important for range expansion, especially upstream. Whilst they are capable of movements against flows, the impact of flood events may be important; upstream movements of the crayfish *Orconectes nais* (Faxon) to depopulated areas following floods has been recorded (Momot, 1966). High flows may contribute to downstream expansion of populations through passive movements, but may also cause flood-related mortality (Parkyn, 2000; Robinson, Thom & Lucas, 2000) and reductions in density (Light, 2003).

A thorough understanding of the spatial and temporal patterns of movement and dispersal of signal crayfish is relevant to understanding and predicting their colonisation abilities. Moreover such information for signal crayfish is valuable in the context of providing a model of the dispersal characteristics of a well-known invasive aquatic macro-invertebrate. The conservation value of populations of native crayfish within catchments that contain expanding populations of signal crayfish is dependent on the permeability of the intervening habitat to invasion. Any possible future control or management is reliant on information on the dispersal and movements of signal crayfish.

The aims of this study were to measure the extent of movements of adult signal crayfish at fine spatial and temporal scales in upland rivers, to establish their relationship with environmental conditions and to model dispersal behaviour. Two populations in

neighbouring rivers, the Wharfe and Ure, in northern England, were chosen for study. Both rivers have substantial populations of native crayfish that are threatened by the expansion of introduced signal crayfish populations. We hypothesised that movements recorded in an established high-density population (Wharfe) would be greater than within a colonising low-density population (Ure) because of an increased likelihood of density-dependent dispersal (Anholt, 1995).

Methods

Site histories

The sources of both riverine populations of signal crayfish used in this study are fishing lakes into which signal crayfish were deliberately introduced for the purposes of supplying the restaurant trade and the control of aquatic vegetation. Signal crayfish became established in these lakes and subsequently moved through the outflows of the lakes that are linked to the rivers Ure and Wharfe in North Yorkshire, northern England.

River Ure

Signal crayfish were introduced into the trout fishing lake adjacent to the River Ure in the late 1980s and were first recorded in the Ure in 1997. In 1988 they were recorded over a total linear range of 100 m in the area adjacent to the discharge pipes from the fishing lake. During the summers of 2001 and 2002, extensive survey work was carried out to determine the extent of the populations of signal crayfish (Bubb, Lucas & Johnson, 2002a; D. Bubb, unpubl. data). Areas of riverbed which provided suitable crayfish habitat (abundant stable refuges, low flow) and in which potential refuges could be effectively searched were identified by the same experienced surveyor (D.H.B.). Sites approximately 50 m apart, the exact location of which was dependent on the availability of suitable sites, were selected and hand-searched by experienced surveyors for 30 person-minutes per site (Thomas & Ingle, 1971). Crayfish were recorded a maximum of 184 m upstream and 824 m downstream from the site of introduction into the river. No white-clawed crayfish were recorded, although there are abundant populations further upstream (C. Johnson pers. comm.).

River Wharfe

Signal crayfish were introduced into trout fishing ponds adjacent to the River Wharfe in 1983 and had reached the main river by the late 1980s (Peay & Rogers, 1999). By 1997 they had spread downstream over a distance of 10.4 km (Peay & Rogers, 1999). In 2002, extensive survey work was carried out to determine the extent of the populations of signal crayfish (D. Bubb, unpubl. data). A general survey of the River Wharfe was carried out in a 40-km stretch of river around the introduction focus. More intensive sampling was conducted at the apparent limits of the populations to identify the leading edge of the population. Near the limits of the population, sites of suitable habitat (selection criteria as for Ure), 500 m apart, were hand searched by experienced surveyors for a total of 60 person-minutes per site to determine the extent of the population. In 2002, signal crayfish were recorded 3.8 km upstream and 22.9 km downstream from the source of introduction into the Wharfe. White-clawed crayfish were also recorded over the lower 11 km river-length of the zone inhabited by the signal crayfish population, as well as further downstream.

Study sites

The study was carried out on the rivers Wharfe and Ure, northern England. The rivers are broadly similar in character, both being eroding upland rivers, and they have adjacent upper catchments in the Yorkshire Dales. They flow for much of their length over limestone and as a result are rich in dissolved calcium carbonate. Fieldwork on the Wharfe was centred upon a 1.5 km section of river (54°04′N 2°00′W). Fieldwork on the Ure was centred on a 1 km section of river (54°11′N1°35′W). The rivers at both study areas are approximately 30 m wide. The Ure site is bordered for much of its length on both sides by deciduous woodland, whilst the Wharfe site is bordered on one side by woodland with pasture predominant on the other. At both sites the substratum varies from large boulders on exposed bedrock to silt, although at both sites cobble is the dominant substrate. Both sites include areas of riffle, glide and pools with deeper water. The Wharfe is partially regulated by a weir at the downstream end of the study site. The gradient of the two rivers is similar; the Ure (in the 4 km stretch

surrounding the introduction focus) has a gradient of approximately 1 : 430 and the upper Wharfe (over the current extent of signal crayfish population) has a gradient of approximately 1 : 270. Water velocities across the study sites are highly variable depending on the microhabitat, ranging during low flow conditions ($<Q_{25}$) from <0.05 ms^{-1} in pools to 0.88 ms^{-1} in riffles, and during high flow conditions ($>Q_{75}$) velocities >1.5 ms^{-1} were recorded (all velocities measured 5 cm from riverbed).

Both study sites contained only signal crayfish. The Wharfe site was 5 km downstream from the site of introduction of signal crayfish. The population is well established, with signal crayfish having been present for over 10 years. Quantitative surveys in 2002 at this site using modified Surber sample quadrats (0.49 m^2) estimated the density to be approximately 20 signal crayfish/m^2 for all age groups combined (D. Bubb, unpubl. data). The Ure site was the area surrounding the discharge pipes from the fishing lake. Densities of signal crayfish there were much lower than at the Wharfe site and although no absolute density estimates were carried out, standardised-effort searches using identical methodology carried out at both sites suggest the Ure signal crayfish densities are between 5 and 10% of those recorded at the Wharfe site.

Environmental measurements

Water temperature at the study sites was measured at 60 min intervals during the study period using Tinytalk temperature loggers (Gemini Data Loggers, Chichester, U.K.). The flows during study periods in the Upper Wharfe and Ure were measured at Addingham and Kilgram gauging stations, respectively. Although the gauging stations are several kilometers downstream from the study sites the pattern of discharge between the study sites and gauging weirs are very similar (D. Bubb, unpubl. data).

Capture and radiotagging

Crayfish were caught by hand-searching in accessible areas of the river. The carapace length (CL) of crayfish, from the rostral apex to the posterior median edge of the cephalothorax, was measured to the nearest 0.1 mm using vernier callipers. The wet mass of crayfish was measured to the nearest 0.1 g using an electronic balance. Excess water was removed from crayfish prior to weighing.

Radio-transmitters (type PIP powered by an Ag 392 battery; Biotrack, Wareham, U.K.) were used to track crayfish. Tags measured 17 × 8× 6 mm, with a whip antenna length of *c.* 10 cm and were potted in dental acrylic. Frequencies between 173.700 and 173.950 MHz, with a nominal spacing of 10 kHz were used to identify individual crayfish. The radiotags had a lifespan of over three months. Each tag was attached to a chela using a combination of cyanoacrylate adhesive and dental acrylic (see Bubb, Lucas & Thom, 2002b for further details). Crayfish were retained for about 30 min until the acrylic was set. Care was taken to return crayfish as close as possible (<0.5 m) to the capture location. Total tag mass was not more than 1.8 g, which represented 1.4–9.8% of body mass. This is a similar tag mass : body mass ratio as in other telemetry studies of crayfish (Bohl, 1999; Schütze, Stein & Born, 1999; Gherardi & Barbaresi, 2000; McCreesh, 2000; Robinson *et al.*, 2000) none of which reported interference with behaviour or survival.

Tracking

Radio-telemetry data collection was separated into four site-season specific component studies: (i) River Wharfe, winter 2000/01, (ii) River Ure summer to autumn 2001, (iii) River Ure summer 2002 and (iv) River Wharfe summer 2002. The details and number of crayfish tagged in each period are given in Table 1.

Crayfish were tracked using a modified Yaesu FT290R receiver (Argus Electronics, Great Yarmouth, U.K.) or Mariner M57 receiver (Mariner Radar, Lowerstoft, U.K.) both with a collapsible three-element Yagi antenna. During tracking on the Ure and Wharfe in 2002 the positions of crayfish were recorded every other day. On the Ure in 2001 intensive tracking every other day was carried out during September and less frequently, usually twice a week, in August and October. During the winter tracking in the Wharfe, crayfish were usually tracked once or twice a week. All tracking was carried out during daylight hours; locations therefore represent daytime refuge sites but are indicative of long-term movements. This was confirmed by periodic night-time visits.

When water levels permitted entry to the river (>75% of the time) the positions of radiotagged

Table 1 Details of crayfish tagged during the four periods of radiotagging

		Number tagged	Number successfully tracked (M : F)	Track duration* (days) mean (SD)	Carapace length* (mm) mean (SD)	Mass* (g) mean (SD)
Wharfe 2000/01	October to February	20	18 (9 : 9)	120 (10.4)	45.7 (6.9)	36.9 (21.8)
Ure 2001	August to September	15	15 (3 : 12)	32.9 (7.7)	42.8 (5.3)	32.8 (8.5)
Ure 2002	June to August	14	12 (5 : 7)	29.3 (7.24)	34.7 (17.9)	48.1 (8.1)
Wharfe 2002	June to August	21	19 (9 : 10)	47.3 (21.4)	44.1 (3.6)	28.0 (6.5)

*of individuals successfully (>21 days) tracked.

crayfish could be located to within 1 m. The accuracy of location was reduced to within 5 m when the position of crayfish was assessed from the bank. When crayfish were located their positions were recorded with reference to riverside features that had been marked on a scale map of the area. Their position upstream or downstream of the release location was calculated. Not all crayfish tagged were successfully tracked. During the study on the Wharfe in winter 2000/01, the radiotags on two crayfish are believed to have become detached soon after tagging (<14 days). During fieldwork in summer 2002 two crayfish each at the Wharfe and Ure sites moulted soon after tagging (<10 days) and so lost their radio-transmitters. The results from these crayfish are not included in the analysis. All remaining crayfish were tracked for more than 3 weeks (Table 1).

Methodological rationale and data analysis

All measurements concerning movements and dispersal of signal crayfish at study sites on the Wharfe and Ure were made by radio-telemetry. Although limited to the study of adult crayfish, this method has the capacity to provide data on the movement patterns of animals on a fine spatial and temporal scale. Moreover it can provide such data where the likelihood of recapture of marked individuals is very low, so it is highly appropriate for the study of movements during winter and in expanding low-density populations, such as at the Ure site.

For each radiotracked crayfish, the total linear range was calculated. This is the difference between the maximum distance upstream and downstream recorded throughout the period a crayfish was tracked. Linear range was correlated with the duration that crayfish were tracked for (Spearman rank correlation, $r_s = 0.342$, $P < 0.05$). Therefore, for comparisons of relative movement between individuals tracked over different durations, the range was divided by the number of days the crayfish was tracked for (range per day tracked). This variable has been used in analyses reported here. During the winter 2000/01 tracking period, previous analysis (Bubb *et al.*, 2002b) had shown two distinct periods of movement. Prior to mid-December a relatively constant amount of movement had been recorded, followed by a substantial decline in movement associated with a rapid decline in water temperature. These two distinct periods are used separately in further analysis of seasonal changes in movement. Because of the differing frequency of positional fixes obtained between some parts of the seasonal study components, calculations of movement per day have been restricted to those periods when fixes were obtained every other day.

Many studies have sought regression equations that best describe the distributions of dispersal distances (e.g. Kot, Lewis & van den Driessche, 1996). Inverse-power functions are commonly used to model the shape of the curve describing the distance moved by marked individuals (Hill, Thomas & Lewis, 1996; Elliott, 2003). The frequency distribution of movements and dispersal recorded in this study showed a typical inverse-power shape, we therefore used an inverse-power function to describe the movements made and dispersal of individuals. In the context of lotic environments, dispersal is essentially bi-directional, upstream or downstream, but the factors (especially flow) influencing directional movement make separate comparison of the direction of dispersal a sensible approach. In the analysis of movements and dispersal data we fitted separate models to the upstream and downstream components. Data were linearly transformed using a double-ln plot, analysed using regression analysis and the upstream and downstream regression lines compared. The upstream and downstream range of tagged animals was used to provide a measure of the dispersal potential of the

tagged crayfish, and to allow comparison of upstream and downstream dispersal. The analysis of ranges includes data from both rivers and all seasons. The relatively small number of crayfish tagged during each seasonal component necessitated this, although when conducting concurrent tracking on both rivers no differences in spatial behaviour were observed (see results). The integration of these data provided a realistic data set of the dispersal opportunities occurring during different environmental conditions over the annual cycle. Whilst the comparison of upstream and downstream ranges may include crayfish tracked for differing durations, at different seasons and sites, it is considered appropriate as each radiotagged crayfish provides a paired sample of an upstream range and a downstream range.

Results

Site and seasonal differences

There were significant differences between the amount of movement recorded in the different tracking periods (Kruskal–Wallis, $K_4 = 41.6$, $P < 0.001$). Maximum movements were recorded during midsummer (July to August) with a decline in recorded movements during late summer (August to September) and further declines in early and late winter (Fig. 1). Comparing the two radiotracking sessions carried out concurrently on the Wharfe and Ure in summer 2002, there was no significant difference in either the daily distance moved (Mann–Whitney *U*-test, $U = 109$, $P > 0.05$) or range per day tracked ($U = 97$, $P > 0.05$). Hence, there seemed to be no clear difference in the spatial strategies of adult signal crayfish during summer from the developing low-density population (Ure) and the established high-density population (Wharfe).

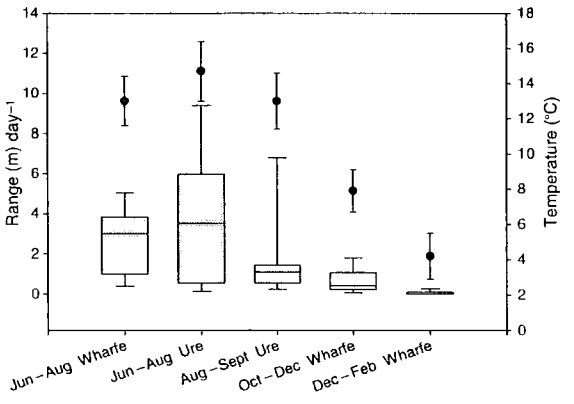

Fig. 1 Comparative ranges and temperature during radiotracking periods. Box plots represent range per day tracked, the 10th, 25th, 50th, 75th and 90th percentiles are shown. Circles represent mean temperature (±SD) during tracking period.

Movements

In all tracking periods there was a large variation between individuals in the amount of movement recorded (Fig. 2). The maximum distance moved by any one crayfish was 790 m and the minimum was 0 m during total tracking periods of 74 and 127 days, respectively. In all periods of radiotracking a similar pattern of movements was observed; crayfish would usually remain in the same location for days to weeks, followed by movement to a new location associated with a refuge. No tagged crayfish returned to a refuge they had previously occupied after they had moved to a different refuge.

Because of the potential differing effects of sex on movements at different periods of the year (i.e. moulting, mating, carrying eggs), the effect of sex was analysed separately in each tracking period. In all periods there was no difference between the amount of movement (range per day tracked) and sex (Mann–Whitney *U*-test, all $P > 0.05$), however the number of animals in each tracking period was low so the analysis may lack power with respect to sex differences. There was no significant relationship between size and amount of movement (range per day tracked) recorded (ANOVA, $P > 0.05$), although the size range

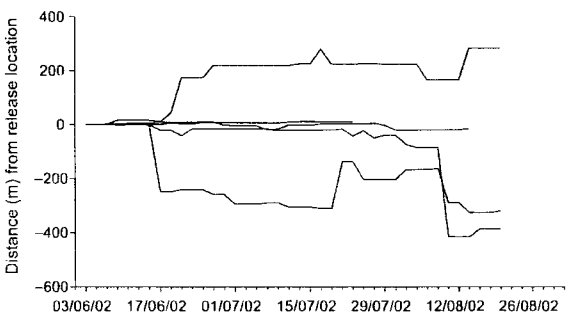

Fig. 2 Example plot of movements of five radiotagged signal crayfish in the River Wharfe, summer 2002, chosen to demonstrate the range of movements recorded. Positive values refer to locations upstream and negative values refer to locations downstream from release location.

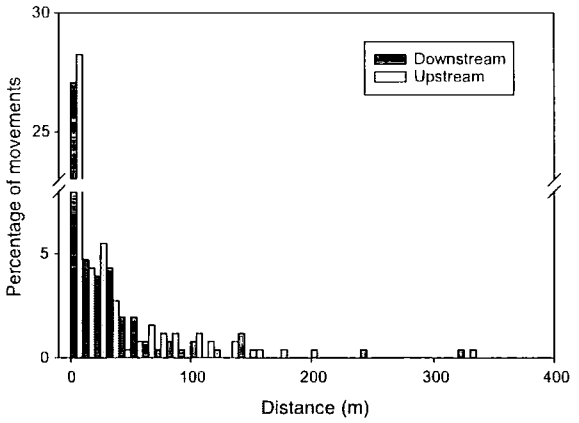

Fig. 3 Frequency distribution of all upstream (n = 126) and downstream (n = 129) movements made by signal crayfish between tracking sessions (every 2 days), all tracking sessions combined.

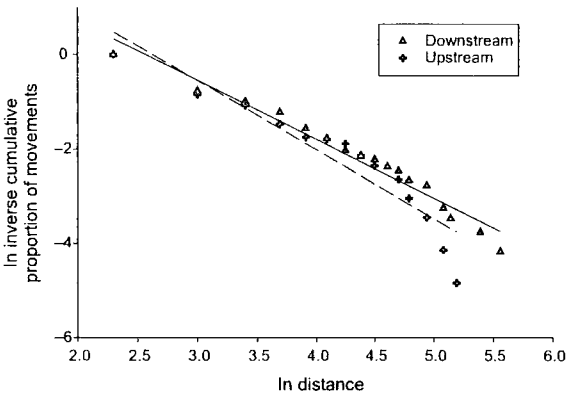

Fig. 4 Double ln plot of inverse cumulative proportion of movements in upstream and downstream directions of signal crayfish plotted separately. The solid line shows the power function of downstream movements and the dashed line the power function of upstream movements.

of radiotagged crayfish was quite limited and all were relatively large.

The analysis of individual movements considered only those periods of radiotracking in which positional fixes were taken every 2 days. Most crayfish (59.8%) remained in the same position between consecutive fixes. The median distance moved (per 2 days) in an upstream direction was 7.5 m and 7.0 m in a downstream direction. There was no significant difference in the number of movements recorded upstream (126) and downstream (129) (Mann–Whitney U-test, $P > 0.05$). The frequency distributions of movements in upstream and downstream directions (Fig. 3) were described by inverse-power models. Using the data from Fig. 3, the inverse cumulative proportion of movements over certain distances upstream were fitted to a inverse-power function where the probability of a movement M having a distance of D (m) was given by:

$$M = CD^{-n}$$

where C and n are scaling constants. ln M was regressed upon ln$D$. $R^2 = 0.867$, $F_{1,12} = 85.8$, $P < 0.001$) (Fig. 4) to produce the equation:

$$\ln M = 3.845(\text{SE} = 0.670) - 1.464(\text{SE} = 0.158) \ln D$$

The same procedure was carried out for downstream movements ($R^2 = 0.957$, $F_{1,16} = 383.7$, $P < 0.001$)

$$\ln M = 3.161(\text{SE} = 0.281) - 1.236(\text{SE} = 0.63) \ln D$$

There was no significant difference between the gradient of the two regression lines ($t_{28} = 0.351$, $P > 0.05$) (Fig. 4).

Dispersal

The upstream and downstream range of a crayfish is defined as the maximum distance moved upstream and downstream from the release location. This was used to provide a measurement of the dispersal potential of the tagged crayfish. The upstream and downstream ranges of all crayfish are given in Fig. 5. Using the data from Fig. 5, the inverse cumulative proportion of individuals ranging over certain distances upstream were fitted to an inverse-power function where the probability of an individual (I) having a range R (m) is given by:

$$I = CR^{-n}$$

where C and n are scaling constants. Ln I was regressed upon ln$R$. $R^2 = 0.895$, $F_{1,9} = 86.23$, $P < 0.001$) (Fig. 6) to produce the equation:

$$\ln I = 2.108(\text{SE} = 0.469) - 1.015(\text{SE} = 0.109) \ln R$$

The same procedure was carried out for downstream ranges ($R^2 = 0.858$, $F_{1,15} = 97.93$, $P < 0.001$)

$$\ln I = 1.662(\text{SE} = 0.371) - 0.786(\text{SE} = 0.079) \ln R$$

There was a significant difference between the two regression lines ($t_{22} = 12.65$, $P < 0.01$), with the upstream ranges having a steeper gradient than the

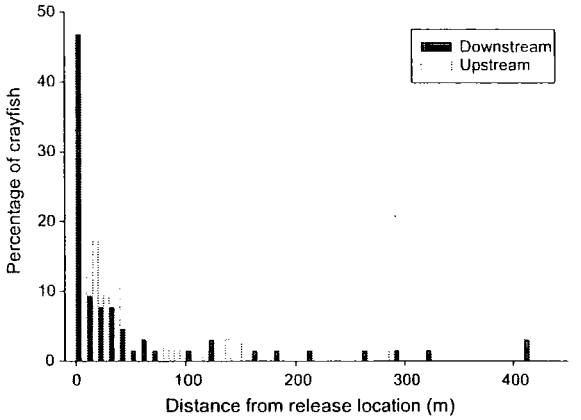

Fig. 5 Frequency distribution of upstream and downstream ranges of radiotracked signal crayfish. Values of maximum distance upstream and downstream of all radiotracked crayfish (n = 64) shown.

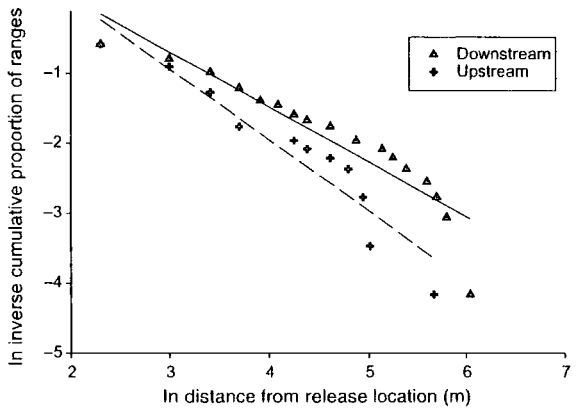

Fig. 6 Double ln plot of inverse cumulative proportions of paired upstream and downstream ranges of radiotagged signal crayfish (n = 64). The solid line shows the fitted power function of downstream ranges and the dashed line the power function of the upstream ranges.

downstream ranges (Fig. 6). The difference in distribution appears to be strongly influenced by the longer tail in the downstream ranges with a much greater tendency for large ranges to be in a downstream direction.

Environmental factors

With all crayfish in all tracking periods combined, there was a significant positive relationship between mean water temperature and range per day tracked (r^2 = 0.24, P < 0.001) (Fig. 7). The influence of environmental factors on movements within the two

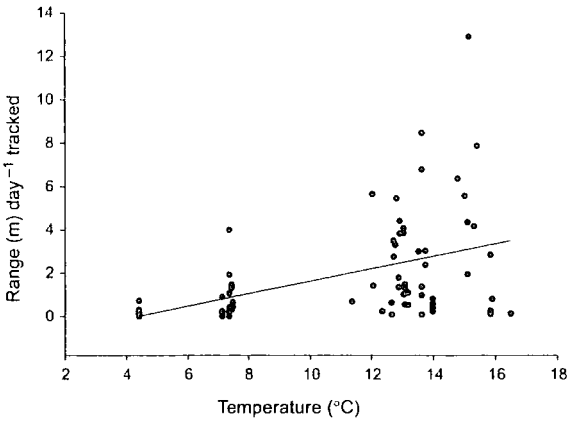

Fig. 7 Plot of range per day tracked of 64 radiotagged signal crayfish and temperature. Regression line r^2 = 0.24, P < 0.001.

midsummer 2002 tracking sessions on the Ure and Wharfe that were conducted concurrently was also considered. The proportion of crayfish moving between tracking sessions (2 days) was calculated for the Wharfe and Ure combined, and the mean temperature and flow of the two rivers calculated. The flow of the two rivers was highly correlated (flow R_s = 0.948, P < 0.001) as was temperature (temperature R_s = 0.746, P < 0.001), both displaying very similar patterns, although during the summer period the Ure was an average of 1.7 °C warmer. Fixing the effect of temperature, Kendall's test of partial rank correlation between proportion (arcsine transformed) of crayfish moving and flow was negative and significant ($\tau_{\text{movement, flow | temperature}}$ = −0.261, P < 0.05). The partial correlation of movement and temperature, fixing the effect of flow, was not significant ($\tau_{\text{movement, temperature | flow}}$ = 0.126, P > 0.05). During periods of high flow there was an apparent reduction in the number of crayfish moving (Fig. 8). There were no large movements >20 m during periods of high flow during any of the tracking periods.

Discussion

The comparatively slow upstream colonisation recorded in these two upland rivers, coupled with the bias downstream in the direction of dispersal of radiotagged signal crayfish, suggest that gradient or flow conditions may be influencing the invasive potential of signal crayfish in an upstream direction in the Ure and Wharfe. The observed bias towards downstream

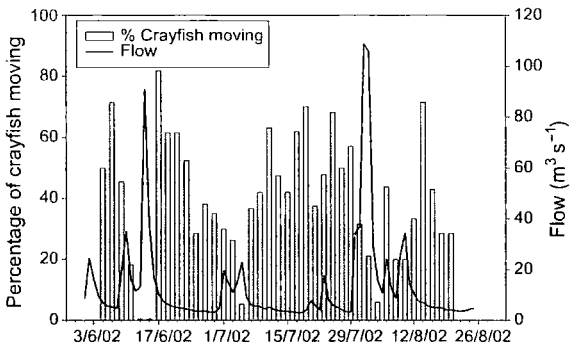

Fig. 8 Plot of proportion of radiotagged crayfish moving and river discharge. Data for proportion of crayfish moving is combined Wharfe and Ure, summer 2002. Discharge data is from Wharfe, information on Ure discharge is not given because of very high correlation ($R_s = 0.948$, $P < 0.001$) with Wharfe.

colonisation in the two upland rivers reported here (upstream : downstream ratio of distance colonised from focus of introduction; River Wharfe 1 : 6.0, River Ure 1 : 4.5), contrasts with records from lowland rivers. Guan & Wiles (1999) reported that the expansion of a signal crayfish population in the River Great Ouse in eastern England was only weakly biased in a downstream direction (4.3 km upstream : 5.8 km downstream from the focus of introduction). A similar pattern of weak bias towards downstream colonisation was reported in the River Bain (eastern England), with 3.5 km upstream and 4.5 km downstream colonised from the focus of introduction (Holdich *et al.*, 1995). The gradient of the Great Ouse is less than half that of the Ure and Wharfe (Great Ouse 1 : 850, Ure 1 : 430, Wharfe 1 : 270). The higher gradient of upland rivers is associated with an increased number of riffles and falls, which whilst not forming an absolute barrier to signal crayfish may have a reduced permeability to movements contributing to the observed reduced upstream expansion. Higher gradient is also associated with higher mean water velocity.

Whilst the frequency distribution of upstream and downstream ranges for adult signal crayfish obtained in this study might not reflect the true annual distribution of ranges, and was formed by pooling data from the different sites at different periods of the year, it is believed to be representative of the dispersal response in signal crayfish in these rivers and does demonstrate the differing distribution of upstream and downstream ranges. The fact that there was no significant difference in movements between the Ure and Wharfe in 2002 supports this approach, as does the similarity in flow and temperature characteristics of the two rivers. Most crayfish remain relatively close to the release location but a few individuals make longer movements. The importance of the differing shapes of the regression curves can be seen from substituting values into the power function. If a range of 1.5 km is substituted into the downstream and upstream power functions probabilities of one in 60 and one in 200, respectively, of an animal achieving that distance are obtained. This example serves to demonstrate the differences between upstream and downstream ranges with respect to the prediction of long distance colonisation, but care should be taken in extrapolating beyond the range of recorded values.

Both the Wharfe and Ure have fluctuating discharge patterns; the rivers respond rapidly to rainfall. High discharges and their associated high water velocities have been reported to cause downstream displacement (Momot, 1966; Parkyn, 2000; Robinson *et al.*, 2000), mortality of crayfish (Robinson *et al.*, 2000; Royo, Gonzalez-Cienfuegos & Muzquiz, 2002) and significant winter or spring spates have been linked to declines in density (Light, 2003). The information from this study suggests that high flows do not have a significant impact on the survival or cause downstream movement of signal crayfish. The results from both the winter (Bubb *et al.*, 2002b) and summer tracking suggest that during periods of high discharge adult crayfish are able to remain in refuges, protected from the high flows. Passive dispersal of adult signal crayfish downstream during high flows would not appear to occur frequently and does not form a major factor in their dispersal.

The information gained from radiotracking adult crayfish suggests that movement of adults has the potential to be responsible for the observed rates of population expansion. The average rate of population expansion on the Wharfe (1987–2002) was approximately 1.5 km $year^{-1}$ (4.1 m day^{-1}) recorded in a downstream direction. The maximum rate of downstream range expansion recorded during this study was 13 m day^{-1}. Although this level of movement occurred during summer only, it would require range expansion of 13 m day^{-1} during four summer months only to equate to yearly movements of 1.5 km.

Although the movements of adult crayfish could account for the observed rates of downstream expansion, the importance of juveniles and smaller size

classes to downstream dispersal is poorly understood. Radio-telemetry is currently limited to tagging large adult crayfish (>35 mm C.L.). Mark-recapture methods involving branding (>16 mm C.L.) and passive integrated transponder remote detection studies (>25 mm C.L.) can mark and provide spatial information on smaller individuals (Abrahamsson, 1965; Bubb *et al.*, 2002c; Light, 2003) but this still does not include 0–1 age class crayfish. Although the smallest age class is unlikely to be capable of making substantial active movements they could be passively transported downstream. The passive downstream drift of many macro-invertebrates contributes to their species' dispersal ability (Bilton, Freeland & Okamura, 2001). It may be that the downstream movements of juvenile crayfish especially during periods of high discharge may form a significant component of the downstream dispersal of signal crayfish populations.

The densities of crayfish at the Ure and Wharfe sites differed greatly. However, there was no significant difference in the amount of movement recorded at the two sites. Refuges and food may be a limiting factor in crayfish populations and competition can be severe (Lodge & Hill, 1994). It was hypothesised that the higher densities of crayfish at the Wharfe site may result in greater competition for refuges and food that would cause greater dispersal. As size is one of the major factors affecting dominance (Vorburger & Ribi, 1999) the tagging of only large adult crayfish may have been why this effect was not observed in the results. The effect of competition may be greater on smaller, less dominant age classes.

Both size and sex did not appear to influence the amount of movement recorded. The lack of a relationship between size and movement may reflect the relatively small size range of radiotagged crayfish, as all tagged animals were relatively large mature adults. The pattern from mark-recapture studies involving a greater range of sizes of signal crayfish is unclear, with Light (2003) reporting larger crayfish moving greater distances whilst Guan & Wiles (1997b) reported no difference in movement with size. Very large movements of males in reproductive condition have been described in red swamp crayfish *Procambarus clarkii* (Gherardi & Barbaresi, 2000). Although our sample sizes were small, there was no apparent difference in the movement patterns of males and females, including during the period when mating occurred (September). Mark–recapture studies have also not demonstrated a sex difference in movements of signal crayfish in river (Guan & Wiles, 1997b) and lake (Kirjavainen & Westman, 1999) populations. However, in a high gradient stream, Light (2003) found larger female signal crayfish tended to move upstream early in the summer and move downstream later in the summer, while there was no particular trend for male crayfish.

Previous studies have shown that there is a strong correlation of activity of crayfish with water temperature (Flint & Goldman, 1975; Lozán, 2000; Barbaresi & Gherardi, 2001; Bubb *et al.*, 2002b). This study demonstrated that movements are also correlated with temperature. Temperature between tracking periods appeared to influence the amount of movement recorded. This relationship was as might be expected in an aquatic ectotherm, and suggests that in temperate climates maximum dispersal and expansion of populations will occur during midsummer when water temperatures reach a maximum.

The pattern of movement of individual crayfish is similar to that recorded in previous studies on other crayfish species (Gherardi, Barbaresi & Villanelli, 1998; Schütze *et al.*, 1999; McCreesh, 2000; Robinson *et al.*, 2000). Crayfish would remain at one refuge for several days to weeks and then make a movement to a different refuge. Once a crayfish had moved from one daytime refuge to another there was no evidence of subsequent return to previously occupied refuge. The occupation of a single refuge for several days or weeks does suggests that signal crayfish may maintain an 'ephemeral home range' (Robinson *et al.*, 2000) during this stationary phase. However the lack of return to any previously occupied refuges and increasing range size with duration tracked suggests the maintenance of a home range is limited at least in the longer term.

This research suggests that while colonisation by signal crayfish in upland rivers is likely to be rapid in a downstream direction, natural colonisation towards headwater tributaries may be much slower. This means that conservation efforts directed towards native crayfish in upriver areas in such rivers may be worthwhile. Nevertheless, more information is undoubtedly needed on the ability of invasive crayfishes to traverse, in an upstream direction, potential natural barriers such as high-velocity rapids and waterfalls, as well as anthropogenic structures such as weirs of varying height and shape and fishways. It is also possible that the greatest factor influencing

upstream colonisation by exotic crayfish in upland rivers may be from human introduction, intentional or unintentional, at new foci upstream, rather than by natural upstream dispersal.

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