

A holistic assessment of the invasion
of signal crayfish (*Pascifastacus
leniusculus*) in Great Britain:
Understanding the invasion of signal
crayfish through their distribution,
variations in traits across their
invasion continuum and the attitudes
of key stakeholders.

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Abstract

Invasive non-native species (INNS) are one the biggest threats to global biodiversity. In Great Britain (GB), signal crayfish (*Pacifastacus leniusculus*) is a particularly problematic INNS. As well as numerous economic, environmental, and social impacts, signal crayfish are believed to be the leading cause behind the decline of white-clawed crayfish (*Austropotamobius pallipes*), the only native crayfish species in GB. Whilst one of the most studied case studies of an INNS in GB, there are still many unanswered questions when it comes to its invasion. There are still important questions around the current state of signal and white-clawed crayfish in GB, the level of variability in the traits of the INNS, and the attitudes of stakeholders towards the whole situation. This thesis aimed to address these questions through three separate but related research chapters spanning these topics.

In Chapter 3, we used observational data from a range of different sources, including citizen science, to map out the current and historic distribution of signal crayfish and white-clawed crayfish in GB. The chapter also used a variety of different datasets (climatic, water quality, land-use etc.) to understand the environmental tolerance of each crayfish species. For Chapter 4, we tested whether there is a difference in morphological and behavioural traits in signal crayfish between sites that they have recently (<5 years) invaded (invasion-front) and those that they have colonized for a longer (>15 years) period (invasion-core). The chapter used established assays to test for these traits in the signal crayfish that are caught in each area. Finally, for Chapter 5, we conducted semi-structured interviews and a small exercise with relevant stakeholders to compare their attitudes towards different aspects of the invasion of signal crayfish in GB. we used thematic analysis to analyse the interviews and establish the prominent themes that mattered most to the stakeholders.

In Chapter 3, we see that the pattern of signal crayfish advances and white-clawed crayfish retreat is still taking place. We identify that signal

crayfish are actively advancing in the areas that contain the remaining populations of white-clawed crayfish (northern England and Wales). Through the principal component analysis (PCA) of factors, we see that the environmental space that signal crayfish have been observed is narrowly wider than that for white-clawed crayfish, with generally similar patterns between the two species. In Chapter 4, we find that signal crayfish at invasion-front sites are significantly smaller than those found at invasion-core sites. As well as seeing that the location along the invasion continuum has a significant impact on some traits, we also see that the river that signal crayfish are found in influences their morphological and behavioural traits. In Chapter 5, we see that the stakeholders tended to agree on certain topics but had different attitudes on others. For example, those stakeholders in larger organisations/government bodies tended to believe that we should limit anthropogenic interactions with signal crayfish (as they believe this was a major driver of their spread), whereas those in smaller/more local organisations felt that individual organisations should have more freedom when it comes to how they manage/interact with the INNS.

The findings of this thesis demonstrate that signal crayfish are a dangerous INNS that can rapidly colonize a large much of GB due to its wide environmental tolerance and variability with its population. Likewise, throughout all the chapters, it is clear the decisions made by humans have had a strong influence on this invasion. From the initial decision to introduce the species, the slow response by policymakers, those who perceive that the economic benefit of signal crayfish still outweighs the dangers it poses and transport them to new areas or the lack of political will to create effective management solutions. It may be too late to effectively manage signal crayfish to protect the white-clawed crayfish in GB, but we must learn from our mistakes so that we can effectively manage the future INNS that pose a threat.

Visual Abstract

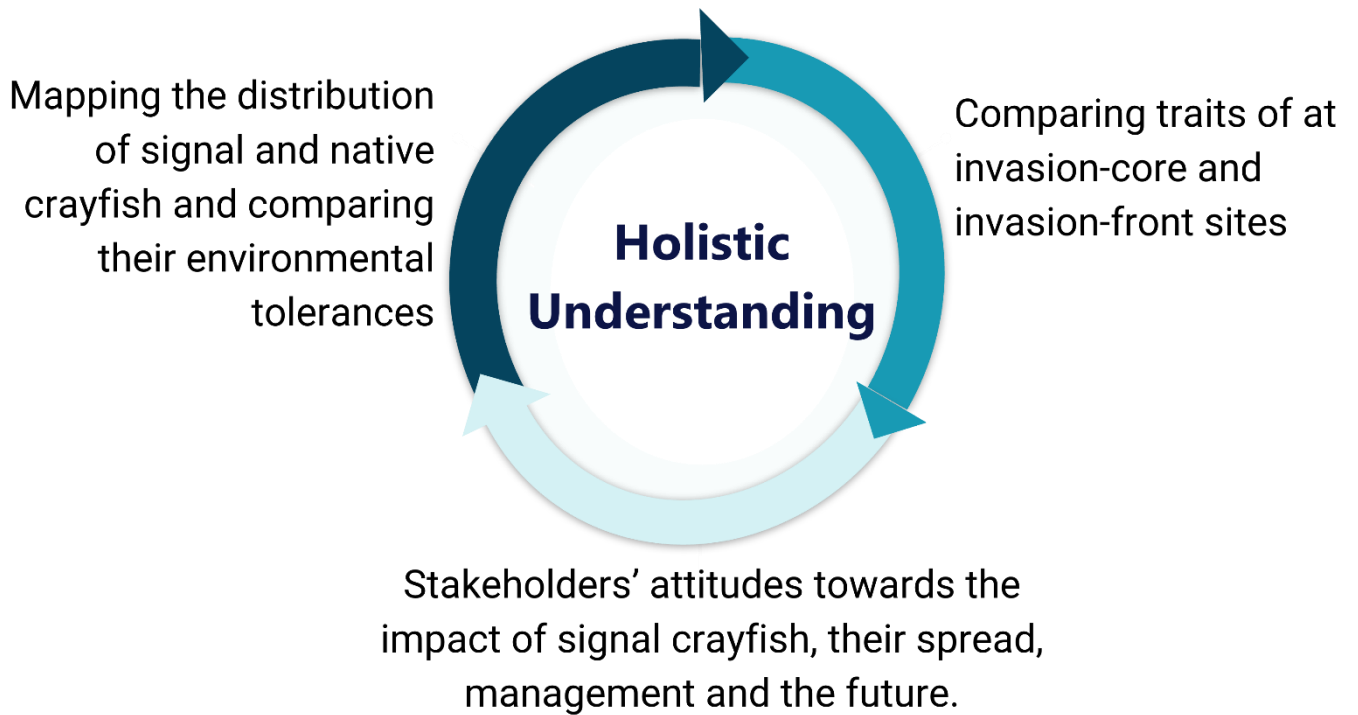


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Chapter 1: Introduction

Biological invasions have been a fundamental force in shaping biogeographical patterns and species assemblages throughout evolutionary history (Williamson, 1996). For example, mass interchanges of biota have regularly taken place in the last 20 million years as previously separated land masses converge (Vermeij, 1991). However, many biological invasions over recent history can be directly attributed to anthropogenic activities (Cassey et al., 2005). Driven by the increasing interconnectedness of the global economic system and rising demand for goods, anthropogenic activities have caused a rapid surge in the intentional and unintentional translocation of species across natural dispersal barriers (Kolar and Lodge, 2001). Biological invasions are now one of the top five threats to global biodiversity (IPBES, 2023).

Although they only account for 2.3% of the Earth's surface, freshwater environments including rivers are particularly biodiverse systems, supporting ~10% of known species (Reid et al., 2019). Additionally, freshwater environments provide critical ecosystem services for human society, including the supply of water, transport and nutrient cycling and carbon storage (IPCC, 2023). However, freshwater systems worldwide are under significant pressure from anthropogenic stressors, including invasive species (Carrizo et al., 2017). Evidence has shown that biological invasions tend to have greater impacts on freshwater environments ecosystems as the addition of novel species can severely disrupt the strong trophic links typically present in these systems (Gallardo et al., 2016).

In Great Britain (GB), a prominent invasive non-native species (INNS) is the signal crayfish (*Pacifastacus leniusculus*). Since their introduction in the 1970s, signal crayfish have significantly impacted the freshwater environments that they have colonised (Holdich et al., 2014). Arguably the most significant impact of signal crayfish in GB has been their

detrimental effect on the native white-clawed crayfish (*Austropotamobius pallipes*). Previous research has analysed various aspects of signal crayfish, from their impact on freshwater biota (Nystrom et al., 2001), their influence on sediment transport (Sanders et al., 2023) and how water temperature affects key traits (Rodríguez Valido et al., 2021). However, there are still important gaps in our knowledge regarding the invasion of this INNS. This thesis aims to address these gaps through a holistic, mixed-method approach that spans the biogeographical, ecological, and social dimensions of the invasion of signal crayfish in GB. Through a holistic approach, the thesis attempts to contribute towards a greater understanding of the invasion of signal crayfish and the factors that have shaped where we are now. A fuller understanding of this biological invasion may allow more effective management and, at the very least, provide important lessons for the future invasions that we must expect.

Chapter 2: Literature Review

2.1. Biological Invasion

Different conceptual models have been created to describe the biological invasion process (Williamson, 1996; Shigesada and Kawasaki, 1997; Blackburn et al., 2011; Richardson et al., 2000). Although there are slight variations between these, they all generally describe biological invasions as a series of 'stages' and/or 'barriers' (**Figure 2.1**) that species can move through (Blackburn et al., 2011). Once introduced outside of their native range (stage i), translocated species can pass through a series of further stages, including (ii) introduction, (iii) establishment, and (iv) geographic spread (Shigesada and Kawasaki, 1997). The classical work by Williamson (1993) suggests that 'the tens rule' applies between each stage, that is, that only 10% of species pass to the subsequent stage in the invasion process (Williamson and Fitter, 1996). A species is described to have reached the last stage (stage iv) when individuals are surviving, reproducing and expanding their range from multiple sites across their new range (Blackburn et al., 2011). Traditionally, a species was labelled as 'invasive' in these models when it had reached the last stage of the biological invasion and had begun having negative economic, social or ecological impacts (Richardson et al., 2000; Williamson and Fitter, 1996). More recently, ecologists have shifted away from the use of the term 'invasive' and related terms such as 'invader' and 'alien' altogether because of their pejorative and value-laden connotations (Pereyra, 2016). As a result, more neutral terms such as invasive non-native species (INNS) are now typically used.

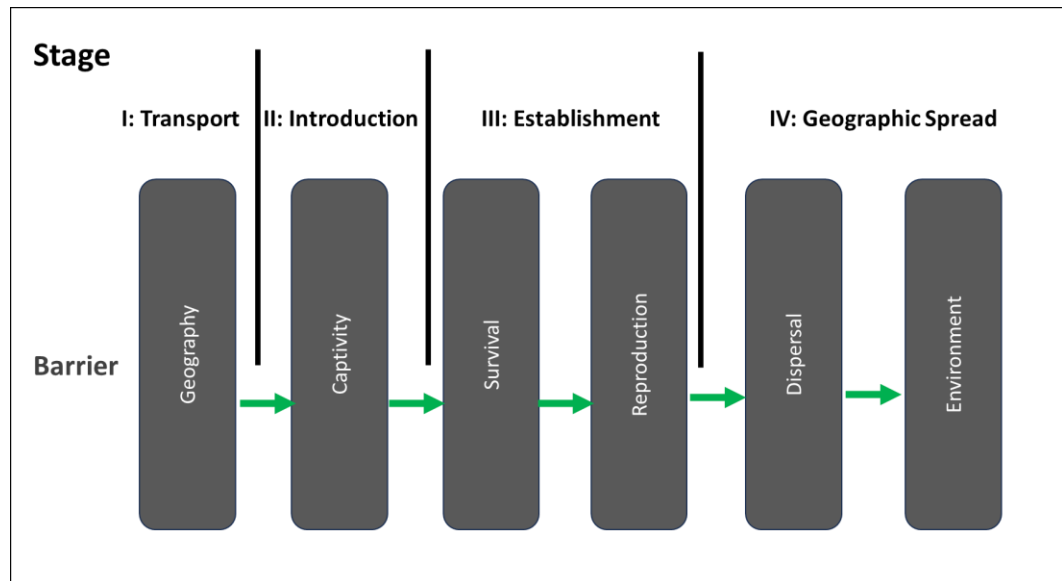


Figure 2.1: Different stages in the invasion process and the barriers that a species must pass through at each point (adapted from Blackburn et al., 2011)

Although the ‘tens’ rule demonstrates that most biological invasions tend to fail (Williamson, 1996), the high frequency and magnitude of introductions associated with anthropogenic activity means that many species still manage to reach invasive status (McNeely, 2006). With increases in international trade forecasted to continue for the foreseeable future, the number of INNS is also expected to continue rising (Levine and D’Antonio, 2003; Sardain et al., 2019). Furthermore, climate change may further exacerbate biological invasions in certain areas by altering conditions at different stages in the invasion process (Hulme, 2017; Bellard et al., 2013). Evidence shows that a climate that is generally warmer and with more extreme events may increase the chance of introduction, thus increasing the number of species at the initial (stage I) in the invasion (Diez et al., 2012). Likewise, other work suggests that climate change may increase their relative performance on INNS compared to native species (Sorte et al., 2013), as well as enabling them to expand their range (stage IV) to previously unsuitable areas (Rahel and Olden, 2008; Dullinger et al., 2017).

Whilst we have a good understanding of the processes that take place in the early stages of the invasion, there are still many unknowns

surrounding the nuances that take place as an INNS expands its range (stage IV). Particularly, there are still big unknowns when it comes to understanding if and how traits may vary spatially between populations of an expanding INNS (Gruber et al., 2017b; Jacob et al., 2012). Recent evidence has shown that, in some INNS, there are variations in traits between individuals in recently invaded areas (invasion front) and those in sites that have been colonized for longer periods (invasion core) (Phillips, 2009; Lindstrom et al., 2013). Several theories have been proposed as to why such variation between invasion front and core may exist in advancing populations of INNS (Shine et al., 2011; Dahirel et al., 2022). The theory of 'spatial sorting' suggests that initial variations in dispersal traits can be progressively amplified at invasion core sites leading to a shift in traits in these individuals (Shine et al., 2011). Whilst this theory suggests that variations in traits are driven by processes taking place at the invasion front, others argue that increased competition at the invasion core can lead to these observed differences (Dahirel et al., 2022). Discovering which INNS display this shift at their invasion fronts and how their traits vary can provide important information for stakeholders to enable them to more effectively manage them and their impacts (Travis and Dytham, 2002).

2.2. Impact of invasions

2.2.1. Ecological impact

Elton (1958) initially observed that human activity, particularly the increase in international trade, was facilitating biotic exchange between previously isolated regions. This breakdown of biogeographic barriers through the spread of INNS reduces the diversity in assemblages between these realms (McKinney and Lockwood, 1999). This increased similarity in the biotic composition of communities, observed across many taxonomic groups, has led to some stating that we are now entering a new era, suitably named 'The Homogocene' (Rosenzweig, 2001). As well as reducing the diversity in assemblages between systems (i.e. lower beta diversity), biotic homogenization from biological

invasions can also lead to extinction of native species through increased competition, predation and other indirect effects (Olden et al., 2004).

Freshwater environments including lakes and rivers are global biodiversity hotspots (Strayer and Dudgeon, 2010; Reid et al., 2019). Whilst they are highly diverse systems, freshwater environments appear to be particularly vulnerable to INNS (Strayer, 2010; Simberloff, 2020). Evidence has shown that freshwater systems display higher rates of successful invasion compared to most other ecosystems (Vitousek et al., 1997). One explanation for why freshwater environments appear more prone to INNS and their impacts is that the addition of novel species can severely disrupt the strong trophic links typically present in these systems, particularly when they also alter the environment (Gallardo et al., 2016). Due to the spread of INNS, freshwater environments are witnessing elevated extinction rates in many areas (Carrizo et al., 2017). Perhaps one of the most infamous examples of a freshwater invasion is the introduction of Nile perch (*Lates niloticus*) into Lake Victoria in Africa in the 1950s. Increased competition and predation from invasive Nile perch contributed to the extinction of over 200 fish species endemic to Lake Victoria (Lowe et al., 2000), including 65% of the endemic cichlids. As the introduction of novel INNS often constitutes the addition of a major new functional component to the recipient community, they can also disrupt natural food webs and generate ecological impacts that propagate through the whole system in a trophic cascade (Walsh et al., 2016). This appears to be particularly an issue in freshwater systems, as organisms here are linked by very strong trophic interactions (Gallardo et al., 2016). The impact of INNS in freshwater ecosystems can vary depending on its position in the food web (Thomsen et al., 2014). For example, the introduction of a species at higher trophic rungs is expected to have a top-down impact that propagates down the food web, influencing abundance/composition at the lower levels (Strayer, 2010). An example of such a top-down trophic cascade is the introduction of two

zooplanktivorous fish species, the common roach (*Rutilus rutilus*) and the common bleak (*Alburnus alburnus*), into Spanish reservoirs, which led to a decrease in the abundance of zooplankton and a corresponding increase the abundance of phytoplankton (Ordóñez et al., 2010). On the other hand, the introduction of INNS at lower trophic levels is expected to have a bottom-up impact that influences the total energy available to organisms at higher trophic levels (Thomsen et al., 2014). Finally, the introduction of other species including the infamous zebra mussels (*Dreissena polymorpha*) and omnivorous invasive crayfish (see **Section 4**) can have both top-down and bottom-up impacts on ecosystems, allowing them to impact food webs via multiple processes (Gallardo et al., 2016). These examples demonstrate the ability of invasive species to have complex ecological impacts on the structure and processes of ecosystems (Strayer, 2010).

Table 2.1: Example of some of the ecological impacts of invasive non-native species (INNS).

Ecological Impact	Direct or Indirect	Example
Predation	Direct	Nile Perch (<i>Lates niloticus</i>)
Competition	Direct	Nile Perch (<i>Lates niloticus</i>)
Change in species composition	Indirect	Common roach (<i>Rutilus rutilus</i>)
Change in resource abundance (e.g., oxygen)	Indirect	Zebra mussels (<i>Dreissena polymorpha</i>)
Disease	Indirect	Signal crayfish (<i>Pacifastacus leniusculus</i>)

2.2.2. Environmental impact

INNS can also have drastic impacts on the environmental conditions in their invasive range. Ecosystem engineering, a term first introduced by Jones et al. (1994), is the direct or indirect modification of resources

and the physical environment by organisms. INNS can act as powerful ecosystem engineers, modifying natural ecosystem processes in their new invasive range (Vitousek et al., 1997). This can result in physical state changes that have ramifications throughout a system (Crooks, 2002). For example, the introduction of common carp (*Cyprinus carpio* L.) to Japanese lakes has increased suspended sediment concentrations, leading to a suppression of the macrophyte community (Matsuzaki et al. (2009). Likewise, increased sediment suspension from invasive red swamp crayfish (*Procambarus clarkii*) switched Chozas Lake in Spain from its typical clear-water state, characterised by high macrophyte abundance and low turbidity, to a turbid state dominated by phytoplankton (Rodríguez et al., 2005). This in turn resulted in reductions of biomass and diversity of the lake's macrophytes, invertebrates and amphibians (Rodríguez et al., 2005). Similarly, invasive signal crayfish have been shown to substantially increase fine sediment transport in UK rivers (Harvey et al., 2014), detrimental to the development of salmon progeny (Greig et al., 2005). Burrowing by invasive crayfish has also been shown to alter morphological properties of rivers, including the rate of bank erosion (Harvey et al., 2011) and overall sediment transport (Johnson et al., 2011).

Table 2.2: Some of the environmental impacts of INNS in freshwater environments.

Environmental Impacts	Example(s)
Increase sedimentation	Common carp (<i>Cyprinus carpio</i> L.) Signal crayfish (<i>Pacifastacus leniusculus</i>)
Decrease sediment transport	Caddisfly (<i>Trichoptera</i>)
Habitat alteration	Zebra mussels (<i>Dreissena polymorpha</i>) Signal crayfish (<i>Pacifastacus leniusculus</i>)

2.2.3. Impact on society and human wellbeing

Ecosystem services are defined as “the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life” (Daily, 1997; p. 3). These ecosystem services are essential to human well-being, defined as access to secure livelihoods, health, good relations, security, and freedom (Mooney, 2005). However, the spread of INNS and their ecological and environmental impacts can severely disrupt the provision of key ecosystem services (Pejchar and Mooney, 2009), posing a clear global threat to human wellbeing (Charles and Dukes, 2008).

One method of quantifying the effects of INNS on human society is their economic impact (Pimentel et al., 2005). One of the most infamous examples of the significant negative economic impact of INNS is that of zebra mussels, which were introduced into the Great Lakes system from their native range in Europe via the ballast water of large commercial vessels (Griffiths et al., 1991; Connelly et al., 2007). Zebra mussels congregate in very high densities and clog water intake pipes, disrupting key industries (e.g., power generation; (Griffiths et al., 1991; Lovell et al., 2006). Estimates put the combined annual cost of the damages from zebra mussels to key industries and management schemes to control their invasion at up to \$1 billion (Pimentel, 2005). The spread of many other INNS around the world also has a substantial economic impact, with other notorious examples including Japanese knotweed (*Fallopia japonica*) (Williams et al., 2010) and cane toads (*Rhinella marina*) (Shine, 2010). Research suggests that the global cost of biological invasions could be as high as \$162.7 billion per year (Diagne et al., 2021).

As well as the economic cost, INNS can have other impacts on human well-being. For example, INNS can have detrimental impacts on the aesthetics of freshwater environments but also alter how groups interact with these systems (Kilroy, 2014). One example is the invasive alga *Didymo*, also known as ‘rocksnot’ (*Didymosphenia geminata*),

which affects recreational angling as well the natural beauty of the rivers it has colonized in New Zealand and Canada (Beville et al., 2012; Kilroy, 2014). INNS are capable of having strong impacts on human health (Mazza et al., 2014). Around 61% of the 1400 infectious diseases are 'zoonotic', meaning that they also infect animals (Jones et al., 2008). When animals are translocated by human activity, they can also spread the dangerous diseases that they carry (Mazza et al., 2014). An example in aquatic environments is the marsh snail (*Biomphalaria glabrata*), which has been translocated outside its native range through the aquatic plant trade and can act as a hosts for the dangerous *Schistosoma mansoni* parasitic worms that affect around 83 million people around the world (Morgan et al., 2001). Likewise, invasive pathogens such as *Vibrio cholerae* have also been directly translocated through the ballast waters of cargo ships (Ruiz et al., 2000). Although under-studied, INNS can also have an impact on Indigenous culture (Siegert et al., 2023). For example, the introduction of Nile Perch led to changes to fishing practices in Lake Victoria, shifting from more traditional approaches to commercial fishing practices (Molony et al., 2007).

Table 2.3: Impact on society and human-wellbeing from INNS in freshwater environments.

Impact on society	Example(s)
Economic (Direct damage, loss of ecosystem services and/or management cost)	Zebra mussels (<i>Dreissena polymorpha</i>) Japanese knotweed (<i>Fallopia japonica</i>) European green crab (<i>Carcinus maenas</i>) <i>Hydrilla</i>
Recreation/aesthetic	Didymo ('Rocksnot') (<i>Didymosphenia geminata</i>)
Health	Marsh snail (<i>Biomphalaria glabrata</i>) <i>Vibrio cholerae</i>

	Ragweed (<i>Ambrosia artemisiifolia</i>)
Cultural practices	Nile Perch (<i>Lates niloticus</i>)

2.3. Overview of crayfish with reference to their status in the UK

2.3.1. Overview of crayfish

The first known scientific reference to crayfish is in Aristotle's History of Animals where he mentions of the "small *Astaci* which breed in the river". Belonging to the decapod infraorder Asticadea, crayfish are the largest mobile freshwater invertebrates (Holdich, 2002). The earliest records of freshwater crayfish date back to the Triassic period (185 – 225 Mya) (Crandall and Buhay, 2008). Crayfish are monophyletic in origin (Crandall et al., 2000), with a single ancestor species that is believed to have made the transition from marine into freshwater environments between the Permian and Triassic periods (Souty-Grosset and Fetzner, 2016). Modern crayfish are classified into two major groups with distinct natural distributions and morphology (Lodge et al., 2012). The first group, the Astacoidea, is comprised of two families (Astacidae and Cambaridae) that are both confined to the Northern hemisphere (Hobbs, 1989). Astacoidea are thought to have originated around eastern Asia and subsequently spread westward into Europe and eastward into North America via the Bering land bridge (Souty-Grosset and Fetzner, 2016). The Parastacoidea group (single family: Parastacidae) are confined to the Southern hemisphere, occurring in Madagascar, South America, New Zealand and Australia (Crandall and Buhay, 2008). The disjunct distribution between the Astacoidea in the northern hemisphere and the Parastacoidea in the southern hemisphere is believed to have occurred during the break-up of the supercontinent Pangea (~195 Mya) into northern Laurasia and southern Gondwana supercontinents, respectively (Souty-Grosset and Fetzner, 2016). Today there are currently 644 known species of

crayfish and they are naturally found throughout every continent except Africa and Antarctica (Lodge et al., 2012).

Crayfish are typically considered keystone species in the freshwater systems where they present (Kouba et al., 2014; Nystrom et al., 1999; Lodge et al., 2012). As already mentioned, crayfish are the largest mobile freshwater invertebrate, with some species reaching 4.5 kg in weight (Holdich, 2002). Crayfish are also omnivorous, consuming other invertebrates, aquatic macrophytes, leaf litter, fish, and even other crayfish (Nystrom and Strand, 1996; Nystrom et al., 1999; Dunoyer et al., 2014; Findlay et al., 2015). Crayfish populations can reach very high densities, over 100 animals m⁻² (Chadwick et al., 2020). Crayfish are also amongst some of the longest-lived freshwater invertebrates, with individuals living 15+ years (Gherardi et al., 2011; Holdich, 2002). In combination, these factors mean that crayfish play a significant role in the transfer of energy in freshwater systems, providing both top-down and bottom-up control on trophic interactions (Danilović et al., 2022). Some crayfish can also alter the physical environments through their feeding activity and burrowing (Faller et al., 2016; Mathers et al., 2020a).

As with other arthropods, crayfish have a protective rigid exoskeleton (Huxley, 1880). This means that crayfish do not grow continuously but, instead grow in a stepwise pattern through the regular moulting of their exoskeleton (Reynolds, 2002). While internal physiological growth takes place constantly, the external size and weight of crayfish typically increases when they shed their old exoskeleton and replace it with a larger new one (Aiken and Waddy, 1992). As with other decapods, crayfish have 10 legs that are used for locomotion (pereiopods) (Souty-Grosset and Fetzner, 2016). The first pair of pereiopods are generally referred to as the chelipeds as they contain large chela (claws) that are used for antagonistic behaviour and courtship (Holdich, 2002). Crayfish typically use the other 8 legs for propulsion via walking and climbing, but can also swim by using their tail, often when escaping disturbance. The number of eggs that female crayfish can lay is generally

proportional to their size, with large, female *Procambarus clarkii* known to be able to lay over 700 eggs (Reynolds, 2002).

2.3.2. Crayfish as an INNS

Crayfish are known to many people as a luxurious food item (Gherardi and Holdich, 1999), with research suggesting that crayfish have been consumed as food in England since the 10th century (Swahn, 2004). As a result of this commodification, there's been a large economic interest in harvesting crayfish (Skurdal et al., 1999). Aquacultural interest has led to many crayfish species being widely introduced outside of their native range into North America, Europe and Asia, to the point that they are now regarded as one of the most successful and widely distributed invasive species in the world (Holdich et al., 2014). There's been a particularly large movement of crayfish from North America to Europe, with species such as the red swamp crayfish (*Procambarus clarkii*) translocated to numerous countries, including Italy, Spain, UK and France (Gherardi et al., 1999; Rodríguez et al., 2005; Holdich and Reeve, 1991; Arrignon et al., 1999). In England, the range of invasive crayfish appears to be increasing (Soto et al., 2023). The large movement of metropolitan crayfish species around the world has in part contributed to the local extinctions of many species (Manenti et al., 2019). Research suggests that around 32% of all crayfish species are threatened by extinction, with competition from invasive crayfish as one of the main causes (Richman et al., 2015).

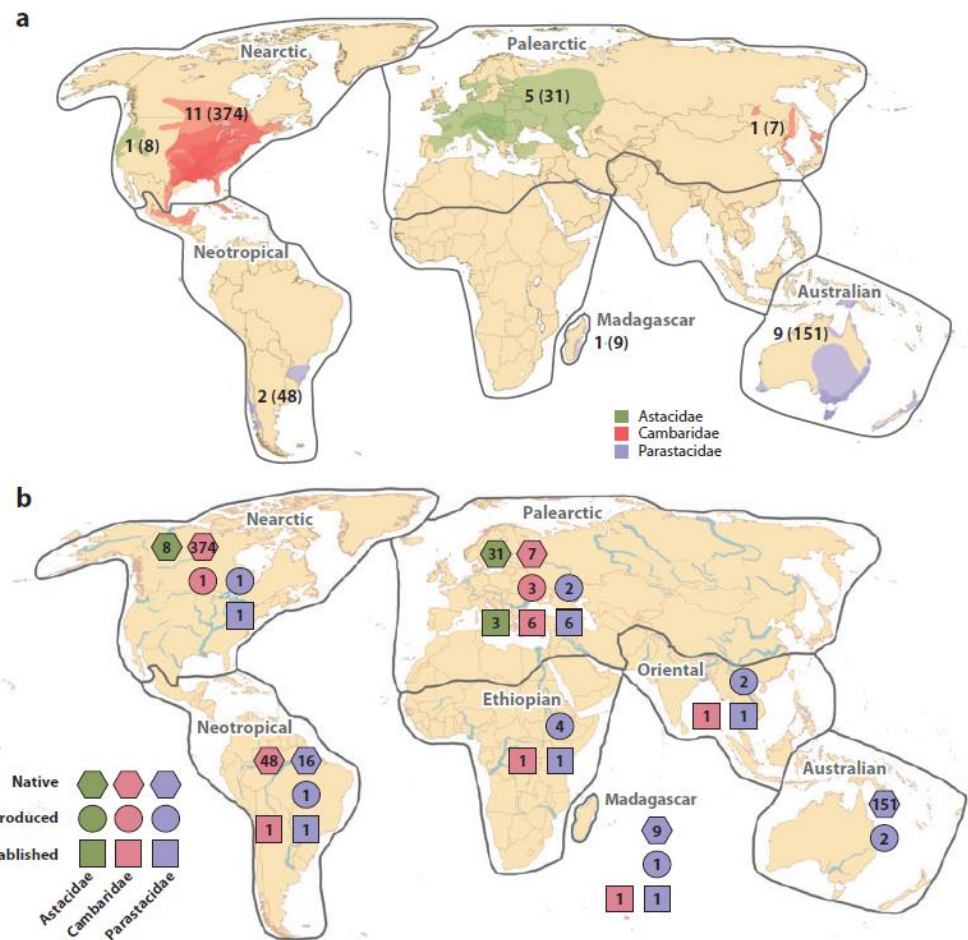


Figure 2.2: (a) Global distribution of the three families of freshwater crayfish. Increasing colour intensity indicates increasing genera richness whilst number indicates the number of genera (with number of species in parentheses). (b) Number of native, introduced and established species in each biogeographic realm (Modified from Lodge et al., 2012).

2.3.3. Crayfish in Great Britain

Great Britain has only one native crayfish species, the white-clawed crayfish (*Austropotamobius pallipes*; (Holdich et al., 1999). The white-clawed crayfish (**Figure 2.4**) typically inhabits clean, mineral-rich waters with calcium concentrations above 5 mg/l, water temperatures below 18°C and pH between 7 and 9 (Foster, 1995; Holdich, 2002). However, some studies have found white-clawed crayfish to be able to tolerate temperatures above 20°C and lower-quality water chemistry for several days (Trouilhé et al., 2007). White-clawed crayfish are also known to prefer habitats with lots of structural complexity and refugia (Rosewarne et al., 2017). With adequate conditions, white-clawed crayfish can occur

in a wide range of water bodies including lakes, reservoirs, quarries, streams and rivers (Holdich et al., 1999). The origin of white-clawed crayfish in the UK is still unclear, with some arguing it colonized naturally from mainland Europe (Laurent, 1988) and others believing it may have been brought over by humans (Albrecht, 1983). However, historical evidence confirms that they were present in the UK prior to 1500, and as such accepted by the International Union for the Conservation of Nature (IUCN) as native to the UK (Holdich et al., 1999). Although the location of white-clawed crayfish was rarely recorded prior to 1970, evidence (**Figure 2.3**) suggests it had a wide distribution throughout the UK before the expansion of invasive crayfish (Sibley et al., 2002).



Figure 2.3: Distribution of white-clawed crayfish in Great Britain. Grey triangles represent records made before 1991 and white triangles show records made between 2009–2013, with each triangle representing one population (Taken from Holdich et al., 2014).

Research now suggests that there are currently eight invasive crayfish species present in the UK, including the European noble crayfish [*Astacus astacus* (Linnaeus 1758)], narrow-clawed/Turkish crayfish [*Astacus leptodactylus* Eschscholtz 1823)], the red swamp crayfish (*Procambarus clarkii*), the spiny-cheek crayfish (*Orconectes limosus*), the virile crayfish (*Orconectes virilis* (Hagen 1870)], the white river crayfish [*Procambarus acutus* (Girard 1852)], and the signal crayfish [*Pacifastacus leniusculus* (Dana 1852)] (Holdich et al., 2014). All of these species were introduced into the UK for aquacultural purposes or as a result of the aquatics trade (Holdich et al., 1999), but only the signal crayfish is currently widespread and, as such, it is considered one of the most problematic invasive species in the UK.



Figure 2.4: White-clawed crayfish (*Austropotamobius pallipes* - left) and invasive signal crayfish (*Pacifastacus leniusculus*). Photo of *A. pallipes* taken from Sibley et al., 2009.

2.4. Signal crayfish (*Pacifastacus leniusculus*)

2.4.1. Ecology and Behaviour

One of the most notorious invasive crayfish species is the North America signal crayfish, a member of the Astacidae group (Holdich et al., 2014). The native range of signal crayfish stretches from British Columbia in the north, central California in the south and Utah in the

east (Lewis, 2002). Signal crayfish have a life cycle typical of other crayfish species, reaching maturity in 1-3 years (Abrahamsson, 1971). However, they typically show faster growth rates than the UK-native white-clawed crayfish and many other native European species (Alderman and Wickins, 1996). They can reach a carapace length of 50-70mm and some have been found to live up to 16 years (Lewis, 2002). Evidence suggests that signal crayfish can be found in high densities in their invasive range, sometimes in excess of 100 animals m⁻² (Chadwick et al., 2020). The diet of signal crayfish is omnivorous and typically displays an ontogenetic shift from feeding predominantly on insects as juveniles to a more balanced diet in adulthood that includes macrophytes (Lewis, 2002). Likewise, research suggests that their habitat preference also shows ontogenetic shifts, with younger/smaller crayfish preferring shallower sections with more boulders and older/bigger individuals favouring deeper water with finer sediment (Wutz and Geist, 2013). This preference for deeper water by larger signal crayfish is supported by data from aquaculture, that shows that the greatest number of individuals can be found between 10-20 m deep (Abrahamsson and Goldman, 1970). This phenomenon may be driven by the avoidance of predators, with shallower gravel-dominated sites providing refugia for juveniles and deeper pools providing more appropriate shelter for larger adults (Wutz and Geist, 2013). Signal crayfish occur in a wide variety of habitats, including from small upland streams to large lowland rivers, as well as lakes and reservoirs (Lewis, 2002).

The signal crayfish is typically regarded as a temperate, cool water species in its native range (Lewis, 2002). However, invasive signal crayfish have a large thermal performance breadth and can thrive at relatively high temperatures, reaching peak performance between 20-26°C (Simcic et al., 2014; Firkins, 1993; Rodríguez Valido et al., 2021). The influence of temperature also creates seasonal variations in signal crayfish activity, with maximum activity taking place during the warmer summer months, with minimal activity taking place in winter (Johnson et

al., 2014; Bubb et al., 2004). Studies have found that after around mid-December signal crayfish movement drops drastically (Bubb et al., 2002), with animals entering a diapause, sometimes referred to as 'winter torpor', that is also observed in other crayfish species (Brewis and Bowler, 1982). As well as seasonal shifts in activity, signal crayfish show diurnal variation in their activity, with most of their activity taking place at night (Johnson et al., 2014; Guan and Wiles, 1998). As well as temperature, flow conditions influence signal crayfish activity, with lower activity at deeper depths and during high flow events (Johnson et al., 2014), perhaps because larger animals take shelter in deep pools and other refugia during such events (Light, 2003). Whilst high-flow events are not typically considered an important factor behind the spread of adult crayfish, it has been suggested that they may allow smaller individuals to passively spread downstream (Bubb et al., 2004).

The study by Bubb et al. (2004) found that adult signal crayfish in upland rivers in the UK tended to preferentially migrate downstream, perhaps due to the high gradients and associated higher water velocities. Signal crayfish at varying life stages have also been found to disperse overland (Thomas et al., 2019) and are capable of surviving extended periods outside of the water (Banha and Anastácio, 2014). In their native range of North America, signal crayfish are not considered a burrowing species and have only been observed to burrow during extreme weather conditions to avoid the impacts of very low flows (Shimizu and Goldman, 1983; Sanders et al., 2021) and some reports suggest that the species is not capable of burrowing (Kouba et al., 2016). However, signal crayfish in their invasive range burrow extensively, creating complex burrow systems into bank and bed material when there is adequate geology (Guan, 1994; Sanders et al., 2021; Faller et al., 2016).

2.4.2. Introduction in the UK

The introduction of signal crayfish from North America into Europe began in the late 1950s in order to replace native crayfish populations

that had been devastated by the crayfish plague, a disease transmitted by the fungus *Aphanomyces astaci*, with a plague-resistant species (Holdich and Reeve, 1991). As well as being plague-resistant, signal crayfish were also selected by the aquaculture industry because of their faster growth rate compared to native European species, which was seen to provide a commercial advantage (Alderman and Wickins, 1996). Initially introduced into a hatchery in Sweden, signal crayfish were subsequently introduced throughout Europe and Japan (Lewis, 2002).

Signal crayfish were first introduced into the UK from Sweden in the 1970s. They were implanted into around 300 fish farms across southern England (Holdich et al., 2014). However, the commercial harvest of signal crayfish generally failed and only five fish farms were registered to grow them by 2006 (NNSS, 2011). As a result of this economic failure, signal crayfish were released into the wild, with many further individuals escaping due to poor biosecurity at the fish farms that had stocked them (Peay et al., 2010; Alderman and Wickins, 1996). Signal crayfish have subsequently spread further through migratory activity and by people unintentionally and intentionally moving them to new sites (NNSS, 2011). In combination, these factors have led to the population of signal crayfish quickly spreading across the UK, to the point where they now cover much of England and have also reached certain parts of Wales and Scotland (Holdich et al., 2014). The study by Bubb et al. (2005) found that the rate of expansion of signal crayfish in upland rivers in England is increasing, with the most recent analysis showing rates up to 2.4km year^{-1} . Whilst we have a good understanding of how signal crayfish arrived in the UK, we still do not fully understand the factors influencing where and how fast they are spreading.



Figure 2.5: Geographic distribution of signal crayfish in Great Britain. Black circles indicate records made before 1991, whilst white circles indicate records made during and after 1991 (Taken from Holdich et al., 2014).

2.4.3. Signal crayfish impacts

The spread of invasive signal crayfish has been particularly detrimental to the native crayfish species in the UK; the white-clawed crayfish (Holdich et al., 1999; Sibley et al., 2009). The population of the native white-clawed crayfish has plummeted after signal crayfish introductions and has been regarded as endangered in the UK since 2010 (Bubb et al., 2004). Much of the decline in the population of white-clawed crayfish can be attributed to the spread of crayfish plague (Holdich and Reeve, 1991). Although signal crayfish are themselves generally resistant to crayfish plague due to co-evolution with the disease (Persson and Soderhall, 1981), they can still act as vectors for the fungus (James et al., 2017). As a result, the expansion of signal crayfish has facilitated the spread of the disease, and this has resulted

in the decimation of many vulnerable white-clawed crayfish populations, for whom crayfish plague is lethal (James et al., 2017). Even where there is little interaction between the species, the presence of signal crayfish that are infected with crayfish plague typically causes the complete elimination of white-clawed crayfish (Bubb et al., 2005).

In addition to spreading crayfish plague, signal crayfish have also been shown to displace native white-clawed crayfish populations (Holdich et al., 2014; Lewis, 2002). As previously mentioned, signal crayfish have a faster growth rate compared to white-clawed crayfish (Alderman and Wickins, 1996) and larger overall body size and bigger chelae (claws) than native white-clawed crayfish, both important factors in deciding antagonistic encounters between crayfish (Levenbach and Hazlett, 1996). Additionally, signal crayfish are generally considered to be more aggressive than white-clawed crayfish (Ibbotson and Furse, 1995). As a result of these competitive advantages, signal crayfish typically outcompete white-clawed crayfish for resources crucial to survival (such as refugia and food) and even predate on them during moulting (Dunn et al., 2009; Ibbotson and Furse, 1995). As a result, even disease-free signal crayfish can completely replace white-clawed crayfish within a few years (Holdich et al., 1995; Bubb et al., 2005).

Although additional stressors such as habitat degradation and poor water quality are thought to have impacted white-clawed crayfish populations (Holdich and Reeve, 1991), the invasion of signal crayfish is regarded as the biggest contributor to their decline in the UK (Sibley et al., 2009; Soto et al., 2023). Research suggests that in some parts of the UK, the population of white-clawed crayfish has declined up to 95% since the introduction of signal crayfish (Holdich and Sibley, 2009).

The ability of signal crayfish to sustain high population density (Chadwick et al., 2020) and their position as a keystone species means that they can have many complex ecological and trophic influences in river systems (Reynolds et al., 2013). Invasive signal crayfish have been found to have substantial influences on macrophyte communities

(Nystrom and Strand, 1996). Studies have found that signal crayfish were more voracious grazers of macrophyte compared to other native European crayfish, resulting in a loss of biomass of certain species such as *Chara hispida* (Nystrom and Strand, 1996; Nystrom et al., 1999). Likewise, signal crayfish have been found to also have strong effects on invertebrate communities (Nystrom et al., 2001). The study by Sanders and Mills (2022) found that signal crayfish caused non-lethal damage to 100% of native bivalve species in the UK. Likewise, the study of Beatty et al. (2020) also showed that signal crayfish can be particularly detrimental to native invertebrate species. Their study showed that signal crayfish reduced the survivorship of all four amphipod species that they tested; however, the native *Gammarus pulex* species showed the lowest survivorship in the presence of signal crayfish (Beatty et al., 2020). Similarly, the study by Dunoyer et al. (2014) also found that signal crayfish consumed more *G.pulex* than native European crayfish. Studies in the UK have found permanent reductions in the abundance and diversity of many invertebrate taxa in rivers following the invasion of signal crayfish (Mathers et al., 2016; Mathers et al., 2020b). Likewise, studies have shown that the removal of invasive signal crayfish from UK rivers can result in increases in the richness and number of macroinvertebrates (Moorhouse et al., 2014). Several studies have shown that signal crayfish have a particularly negative impact on the abundance of grazers, such as snails (Nystrom et al., 1999; Nystrom et al., 2001; Nystrom and Strand, 1996). This impact on grazers in river systems can result in increases in the abundance of algae, including bloom-forming filamentous algae species (Scordo et al., 2023). Similarly, signal crayfish are also believed to indirectly increase epilithic algae production due to the removal of detritus from rocks and the re-suspension of nutrients associated with their geomorphic activity (Stenroth and Nystrom, 2003).

Signal crayfish have been found to have detrimental direct and indirect impacts on fish (Reynolds, 2011a). Signal crayfish can directly predate on salmon (*Salmo salar*) fry, leading to higher fry mortality compared to

aquaria with native white-clawed crayfish (Edmonds et al., 2011). Findlay et al. (2015) found that adult crayfish significantly reduced the survival of salmon eggs and that even juvenile crayfish may pose a predation threat to salmon eggs (Findlay et al., 2015). As well as through direct predation, signal crayfish can also impact fish species indirectly through various ways (Wood et al., 2017). For example, signal crayfish may reduce the survival of salmonid eggs indirectly through an increase in fine sediment transportation (Mathers et al., 2022), which can decrease oxygen levels in salmonid nests (called redds) (Greig et al., 2005; Statzner et al., 2003). As mentioned previously, invasive signal crayfish can reduce the abundance of macrophytes in rivers (Nystrom and Strand, 1996), which can negatively affect fish populations that use macrophytes as spawning habitat and for shelter (Holdich et al., 2014). Research in the UK has found that signal crayfish can reduce the growth rate of young chub (*Squalius cephalus*), potentially due to greater competition or predation (Wood et al., 2017). Other studies in the UK have shown a negative relationship between the presence of signal crayfish and that of Atlantic salmon and sea trout (*S. trutta*) in headwater streams (Peay et al., 2009). Likewise, a more recent study has found a decrease in the abundance of benthic fish and young-of-year (YoY) salmonid in a UK river impacted by signal crayfish (Galib et al., 2020). Research on the River Great Ouse in England found a negative correlation between the abundance of signal crayfish and that of benthic fish species such as bullhead (*Cottus gobio*) and stone loach (*Noemacheilus barbatulus*) (Guan and Wiles, 1997). The direct and indirect impact of signal crayfish on fish populations, particularly those of highly valued salmonids, also carries substantial economic impacts (Holdich et al., 2014).

Invasive signal crayfish are also considered to be an adverse ecosystem engineer in river systems (Rice et al., 2016). As previously mentioned, signal crayfish in their invasive range are known to burrow (Guan, 1994). Signal crayfish burrows in UK rivers have been found to be patchy and are preferentially found in banks with cohesive material

and steep profiles (Faller et al., 2016). Although signal crayfish burrows are rudimentary, they can make extensive burrow systems just below the water surface (Harvey et al., 2011). When present in high densities, signal crayfish burrowing has been shown to accelerate bank erosion in the UK by up to 253% (Sanders et al., 2021). Faller et al. (2016) calculated that signal crayfish burrowing into banks could contribute around 3 tonnes km⁻¹ for areas affected. As well as through their burrowing, signal crayfish activity, including foraging and fighting can also increase sediment transport (Johnson et al., 2011).

Related to the above, various studies have subsequently found that invasive signal crayfish can alter sediment transport regimes in UK rivers (Rice et al., 2016; Mathers et al., 2022; Johnson et al., 2011). Harvey et al. (2014) found that invasive signal crayfish presence increased fine sediment transport rates in the laboratory and in the wild. Likewise, Mathers et al. (2022) also found that signal crayfish increased fine sediment transport, contributing on average 18.5% extra baseflow than through fluvial forces alone. Rice et al. (2016) on the River Nene (Northamptonshire, UK) identified a diurnal cycle of fine sediment flux which was driven primarily by the nocturnal peaks in signal crayfish activity. Their study found that, on average, signal crayfish activity accounted for 32% of monthly suspended sediment load in their study reach (Rice et al., 2016). Johnson et al. (2011) found that signal crayfish activity may also increase coarse sediment transport in rivers. This is because their activity changes the protrusion of gravel grains and means that they can be more easily entrained by the flow of water (Johnson et al., 2011; Johnson et al., 2010).

These changes in the environmental processes of rivers where invasive signal crayfish have established may lead to complex environmental responses. For example, the reworking of coarse sediment by signal crayfish has been shown to alter the topography of river beds (Johnson et al., 2010). As many organisms live on the riverbed, shifts in its topography may alter the composition and diversity in these spaces (Leitner et al., 2015). Likewise, as water levels are a product of river

discharge and width, increasing bank erosion associated by signal crayfish activity may also lead to wider and shallower river sections (Faller et al., 2016; Guan, 1994). Lower water levels would also lead to slower flows, which can in turn lead to greater deposition of fine sediments on the riverbed (Wood and Armitage, 1997). Situations such as this show how signal crayfish activity, whether it be as a result of geomorphic or feeding activity, can ultimately cascade into complex interactions that alter the fundamental physical characteristics of affected rivers (Harvey et al., 2011). This is exemplified by the possible effect of signal crayfish on the survival of salmonid eggs on the river bed due to increased fine sediment transport (Greig et al., 2005) or the increase in epilithic algae due to the removal of detritus from rocks (Statzner et al., 2003).

Managing the impacts of invasive signal crayfish on freshwater systems is an economic burden in the UK (NNSS, 2011). Between the necessary conservation activity for white-clawed crayfish, river bank restoration for affected streams, and impacts on recreational angling, the cost of signal crayfish in the UK is estimated to be over £2.5 million annually (Williams et al., 2010). The expansion of signal crayfish into Scotland, where recreational angling of salmonids contributes nearly £80 million annually (Radford et al., 2004), could increase this economic impact further. Warmer river temperatures as a result of climate change may also increase the performance of signal crayfish (Hellmann et al., 2008; Rahel and Olden, 2008), potentially increasing their overall impact in the UK (Rodríguez Valido et al., 2021).

2.5. Social dimensions of signal crayfish invasion in GB

Natural systems (or resources) that humans interact with are embedded in complex social-ecological systems (SEs; (Ostrom, 2009; Binder et al., 2013). These SEs comprise complex relationships where social and ecological factors intertwine and influence each other (Newell et al., 2005). With many of the largest environmental issues we face

(INNS, climate change habitat destruction etc) having strong social dimensions, there is a growing appreciation that we require a holistic approach (Partelow, 2018). Many argue that interdisciplinary research that tries to understand both the social and ecological aspects of environmental problems can improve our management of them (Bennett et al., 2017).

As seen, there has been vast work on the drivers of INNS, as well as on the impacts that signal crayfish and other species have in the UK (Galib et al., 2020; Guan and Wiles, 1997; Peay et al., 2009). However, the social dimension of invasion has, by comparison, been relatively neglected (Carter et al., 2021). As discussed, humans are commonly responsible for the introduction of INNS, can facilitate their spread, may be the victims of their impacts and can manage invasive species (Witmer et al., 2009). Therefore, to properly understand an invasion, it is critical to take a more holistic view that also includes analysing their social dimension (Bennett et al., 2017).

One area that is particularly important when trying to understand and manage INNS is to understand the attitudes of key stakeholders (Reed, 2008). Successfully managing INNS and their impacts requires cooperation between different key stakeholders (Stokes et al., 2006). However, each stakeholder can have different relationships and interests towards INNS and their management, which can sometimes make cooperation difficult (Caplenor et al., 2017). Understanding the attitudes of stakeholders can shine a light on where there may be conflict or consensus between different groups (Bendtsen et al., 2021). Therefore, understanding the role and attitudes of stakeholders is critical for effective INNS management (Shackleton et al., 2019). Previous research has looked at the attitudes of stakeholders towards a variety of INNS, such as wild hogs (*Sus scrofa*) in the United States (Caplenor et al., 2017), grey squirrels (*Sciurus carolinensis*) in the UK (Dunn et al., 2021), and invasive plants in Spain (Touza et al., 2014). These investigations have discovered the complex attitudes that different stakeholders have towards these INNS and how these affect

the effectiveness of their management. Understanding the attitudes of stakeholders when managing an INNS is critical for several reasons, but some of the most important are: i) allows different types of knowledge and opinions to be voiced, ii) increases the opportunity for dialogue iii) reduces conflict between groups iv) increases management support (Shackleton et al., 2019; Stokes et al., 2006).

As seen, there has already been considerable research looking at the impacts (Mathers et al., 2016) and ecology of invasive signal crayfish in the UK (Johnson et al., 2014). However, so far there has been little research attempting to understand the attitudes of stakeholder towards this aquatic INNS. The only previous investigation that has looked at signal crayfish was Adams (2016), that focused on the attitudes of stakeholders towards their management. This study provided important information on stakeholders' perceptions of different management techniques in the UK and factors influencing their effectiveness in controlling signal crayfish (Adams, 2016).

However, there remains the need for further research to understand how stakeholders feel towards other aspects of signal crayfish, including their impact, the factors influencing their spread and recent policy changes. Likewise, there is now the appreciation that multiple forms of knowledge from different sources (e.g. scientific, local) are needed to create new insight (Tengö et al., 2014). This chapter contributes to this idea of multiple forms of knowledge by interviewing stakeholders from a variety of different groups (e.g. government, practitioners, locals, and academics). New evidence on management approaches and large policy shifts associated with Brexit have altered how we manage INNS like signal crayfish in the UK (Black and Bartlett, 2020; Green et al., 2020; Browne et al., 2019). A greater understanding of how stakeholders feel towards different aspects of the invasion of signal crayfish in the UK will allow for greater opportunities to co-operate and find effective management solutions.

2.6. Thesis aim and hypotheses

The overarching aim of this thesis is to improve our understanding of the invasion of signal crayfish through further study of three important areas. These are, in order of study: how their distribution has changed in comparison to native white-clawed crayfish (Chapter 3); how their environmental tolerance compares to the native species (chapter 3); if/how their traits vary at invasion-front sites (chapter 4), and comparing the attitudes of stakeholders towards different aspects of their invasion (chapter 5). Whilst these three areas may not appear related at first, they each have played an important role in the way signal crayfish have spread throughout GB. Studying these three areas and demonstrating how they interlink with one another allows us to have a more holistic understanding of them and the invasion of signal crayfish overall, something which may otherwise be difficult if studied individually.

The thesis tests the following hypotheses relating to the invasion of signal crayfish in GB:

- **Hypothesis 1:** Signal crayfish are found in more diverse environmental conditions than white-clawed crayfish (Chapter 3).
- **Hypothesis 2:** Signal crayfish in GB are bigger, more active and have higher exploration at invasion-front compared to those invasion-core sites. (Chapter 4).
- **Hypothesis 3:** Those who create and enforce environmental regulation have different attitudes towards the invasion of signal crayfish compared to those whose activities are impacted by the regulation (i.e. 'the regulated') (Chapter 5).

After a literature review chapter (Chapter 2) this study is comprised of three results chapters (Chapters 3, 4 and 5) and a subsequent synthesis chapter (Chapter 6).

Chapter 3 addresses Hypothesis 1 by analysing spatial and environmental secondary datasets to determine the key factors influencing the distribution of invasive signal crayfish and native white-

clawed crayfish in the UK. The study uses occurrence data collected from a mixture of government and citizen-science sources alongside environmental and social datasets. As well as presenting how the invasion of signal crayfish has progressed since its introduction, the chapter tests whether there are any conditions where white-clawed crayfish are present that may not be suitable to signal crayfish and thus act as natural ark sites for the endangered species.

Chapter 4 addresses Hypothesis 2. This Chapter tests theories being developed in rapidly growing areas of research in invasion front and population expansion ecology. The study tests whether signal crayfish at recently invaded (invasion front) sites have different morphological and behavioural traits compared to those in long-established (invasion core) sites. Evidence of trait shifts have been observed in other species and recent evidence suggests it may also be taking place in signal crayfish. This study uses fieldwork in five rivers to test whether there are differences in signal crayfish between populations, which may allow managers to better predict the advance, and thus the impact, of signal crayfish in the GB.

Chapter 5 answers Hypothesis 3. The study uses qualitative methods to conduct a short task and semi-structured interview with different key stakeholders associated with signal crayfish in the GB. There is a paucity of research looking into the social dimension of the signal crayfish invasion and evidence suggests that proper understanding of stakeholders is crucial to management that is effective and widely supported. The study tests whether stakeholders have different or similar attitudes towards key topics around the invasion of signal crayfish in the GB. The study also provides insight into how participants view the role of other key stakeholders associated with signal crayfish in the GB. This study's findings provide insight into key groups' attitudes in the management of signal crayfish in the GB, which may allow for more effective collaboration and communication between these important stakeholders.

Finally, Chapter 6 synthesises the information gathered from the previous three chapters (Chapters 3, 4 and 5) and presents suggestions for how the new understanding presented in this thesis can improve the management of signal crayfish and INNS more generally in the GB.

Chapter 3: Understanding the distribution of signal (*Pacifastacus leniusculus*) and white-clawed crayfish (*Austropotamobius pallipes*) in Great Britain using citizen science and traditional records.



A system maintains a certain fluid stability that can be destroyed by a misstep in just one niche. A system has order, flowing from point to point. If something dams that flow, order collapses. The untrained might miss that collapse until it was too late. That's why the highest function of ecology is the understanding of consequences.

- **From “Dune” by Frank Herbert**

3.1. Abstract

The introduction of signal crayfish (*Pacifastacus leniusculus*) to Great Britain in the 1970s has played an important role in the decline of native white-clawed crayfish (*Austropotamobius pallipes*) populations over the same period. However, due to a lack of comprehensive recording schemes, their historic and/or current distributions have not been accurately or adequately mapped. In this study, we combine observations from iNaturalist, (made up exclusively of citizen science observations from the public), with data from the National Biodiversity Network (NBN) Atlas. We use this collated record to map the historic and current distribution of both crayfish species, as well as to understand the environmental conditions where each is found. We find that the pattern of signal crayfish expansion and white-clawed crayfish loss continues at a rapid pace. Signal crayfish are rapidly expanding into the remaining uninvaded areas where white-clawed crayfish populations persist. Our results suggest that signal crayfish can thrive in the same conditions as white-clawed crayfish and appear to have a wider environmental tolerance, which makes the work of determining suitable ark sites aiming to protect the native species particularly difficult. Our study also demonstrates that the role of citizen scientists in our understanding of where crayfish are in Great Britain is critical and increasing.

3.2. Introduction

Since its initial introduction in the 1970s, the invasive signal crayfish (*Pacifastacus leniusculus*) has spread rapidly throughout large parts of Great Britain (Holdich et al., 2014). The most infamous impact of this spread has been the associated decline it has caused in the population of white-clawed crayfish (*Austropotamobius pallipes*), the single native crayfish species in Great Britain. Whilst populations of this native species were already declining before the 1970s due to anthropogenic activity (Dunn et al., 2009), the spread of signal crayfish and the

crayfish plague that they carry has led to a sharper decline in the remaining populations of white-clawed crayfish (Holdich et al., 2014). The only country within the UK where white-clawed crayfish are not threatened by signal crayfish is Northern Ireland, where the latter has yet to reach (Reynolds, 2011b).

Past research has mapped the historical and current distributions of signal and white-clawed crayfish in Great Britain [e.g., Chadwick (2019), Holdich et al, 2014, Rogers and Watson, 2010, and Sibley, 2003), Soto et al. (2023), Kouba et al. (2014)]. Many of these pieces of research have relied on official observations from government agencies and regulators, such as the Environment Agency (EA), Natural Resources Wales (NRW), the Scottish Environmental Protection Agency (SEPA), or other non-governmental organisations (NGOs) whose remit includes crayfish management. However, as many of these organisations lack the funding or resources to conduct regular sampling of crayfish populations, there are questions about whether we truly understand the historical and current distribution of these two important crayfish species in Great Britain (Rogers and Watson, 2010). It is also important to regularly update the distribution of signal and white-clawed crayfish in the UK as this can be very beneficial to help future research and for management purposes.

An accurate database that describes the historical and current distribution of signal and white-clawed crayfish in Great Britain is critical. A precise understanding of the present distribution of signal crayfish populations empowers environmental managers to implement effective management approaches, such as physical barriers. Likewise, understanding the historical and current distribution of white-clawed crayfish can inform where we should concentrate conservation efforts. The currently preferred approach to conserving the remaining populations of white-clawed crayfish has been to translocate them to locations where they will be safe from signal crayfish and crayfish plague (Nightingale et al., 2017). To ensure that these 'ark sites' have the greatest chance of success, they should ideally be located in

locations that are suitable for white-clawed crayfish but difficult for signal crayfish to invade or persist in (Nightingale et al., 2017).

Issues with incomplete distribution data are not unique to signal and white-clawed crayfish in Great Britain. It also affects many important invasive non-native species (INNS) and others that are being threatened by these or other ecological threats (Delaney et al., 2008). Citizen science, the participation of non-professional volunteers in scientific work, has the potential to rapidly increase the amount and geographical extent of observations that are made for native and INNS (Brown and Williams, 2019). Several studies have already begun to utilise records collected using citizen science to more accurately describe the presence of INNS and native species in other countries (Delaney et al., 2008; Gallo and Waitt, 2011; Earp and Liconti, 2020).

Considering the above, the current study aims to use a range of data sources to provide an updated account of the historical and current distribution of signal and white-clawed crayfish in Great Britain. Given that the last published report on the signal crayfish invasion was ~10 years ago (ie. Holdich et al. 2014), and considering the rate progression of the invasion, such information is crucial for the management of this INNS. Our specific objectives are: 1) to provide up-to-date information on the current and historic distribution of signal and white-clawed crayfish in Great Britain using a range of different sources of observation data, including those collated through citizen science; 2) to compare the environmental conditions where signal crayfish and white-clawed crayfish have been observed in Great Britain and 3) synthesise this information to provide commentary on the state of signal and white-clawed crayfish in Great Britain, as well as the role of citizen science in invasive species monitoring more generally.

3.3. Methods

3.3.1. Data

For the observation data for invasive signal crayfish and native white-clawed crayfish, we collated records from the National Biodiversity Network (NBN) Atlas, and observations from the iNaturalist citizen science programme. The NBN Atlas represents the UK's largest repository of biodiversity data that is available to the public, with many government bodies (such as the Environment Agency) and non-governmental organisations (NGOs) contributing data on the distribution of species (Ratcliffe and Jones, 2022). Many of the bodies collect information on the presence of crayfish species from the routine monitoring that they do. For this study, we only used confirmed observations from the NBN Atlas. On the other hand, iNaturalist describes itself as a “crowdsourced species identification system” where individuals can contribute observations in the format of photographs of species they find in nature (Matheson, 2014). Each record that is sent to iNaturalist contains the location, date and species included in the photograph (Van Horn et al., 2018). Importantly, if at least one other member of the community checks and verifies an observation, it becomes “research grade” (Van Horn et al., 2018). For this study, we only used the “research grade” observations for signal and white-clawed crayfish in Great Britain. Datasets for each crayfish species from NBN and iNaturalist datasets were all downloaded on the same day in November 2023.

One limitation with this type of data is that both sources contain presence-only data and thus do not contain if a species was absent. This type of data is not as rich and means that it is problematic to accurately establish if a species is no longer present just because it does not appear in later years (Barry and Elith, 2006). Likewise, it may be possible that some records may have been erroneously tagged as

one particular crayfish, although the use of higher-grade data should limit this risk (Ratcliffe and Jones, 2022).

As well as observation data, other environmental and social datasets were included in the analysis to understand whether there exist differences in the environmental range in which signal and white-clawed crayfish are found (**Table 3.1**). These included variables that have previously been suggested to influence the distribution of crayfish (e.g., water quality) (Rosewarne et al., 2017; Lewis, 2002). As environmental data is not available for all years that crayfish data was used, values from the present (2023) were used. To calculate an averaged value for barrier density at each catchment, the density tool was used within ArcGIS (ESRI, 2015).

Table 3.1: Data types and sources that were used in the analysis.

Data type	Variable	Data Source	Reference
Crayfish observation	Signal and white-crayfish observation	National Biodiversity Network's Atlas	(Ratcliffe and Jones, 2022)
		iNaturalist	(Matheson, 2014)
Climatic	Annual precipitation	WorldClim2	(Fick and Hijmans, 2017)
	Annual mean temperature		
Catchment	Sub-catchment outlines	HydroSHEDS sub-catchments (level 9)	(Lehner et al., 2008)
	Area		
	Upstream area		
Topographic	Elevation	SRTM Digital Elevation Data (Version 4)	(Jarvis et al., 2008)
	Slope		
Geological	Bedrock geology	British Geological Society	(EDINA, 2020)
Landcover	% Suburban	EDINA	(EDINA, 2015)

	% Arable		
	% Woodland		
Water quality	pH	Environment Agency	(EA, 2020)
	Water temperature		
	Dissolved oxygen		
	Chloride		
	Nitrate		
	Nitrite		
Physical barriers	Physical barrier density	Amber barrier atlas	(AMBER, 2020)

3.3.2. Mapping and Statistical Analysis

To understand the pattern of crayfish residency across the UK's hydrological network and calculate the first year that signal crayfish arrived, we analysed the collated crayfish observation data in R Studio (R Studio, 2023), aggregating data at the scale of the World Wide Fund's (WWF) HydroSHEDS level 9 (Lehner et al. 2008) sub-catchments. These are small hydrological sub-basins represented by spatial scales that correspond to Pfafstetter level 9. (Verdin, 2017). The shapefiles that were created for these analyses were subsequently exported and mapped using ArcGIS (ESRI, 2015). Values for the environmental and social datasets were averaged at this resolution so the analysis could be conducted at a consistent spatial scale. Additionally, we mapped the observations of signal and white-clawed crayfish before 2015 and after this period. We chose to compare distributions of the crayfish before and after this point, as it represents the year following the last published investigation to carry out this task (Holdich et al., 2014), and thus allows for a comparison between that and the current study. Additionally, this allows us to visualise where there has been a change in the distribution of each species within the last ten years. Furthermore, 2015 is considered to be the peak in

the occurrence of signal crayfish in Great Britain (**Figure 3.1A**), which makes this a particularly interesting year.

To project the hypothetical core and front of the signal crayfish's invasive range in Great Britain, we also used the Hot Spot Analysis tool in ArcGIS (ESRI, 2015). This tool demonstrates where there is a statistically high (and low) concentration of points using the Getis-Ord G_i^* statistic (Oxoli et al., 2018). To understand the environmental variables associated with the observed patterns of signal and white-clawed crayfish distribution, we first extracted all the environmental variables (see Table 2.1) and crayfish residence status for every HydroSHEDS level 9 sub-catchment. We then used principal component analysis (PCA) using the *prcomp* function (Mankin, 2008) in R (R Studio, 2023) to understand whether there were differences in the environmental conditions where different crayfish were found. Because water quality data was missing from certain sub-catchments, we created two PCAs: one with and another without the water quality data included. The PCA analysis *with* the water quality data included a total of 237 sub-catchments whereas the one *without* these variables included 347.

3.4. Results

From the NBN Atlas dataset, there were 10,252 observations of signal crayfish and 13,947 for white-clawed crayfish in Great Britain. In comparison, the iNaturalist dataset had many fewer records, with only 312 confirmed 'research grade' observations for signal crayfish and 13 for white-clawed crayfish. As can be seen in **Figure 3.1A**, the number of observations for signal crayfish increased steadily from 1975 to around 2015 but has since dropped. Although the first iNaturalist observation was in 2007, the number increased considerably since the late 2010s (**Figure 3.1A**). In contrast, the number of records for white-clawed crayfish peaked in the mid-1990s and has decreased ever since (**Figure 3.1B**). For this native crayfish, records on the iNaturalist dataset

date back to 2016 and the highest number of records in a single year has been four (in 2021). Although there are some NBN records for white-clawed crayfish before 1975 (with some records dated as far back as 1800), these are sporadic and make up a small proportion of the overall dataset.

Mapping these records shows that the distribution of white-clawed crayfish was much greater before 2015, although many of these observations were substantially before 2015 with significant declines through the 1990s and 2000s (**Figure 3.2A**). On the other hand, the record for signal crayfish shows that they have consolidated their range and even expanded it in certain areas around Wales and Scotland (**Figure 3.2B**). Inspection of the first year that signal crayfish were observed in different sub-catchments shows that they were first recorded around southern England (**Figure 3.3A**), but have recently expanded their range towards northern England, southern Scotland, and Wales. **Figure 3.3B** shows that 20 sub-catchments contained observations for both species, with the majority of England having this crayfish residency status. 133 sub-catchments have only had signal crayfish observations, predominantly around the edges of their range in the south coast and Scotland (**Figure 3.3B**). 66 catchments had only ever had white-clawed crayfish observations. These were predominantly in Wales and around the north of England (**Figure 3.3B**). The hotspot analysis demonstrates that the core range of signal crayfish is around the south and middle of England (**Figure 3.4**), which roughly corresponds to the location where they were initially introduced (**Figure 3.2A**), with the extreme edge of the invasion range approximately corresponding to the Cambrian Mountains in Wales and the Central Belt and Borders regions of Scotland.

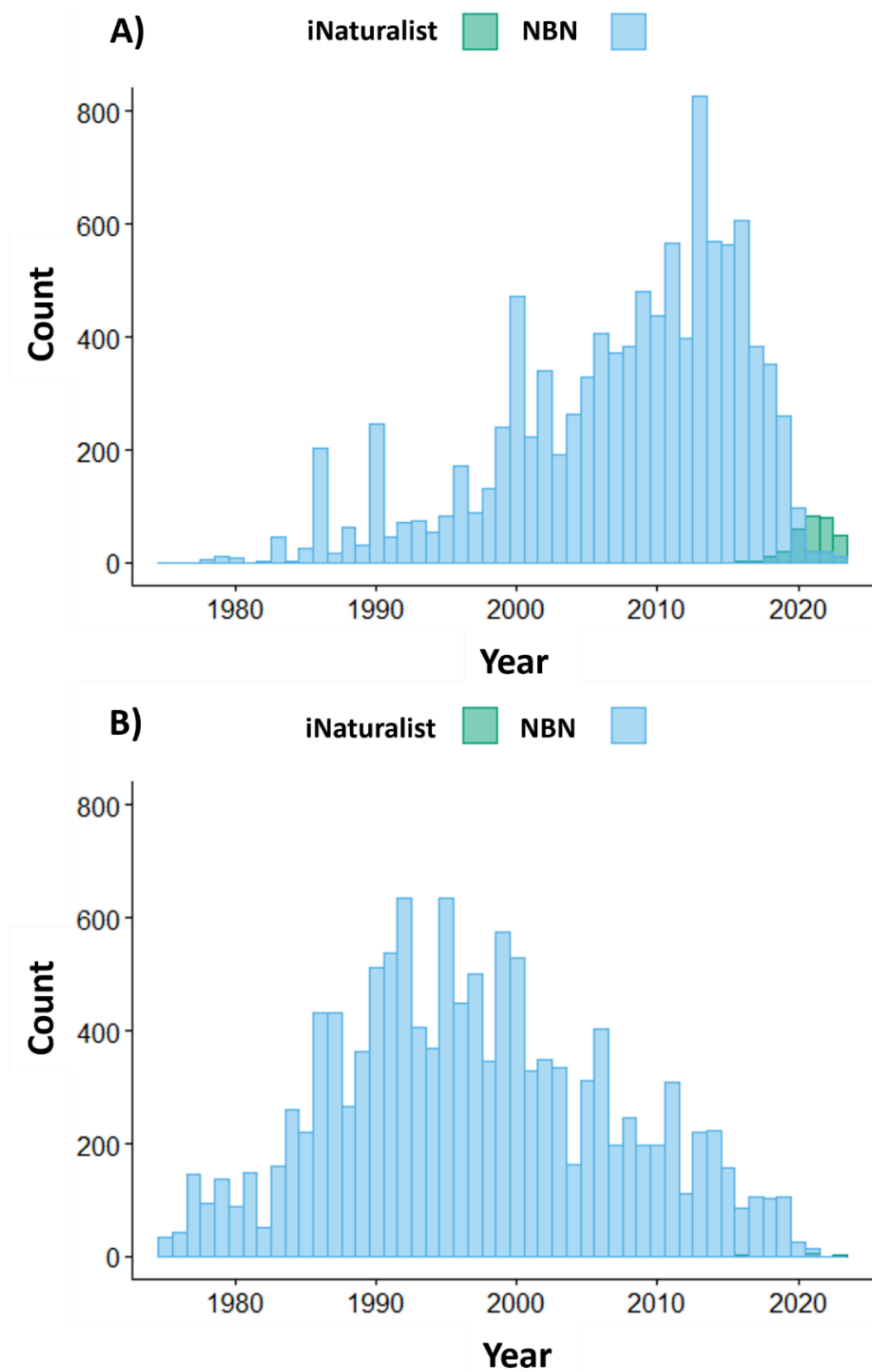


Figure 3.1: Histograms showing the number of observations for **A)** signal crayfish and **B)** white-clawed crayfish from 1975 to 2023. Histograms also show the dataset (NBN or iNaturalist) that they came from.

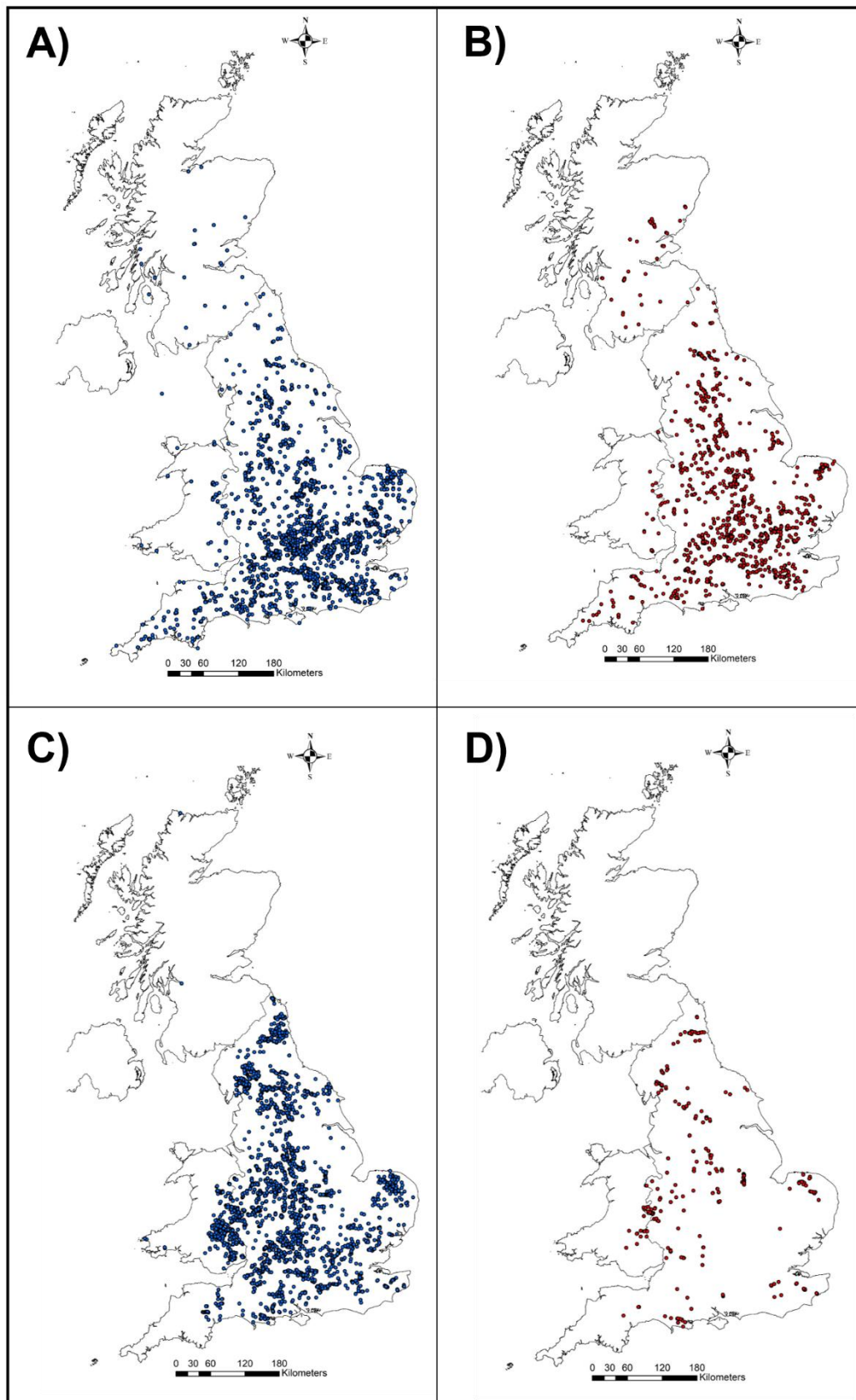


Figure 3.2: Map showing the location of records for the two species of crayfish in Great Britain. **A)** represents signal crayfish before 2015 and **B)** represents for the same species after 2015. **C)** represents white-clawed crayfish before 2015 and **D)** represents for the same species after 2015

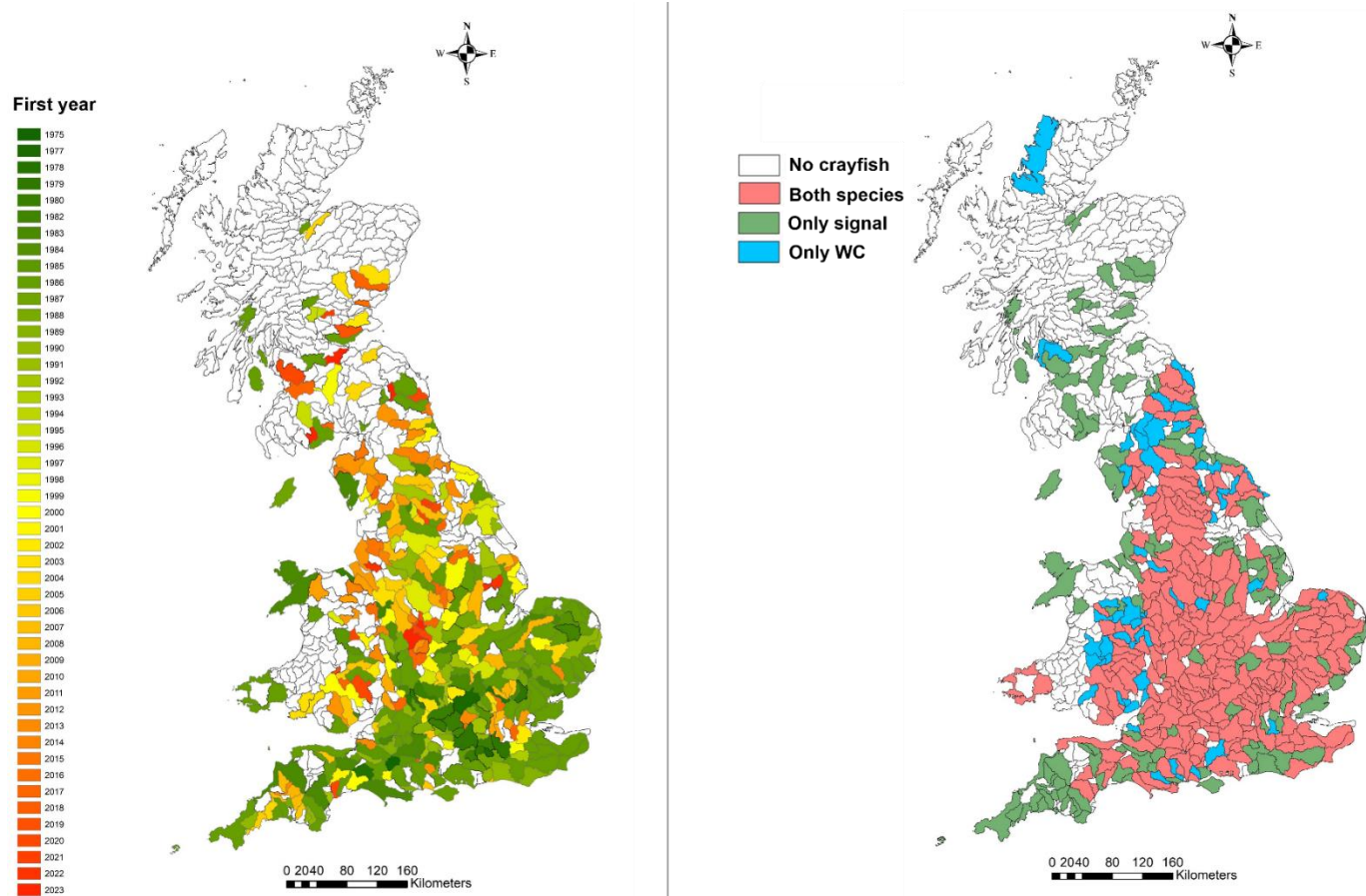


Figure 3.3: Map showing **A)** the first year that signal crayfish were observed and **B)** the crayfish residency status of each sub-catchment in Great Britain (white = no crayfish ever observed, red = both crayfish species observed, green = only signal crayfish observed and blue = only white-clawed crayfish observed here).

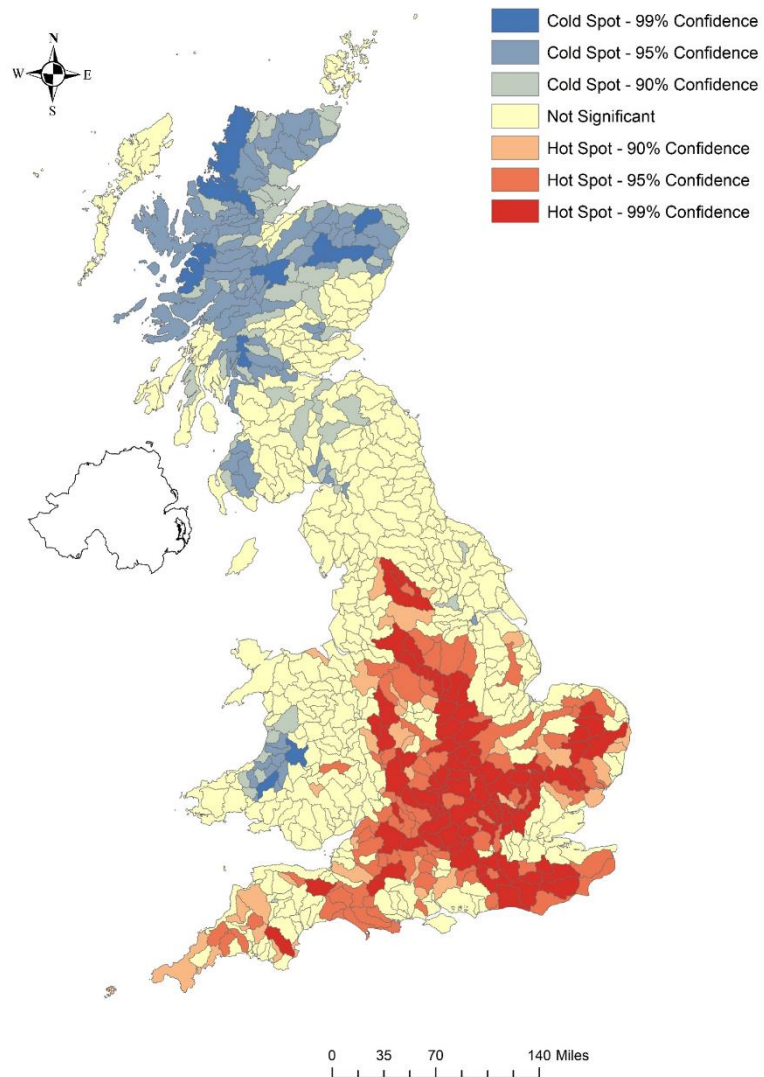


Figure 3.4: Map of Great Britain with the hot spots (in red), representing the core range of signal crayfish. Map also shows cold spots (in blue), which represents areas where the species is relatively less abundant.

For the PCA analysis *without* the water quality variables, the first two (PCs explained 45.6% of the variance explained by the factors (PC1 = 32.8%, PC2 22.8%) (**Figure 3.5A**). This analysis included 347 sub-catchments. For the PCA analysis *including* the water quality variables, the first two principal components (PC) explained 43.6% of the variance by the factors (PC1 = 29.9%, PC2 = 13.7%) (**Figure 3.5B**). This analysis included 237 sub-catchments. Both biplots show that there is a largely nested distribution, with catchments that only encompass white-clawed crayfish entirely contained within the environmental space of those that only contain signal crayfish or both (Figure 3.5).

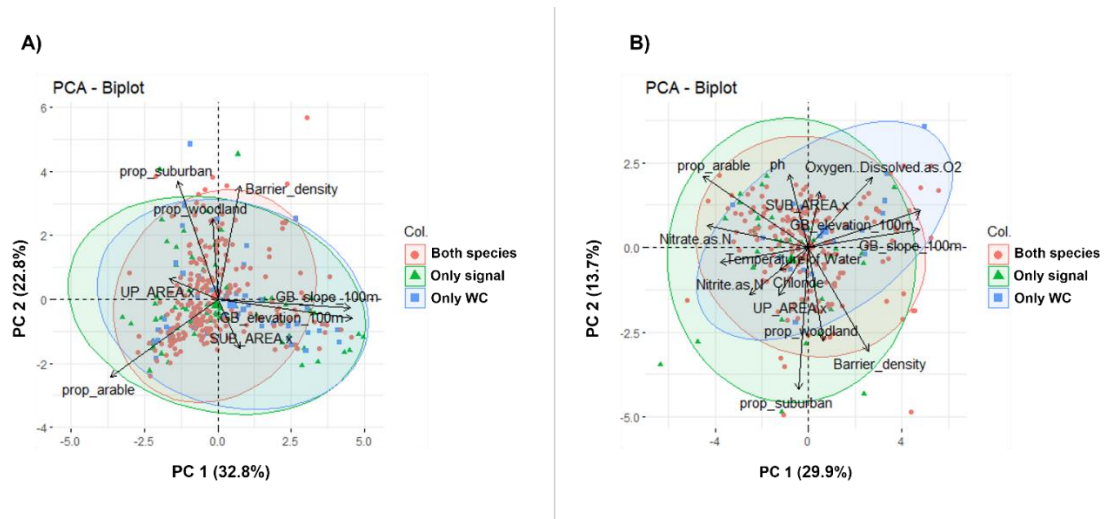


Figure 3.5: PCA biplots showing the environmental conditions at sub-catchments with different crayfish occupancy statuses. **A)** shows a biplot without the water quality variables (dissolved oxygen, pH, water temperature, Chloride, Nitrate and Nitrite) included and **B)** shows a biplot with these variables included.

3.5. Discussion

3.5.1. Distribution of signal and white-clawed crayfish in Great Britain

The results of this study show that the current distribution of white-clawed crayfish has continued to decline since 2015. The maps show that white-clawed crayfish are likely no longer present in much of southern England, which now represents the core range of signal crayfish. The remaining populations of white-clawed crayfish are in northern England and Wales. In comparison, as well as consolidating their distribution around the south of England, signal crayfish have expanded outwards towards northern England and Wales since 2015. This general pattern of signal crayfish expansion and declining white-clawed crayfish populations have been presented in previous reports (e.g., Holdich et al., 2014, Rogers and Watson, 2011). Here we show that these trends remain strong and that if they continue at this pace, signal crayfish will likely soon reach the final remaining populations of white-clawed crayfish.

The maps in this study provide a visual representation of an interesting aspect of the spread of signal crayfish in Great Britain. Unlike other INNS, the pattern of spread of signal crayfish across sub-catchments in Great Britain does not show a progressive expansion of species outwards from a single point, but instead the expansion from multiple subsequent nuclei. This can be seen in **Figure 3.3A**, showing the first year that signal crayfish were observed in different sub-catchments. Whilst there is a concentration of early observations around the south-east of England, we also see early observations in the 1970s in the northern part of the country, west Wales and even in Scotland, and the subsequent expansions from these locations. This pattern of expansion outwards from multiple nuclei is likely explained by the dispersed locations of the fish farms and lakes where signal crayfish were initially introduced (Holdich et al., 2014). Furthermore, in later decades, signal crayfish are observed in sub-catchments far away from where they had previously been spotted. One possible explanation for this apparent 'jump' between far away catchments is the lack of regular crayfish monitoring efforts, which could mean that the record does not always capture the expansion of signal crayfish from one area to another.

However, another explanation is that it shows evidence of the subsequent transfer of signal crayfish between catchments by human actors. This latter explanation is a likely contributor as it is common knowledge that humans, both legally and illegally, have transported signal crayfish to new areas ever since they were first introduced in Great Britain (**see Chapter 5**) (Holdich et al., 2014); however, both explanations have likely played some role in creating this unique pattern of spread.

3.5.2. Factors influencing the distribution signal and white-clawed crayfish

The results from the PCA analyses conducted in this study show that signal and white-clawed crayfish have been observed in locations that share very similar conditions. The PCA without the water quality variables shows that the grouping of sub-catchments that have only ever had white-clawed crayfish are completely contained in the environmental space of those that have only had signal crayfish. Likewise, the PCA analysis including the water quality variables shows that the environmental tolerances of the two species are very similar, with that of signal crayfish being slightly wider. There appears to be one catchment where only white-clawed crayfish has been observed that leans more towards those sites that have higher oxygen concentration and elevation. However, as it is just one site, it cannot be argued that this pattern is a general trend in the analysis. Furthermore, this sub-catchment may have only had white-clawed crayfish because signal crayfish have not had time to reach it yet, instead of it being unsuitable for signal crayfish. This sub-catchment is in the north of England, just north of where signal crayfish were observed in 2014; it is therefore likely that this site could soon also contain signal crayfish if the observed pattern of expansion continues. The PCA analysis suggests that signal crayfish may be able to flourish wherever white-clawed crayfish can exist. Previous authors have commented that the

conditions that make a site suitable for white-clawed crayfish in turn make it suitable for signal crayfish (Holdich and Rogers, 2000), and the results from our study appear to corroborate this conclusion.

These findings also have implications for conservation efforts trying to protect the remaining white-clawed crayfish populations in Great Britain. Ark sites are already recommended to have some degree of isolation (e.g., be an enclosed system) or at least be hard to reach (Peay, 2009). The results of this study suggest that this isolation aspect may perhaps be the most critical part of the selection criteria for ark sites. Without some degree of isolation, it may only be a matter of time before signal crayfish and the crayfish plague seep into these locations. It may also be best to ensure that extra precautionary measures, such as the use of physical barriers or regular monitoring via eDNA, are implemented to ensure that signal crayfish do not colonize these suitable ark sites.

3.5.3. The role of citizen science and data

The results from this study highlight the increasing importance that citizen science plays in the study of INNS and wider ecology. Analysis of the crayfish records that we collated shows that the number of observations from the NBN dataset, which is predominantly provided by government bodies and NGOs (Ratcliffe and Jones, 2022), is decreasing for both species. Although a decrease in the number of observations for white-clawed crayfish can be understood due to their loss from many locations, the decrease in signal crayfish observations since 2015 is surprising due to their otherwise relentless expansion. There may be a 'lag time' between these larger organisations making signal crayfish observations and adding them to the NBN dataset. However, it could also be that there are now fewer routine crayfish monitoring taking place in Great Britain due to declining resources and/or interest in collecting information on the location of this species, in line with their almost ubiquitous expansion. The COVID-19 pandemic

is also expected to have had some impact on the number of observations because of restrictions and changes in the operations of organisations. Whatever the reason, the decline in the number of observations from large organisations is worrying.

In contrast, records on iNaturalist, made up exclusively of observations from citizen scientists (Van Horn et al., 2018), are rapidly increasing. This is particularly the case for signal crayfish. In fact, although the NBN records make up the vast majority of the observations involved in this study, since 2021, there have actually been more confirmed signal crayfish observations on the iNaturalist database than on the NBN Atlas. Although the NBN record is predominantly made up of observations from organisations, an important proportion of it is also provided by citizen scientists. Furthermore, as well as just the volume of number, there were several sub-catchments where the only observation of either species came from the iNaturalist record. To put it another way, the only way we know that there are remaining white-clawed crayfish populations or whether signal crayfish have expanded in certain regions is because of citizen science. This important contribution of citizen science to research on INNS is not new, with previous studies also demonstrating its role in the management of INNS (Gallo and Waitt, 2011; Delaney et al., 2008; Earp and Liconti, 2020).

Citizen science is not perfect, with certain well-known challenges regarding data quality and distribution bias towards areas with high populations (Earp and Liconti, 2020). Likewise, although we include citizen science observations in this study, it is highly likely that our dataset is incomplete and does not capture the true extent of signal and white-clawed crayfish distribution. As well as possible limitations due to incomplete observation records, issues with the distribution of water quality data also impact studies like this one. The lack of regular water quality data for many areas in Great Britain means that many sub-catchments were not included in the PCA analysis. In this study, the PCA analysis *without* these variables included 110 more sub-catchments than the one *with* this data. It is essential that high-quality

environmental data is available for all parts of Great Britain to ensure that studies like this can accurately understand the ecology of important INNS and native species; citizen science may therefore also have a role to play in the collection of more spatial distributed water quality data alongside crayfish observations. For example, Vedia et al. (2016) found that the distribution of signal crayfish in Spain was correlated (positively) with the abundance of certain native fish species as well as (negatively) with the presence of boulders. Additionally, the distribution of signal crayfish may also be negatively correlated with the presence of other INNS of crayfish present in Great Britain, such as the red swamp crayfish (*Procambarus clarkii*) as these could increase the competition for key resources (Sibley, 2003). Having access to reliable and widespread information on these factors may allow future studies to better characterise the biotic and abiotic factors affecting signal crayfish.

The benefits of citizen science extend beyond the contribution it can make to the records of INNS and native species. Promoting citizen science is known to be an effective approach to increasing awareness around a particular ecological issue (Brown and Williams, 2019). This impact could be particularly beneficial in the case of signal crayfish management in Great Britain, where stakeholders often cite that there is a lack of awareness around the species and low political will to manage them (see **Chapter 5**). It would be beneficial for future work to explore the potential that citizen science could have for increasing awareness around crayfish management in Great Britain. A study that can galvanise broad sections of society with an interest in nature, as well as perhaps new technological advancements (e.g., artificial intelligence), may be able to create a more complete picture of the distribution of crayfish in Great Britain than is currently possible.

3.6. Conclusion

This study demonstrates the rapid expansion of signal crayfish and the dire situation for the remaining populations of native white-clawed crayfish in Great Britain. Our findings show that signal crayfish initially expanded outwards from multiple nuclei and continue to migrate rapidly to regions that have only ever contained white-clawed crayfish. It may only be a matter of time before these are colonised by signal crayfish as well, as our environmental data indicates that they can flourish in the same conditions where the native species are found. If the UK government continues to favour the use of ark sites to conserve the native species, it must therefore ensure that these locations are adequately protected and isolated for them to succeed. Citizen science is already proving critical to locate the current distributions of both crayfish species and it could play an even greater role in the future to increase awareness of the plight of white-clawed crayfish in Great Britain.

Chapter 4: Testing for differences in morphological and behavioural traits of signal crayfish (*Pacifastacus leniusculus*) along its invasion continuum in Great Britain.



In the history of all empires, the settlers at the front line of conquest are invariably the most brutal...

- From “Cuba: A New History” by Richard Gott

4.1. Abstract

Individuals at the leading edge of an expanding biological invasion often demonstrate differences in key functional traits compared to those at the core of their invasive range. Invasive Signal crayfish (*Pacifastacus leniusculus*) are advancing across many rivers in the UK, but we still do not understand whether there is consistent variation in traits along their invasion continuum and whether this is influencing the invasion. In this study, we compare key morphological and behavioural traits in signal crayfish at invasion-front and invasion-core sites in five rivers in the UK. We also examined differences in population characteristics (sex ratio, population density) between the populations in the different rivers. Location along the invasion continuum had a significant effect on some morphological traits, with signal crayfish at the invasion-front sites being consistently smaller (lower carapace length, width, and weight). Likewise, invasion-front sites in all five rivers had lower density than the corresponding invasion-core sites. These findings support the idea that the invasion of signal crayfish in the UK represents a 'pushed' wave, where smaller individuals are excluded from the core and driven to the invasion-front sites in the rivers. We also find the river that signal crayfish were caught in significantly influences all the traits, demonstrating that there is great diversity in populations between the rivers. The study highlights the importance of understanding the variability of traits in invasive non-native species throughout their range to effectively manage them and their impacts.

4.2. Introduction

Once introduced into a new area, successful invasive non-native species (INNS) can quickly expand at astonishing speeds (Galib et al., 2022). Numerical modelling can provide environmental managers and policymakers with crucial information on the spread of INNS (Travis and Dytham, 2002). However, attempts to model these biological invasions commonly underestimate their rates of expansion (Erm and Phillips, 2020; Hastings et al., 2005), suggesting that there may be other unaccounted processes taking place. A possible complicating factor for predicting the spread of an INNS is variability in the traits of the population along the invasion continuum (Phillips et al., 2010). Evidence suggests that individuals at the front of an expanding invasion can demonstrate distinct phenotypic traits compared to those in long-established sites at the core of their invasive range (Shine et al., 2011). Shifts in traits associated with the dispersal capacity or performance of individuals at the invasion front can lead to substantial changes in the rate of expansion (Alford et al., 2009). Being able to accurately predict how fast an INNS spreads is critical, as they can have numerous ecological (Vilà and Hulme, 2017; Bellard et al., 2016), environmental (Mathers et al., 2022), social (Siegert et al., 2023) and economic impacts (Diagne et al., 2021).

Species' ranges are spatially and temporally dynamic (Gaston, 2003). This is particularly true for species that do not currently occupy all their available environmentally suitable habitat (Yalcin and Leroux, 2017). Biological invasions typically represent an example of such a nonequilibrium condition, as many INNS have not had sufficient time to occupy all the suitable habitat in their new location, and thus can further expand (Perkins et al., 2013). Whilst earlier studies focused on how traits vary *between* species to understand their invasiveness (e.g. Lodge, 1993; Rejmanek and Richardson, 1996), research in the past decade has extended to analyse variation *within* species (Cote et al.,

2010). Individuals at the front of an expanding population tend to experience novel environmental, demographic, and physiological pressures compared to those at core sites that have been inhabited for a longer period (Chuang and Peterson, 2016). Evidence is growing that these processes can lead to the rise of phenotypic differences between conspecifics at the front and core of invasions (Gruber et al., 2017a; Gutowsky and Fox, 2012).

One theory that has been proposed to explain how these shifts in traits arise at the front of an invasion is the idea of 'spatial sorting' (Shine et al., 2011). The basis of spatial sorting is that evolutionary change can take place in the front of an expanding population due to initial variations in the dispersal rate (Canestrelli et al., 2016). The theory follows that dispersal capacity tends to sort individuals spatially along the invasion continuum, with those that have higher dispersal capacity more likely to be present at the front of the expansion (Phillips and Perkins, 2019). The theory follows that subsequent interbreeding between these fast dispersers produces offspring with even greater dispersal ability (Phillips et al., 2010). As this process continues, the traits associated with dispersal capacity at the front of the expansion become more pronounced due to the preferential selection of individuals that demonstrate a greater dispersal rate (Shine et al., 2011). The traits under selection by this process may be discrete but may also occur in dispersal syndromes when various dispersal-related traits (e.g. activity, leg size and exploration tendency) are selected together (Canestrelli et al., 2016; Sih et al., 2012). Spatial sorting has received lots of interest recently and is supported by various studies showing an increasing rate of expansion in populations (Phillips et al., 2006; Thomas et al., 2001).

As well as via evolutionary change, either via spatial sorting or other processes, a shift in traits at the front of an expanding population may also arise due to phenotypic plasticity (Chuang and Peterson, 2016). Phenotypic plasticity refers to the ability of a genotype to vary its phenotype depending on its context, thus enabling the organism to

maintain high performance in different environments (Bateson and Gluckman, 2011). As individuals at the front of an expanding population may experience novel biotic and abiotic pressures, this plasticity may allow them to adopt certain phenotypic traits without undergoing any genetic modification (Gruber et al., 2017b). This may be particularly important for behavioural traits, which are known to be particularly labile (Snell-Rood, 2013). Common-garden experiments have concluded that at least some observed shifts in invasion-front individuals may be partly explained by phenotypic plasticity, with genetic modification accounting for the other portion (Gruber et al., 2017b).

The concepts previously mentioned (e.g., spatial sorting) all describe situations whereby the population expands due to dynamics at the front. However, shifts in traits may also arise due to processes taking place at the core (Erm and Phillips, 2020). Many theories describe range expansion as a process where individuals at the front ‘pull’ the population forward into new areas (Dahirel et al., 2021), which may be particularly the case in populations where dispersal is greater at low-density conditions typically found at the front (Birzu et al., 2019). However, dispersal and population growth rates can sometimes be lower in low-density conditions, a phenomenon typically referred to as the Allee effects (Tobin et al., 2011; Liebhold and Bascompte, 2003). Furthermore, some populations demonstrate greater dispersal rates at higher density as this can be a mechanism to escape the high levels of intra-specific competition (Harman et al., 2020). These situations can lead to situations where the high-density core ‘pushes’ the expansion of the range (Dahirel et al., 2021). These population dynamics can similarly lead to a shift in traits between core and front populations if individuals with certain traits (e.g., smaller body size or less aggressive) are preferentially ‘pushed’ to the front (Hudina et al., 2014).

Studies have found that many different behavioural and morphological traits can be different at the invasion-front of INNS (**Table 4.1**). Some behavioural traits that have been found to vary include activity levels, exploration, aggression, and boldness. These traits have been

frequently assessed at invasion-front sites as they are believed to be associated with greater dispersal, as well as an overall greater ability to thrive among novel conditions and/or threats (Atwell et al., 2014). For example, Cote et al. (2010) found that mosquitofish (*Gambusia affinis*) in recently invaded sites tended to be more active, more exploratory and show higher boldness in comparison to those in the range-core. Examples such as this have been used to explain increases in the dispersal ability of individuals at the front. Likewise, morphological traits such as body and leg size are also regularly analysed to see whether they differ between invasion-front and invasion-core populations (Phillips et al., 2006). These traits have been of particular interest because they are thought to influence the dispersal and competitive ability of individuals. The most infamous example of this was the finding that the relative leg size of cane toads at the invasion-front was increasing through time, which in turn led to faster expansion of the INNS through Australia (Phillips et al., 2006). Studies have also found a shift towards larger body size towards the front in the invasion of several species (Brandner et al., 2013). This concept has been referred to as “bigger is better”, arguing that a larger body size at the front provides a greater competitive ability and increased survival (Brandner et al., 2013). However, evidence suggests that individuals do not always get bigger at the invasion front, with multiple studies finding smaller individuals at the front compared to those at the invasion core (Hudina et al., 2012; Brownscombe and Fox, 2012). This might be particularly the case when invasions expand from being ‘pushed’ by those at the core, as opposed to being ‘pulled’ from those at the front.

Table 4.1: Examples of traits that have been found to differ at the invasion-front and the species where this has been observed. Arrows represent whether the trait has been found to increase (up-arrow) or decrease (down-arrow) at the invasion-front.

Trait type	Trait	Change at invasion-front	Example(s)	Reference(s)
Behaviour	Activity	↑	• Cane toads (<i>Rhinella marina</i>) • Common myna (<i>Acridotheres tristis</i>) • Mosquitofish (<i>Gambusia affinis</i>)	(Lindstrom et al., 2013) (Burstal et al., 2020) (Cote et al., 2010)
	Aggression	↓	• Signal crayfish (<i>Pacifastacus leniusculus</i>)	(Hudina et al., 2015)
	Boldness	↑	• Cane toads (<i>Rhinella marina</i>) • Round goby (<i>Neogobius melanostomus</i>)	(Gruber et al., 2017b) (Myles-Gonzalez et al., 2015)
	Exploration	↑	• Cane toads (<i>Rhinella marina</i>) • Mosquitofish (<i>Gambusia affinis</i>)	(Gruber et al., 2017b) (Cote et al., 2010)
Morphology	Size	↑	• Ground beetle (<i>Merizodus soledadinus</i>) • Round goby (<i>Neogobius melanostomus</i>)	(Laparie et al., 2013) (Brandner et al., 2013) (Hudina et al., 2017)

			Signal crayfish (<i>Pacifastacus leniusculus</i>)	
	Size	↓	- Signal crayfish (<i>Pacifastacus leniusculus</i>) - Round goby (<i>Neogobius melanostomus</i>)	(Hudina et al., 2012) (Brownscombe and Fox, 2012)
	Leg	↑	Cane toads (<i>Rhinella marina</i>)	(Phillips et al., 2006)
	Relative claw size	↑	Signal crayfish (<i>Pacifastacus leniusculus</i>)	(Hudina et al., 2012)

Whilst many studies have tested for trait shifts at the invasion front of INNS (e.g. cane toads, round goby – see **Table 4.1** for references), there have been relatively few studies focused on signal crayfish (*Pacifastacus leniusculus*) in their invasive range (Galib et al., 2022). Furthermore, nearly all studies looking at invasion front trait shifts in signal crayfish have focused on a single population in the Korana River in Croatia (Rebrina et al., 2015; Hudina et al., 2015; Dragičević et al., 2023). A study here found that signal crayfish at invasion-front sites were in better condition than those at the core and that females at the former exhibited better energetic status of hepatopancreas and gonads, both key factors in determining reproductive capability (Rebrina et al., 2015). Another study in this river also found that signal crayfish were larger at invasion front sites, with the size of individuals decreasing when the site became part of the core (Hudina et al., 2017). In contrast to these results, a different study by the same authors found a greater proportion of smaller signal crayfish at invasion front sites (Hudina et al., 2012). Analysis along the Korana River has also found differences in viral RNA between invasion-core and front sites. Finally, the study by Hudina et al. (2015) that analysed signal crayfish from the invasion front

were less aggressive compared to individuals at invasion core sites. The authors argue that this may be because there is a greater selection pressure for aggression at the invasion-core, due to the higher population density found here (Hudina et al., 2015). More recently, a study in the UK on the River Tees found that the behavioural traits that promote dispersal in signal crayfish tended to differ between invasion core and front sites (Galib et al., 2022). The authors found that dispersal was closely associated with greater boldness and climbing at invasion front sites, whereas at the core sites, activity level had the strongest relationship with dispersal (Galib et al., 2022).

Findings from these previous investigations (e.g., Rebrina et al., 2015; Hudina et al., 2015; Galib et al., 2022), indicate that signal crayfish in the UK may also show shifts in traits between invasion-core and invasion-front sites. Shifts in the behaviour and morphology of signal crayfish at invasion front sites in the UK may result in populations with different levels of performance and/or dispersal ability. This could in turn impact the rate of expansion at the invasion-front as has occurred in other invasions (Phillips et al., 2006). Work in the UK has shown that rates of signal crayfish expansion in some rivers have increased by over an order of magnitude in recent decades (Bubb et al., 2005). While some evidence suggests that signal crayfish traits may differ in invasion-front sites in certain rivers (e.g., Galib et al., 2022) we are still not fully aware whether this is a general pattern across the UK as it has only taken place on a single river. Testing for shifts in key traits across multiple rivers will enhance our knowledge of the population characteristics at the leading front of the signal crayfish invasion and provide managers with actionable information to control their spread.

This study aims to better understand whether signal crayfish differ between invasion-front and invasion-core sites in the UK. Our specific objectives were to: 1) Test whether the location along the invasion continuum (i.e., invasion-front vs invasion-core sites) influences key behavioural and morphological traits in signal crayfish; 2) Understand whether any variation in traits along the invasion continuum is repeated

among different river systems in the UK and 3) synthesise the results to provide the implication it may have on the management of signal crayfish in the UK.

4.3. Methods

4.3.1. Site selection

For this research, invasion-core sites are defined as those sites where the first signal crayfish observation was >15 years ago. Invasion-front sites are defined here as those sites, furthest from the core population for that river, where the first signal crayfish observation was less than five years before the start of sampling. These definitions for invasion-core and invasion-front sites were assigned to correspond with those of previous research in the literature (Gruber et al., 2017a; Galib et al., 2022). Selecting river systems that contain both invasion-front and invasion-cores sites was key, as it allowed us to use a pairwise approach that could test whether any effect that location along the invasion continuum had on signal crayfish traits was a general pattern. Likewise, it was also important that the selected rivers were distributed across the UK to capture any regional differences that may exist. We used a combination of collated observation data (see **Chapter 3**) and discussions with experts such as environmental managers and academics to locate appropriate rivers (see **Chapter 5**). Following this selection stage, five river systems were selected for crayfish sampling. Moving from south to north, these comprised the River Darent (Kent), the River Nene (Leicestershire), the River Soar (Leicestershire), the River Wharfe (Yorkshire) and the River Tees (Durham) (**Figure 4.1**)

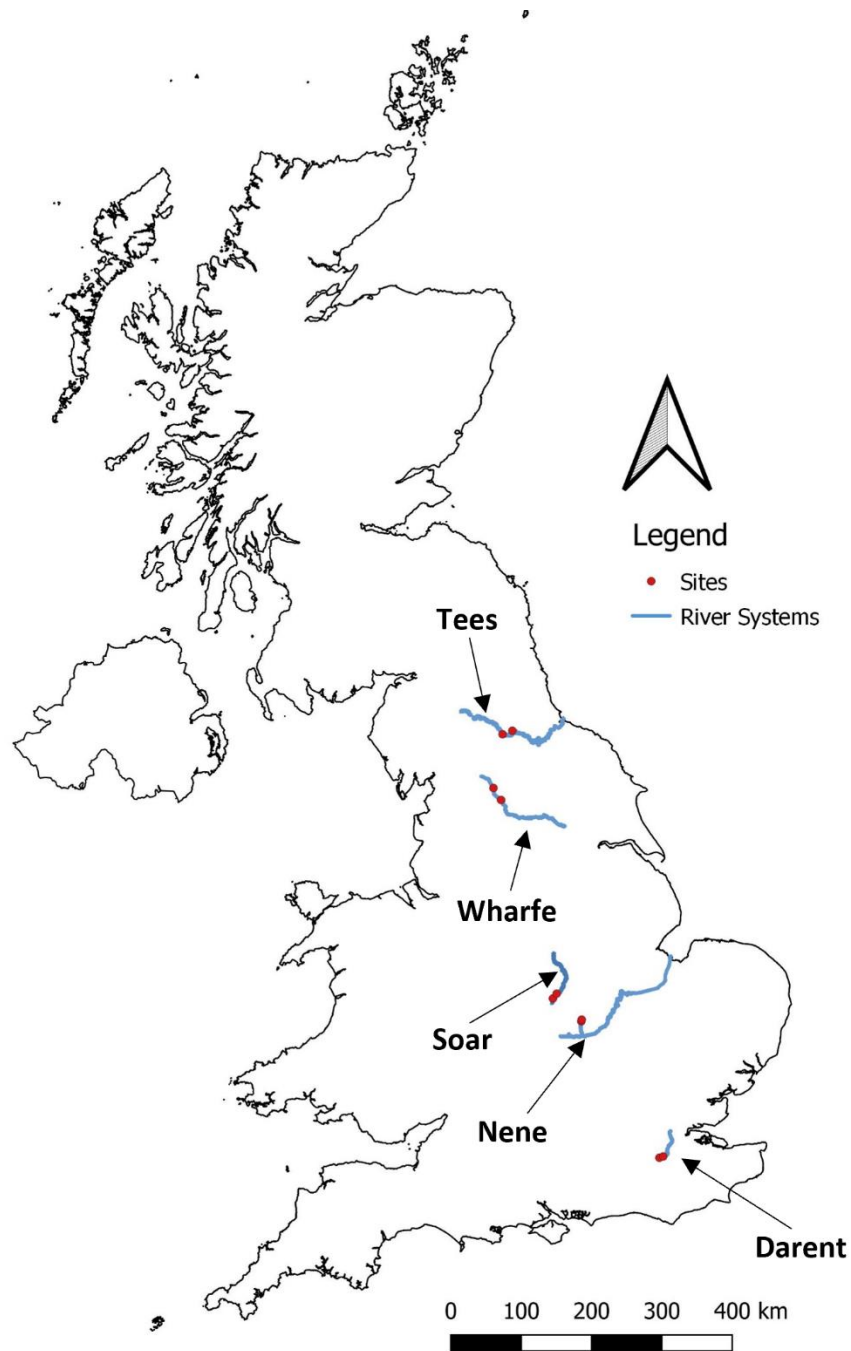


Figure 4.1: Map showing an overview of Great Britain and the location of the five Rivers that were selected for this study (the red dots represent the invasion-front and invasion-core sites within these rivers).

For this chapter, the invasion-core and invasion-front sites consisted of 100m reaches of the rivers, allowing for a comparison of relative signal crayfish density measurements between sites. To select the location of

the invasion-core site on each river system, locations that satisfied the previously mentioned definition (i.e. >15 years of signal crayfish observations) and still contained signal crayfish were identified. The same approach was used to locate the approximate location of the invasion-front sites. However, to ensure that that sampling took place in the current/true front of the invasion in that river, a preliminary survey was established to establish its location. This included searching outwards at 50-metre intervals away from where the last confirmed observation was. This process was repeated until no signal crayfish were recorded at a site, at which point the invasion-front would be determined as the last 100-metre section of the river where signal crayfish were recorded. This followed a previously used approach (Galib et al., 2022).

River Darent

The River Darent is a small chalk stream in northwest Kent that forms part of the larger Thames catchment (Gollock et al., 2011). The catchment of the River Darent is split between heavily developed urban areas of Greater London in the north and west of the catchment and the protected green belt area in the south (Holmes, 2005). Signal crayfish observation data provided by an environmental consultancy firm with experience in this site indicated that this invasive species had been present at this site for 16 years before sampling. The location of the invasion-front site was determined to be just over 4km downstream from the core (**Figure 4.2**).

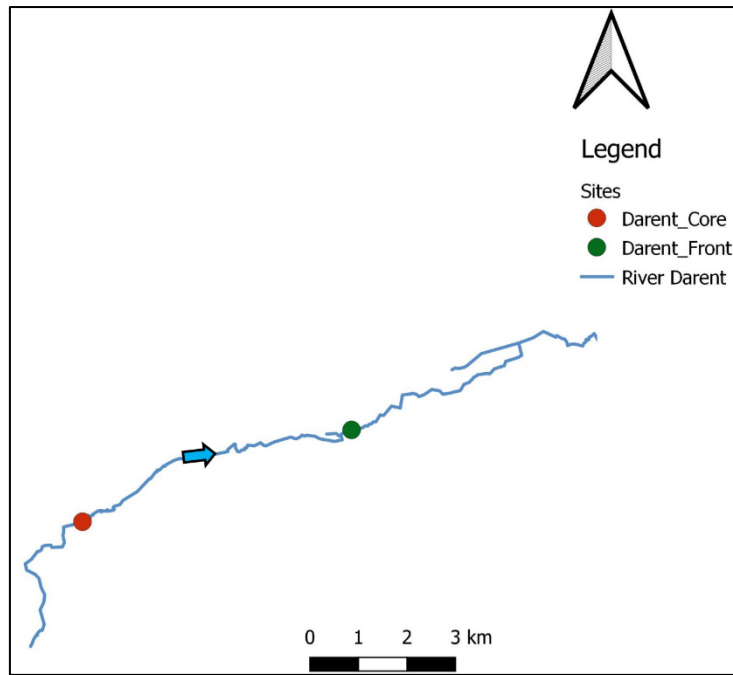


Figure 4.2: Map of the stretch of River Darent with invasion-core (red cricle) and invasion-front (green circle) sites. Arrow shows the direction of the flow of water.

River Nene

The River Nene rises in the west of the county of Northamptonshire and then flows northeast for around 190km before discharging in The Wash, near Sutton Bridge in Lincolnshire (Brierley et al., 1989; Balbi, 2000). The catchment of the River Nene is predominantly clay in the west and some limestone towards the east (Brierley et al., 1989). The location of the invasion-core on the River Nene was northwest of the village of Brixworth. Records from the National Biodiversity Network (NBN) show observations of signal crayfish as early as 2000. The location of the invasion-front was determined to be 1.74km upstream towards the west of the Village of Hanging Houghton (**Figure 4.3**).

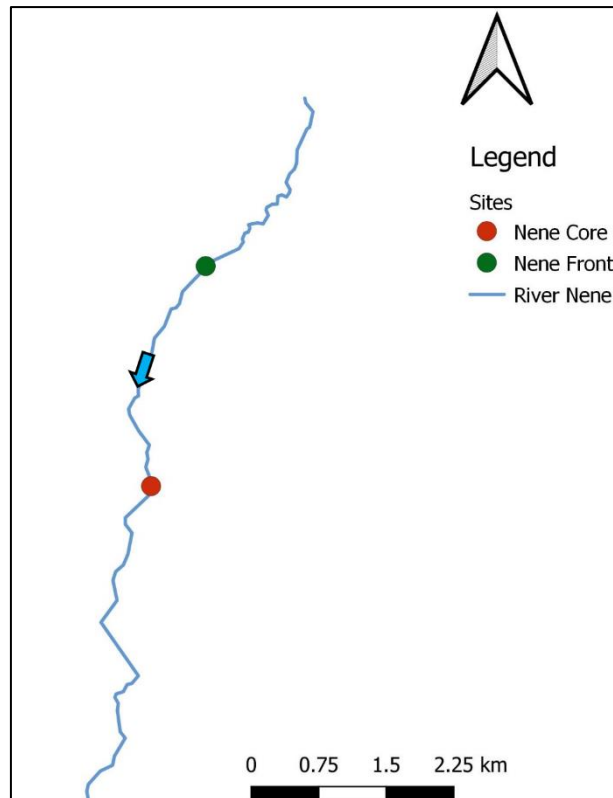


Figure 4.3: Map of the stretch of River Nene with invasion-core (red circle) and invasion-front (green circle) sites. Arrow shows the direction of the flow of water.

River Soar

The River Soar is the principal river in the county of Leicestershire, and it forms part of the wider River Trent catchment. The Soar Valley is part of the geological boundary of harder rock relating to the Pennines and Wales (towards the north and the west) and the softer stones of east and south England (Williams, 1985). The location of the invasion-core on the River Soar is to the east of the village of Sharnford in Leicestershire. Records from the Environment Agency (EA) show observations of signal crayfish in this area as early as 2004. The location of the invasion-front was found to be 7.6km downstream, to the south of the Village of Huncote (**Figure 4.4**).

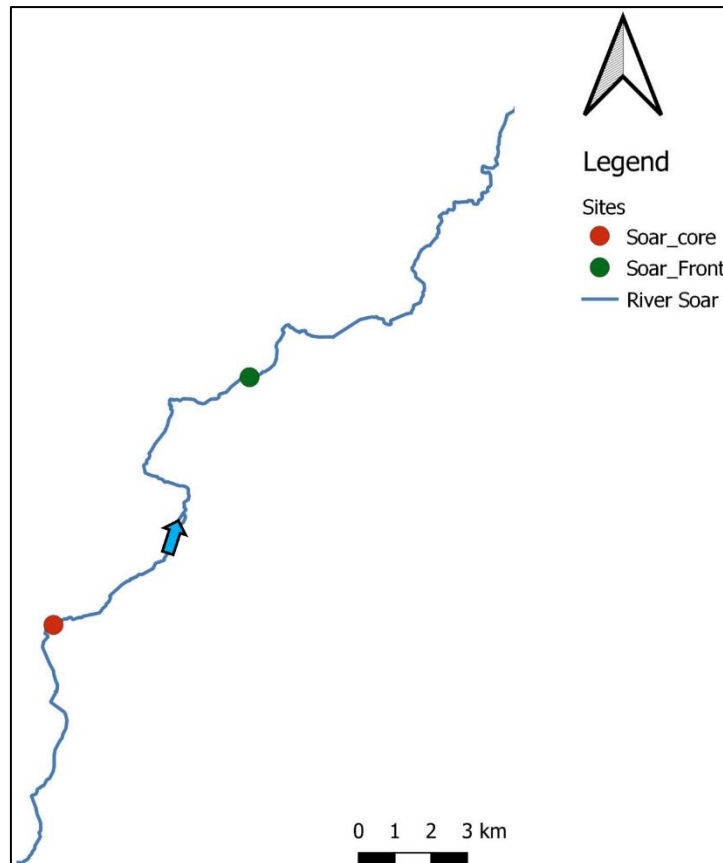


Figure 4.4: Map of the stretch of River Soar with invasion-core (red circle) and invasion-front (green circle) sites. Arrow shows the direction of the flow of water.

River Wharfe

The River Wharfe is a large upland river in the county of Yorkshire. The River Wharfe rises within Yorkshire Dales National Park and flows southeast until it joins the River Ouse downstream of Tadcaster (Yorkshire Dales Park Authority, 2012). Signal crayfish have a relatively long history on the River Wharfe catchment. In 1983, signal crayfish were originally stocked in trout fishing lakes at Kilnsey (Peay et al., 2009). The location of the invasion-core site on the River Wharfe catchment was on the main River Wharfe channel south of Kettlewell. This site is just 3.1km upstream from the Kilnsey trout fishing lakes that were initially stocked with signal crayfish in 1983. The location of the invasion-front on the River Wharfe catchment was around 25k downstream from the IC site, on the confluence between the Barben

Beck and the River Wharfe. A confirmed 2018 iNaturalist record shows that signal crayfish were present in this location (**Figure 4.5**).

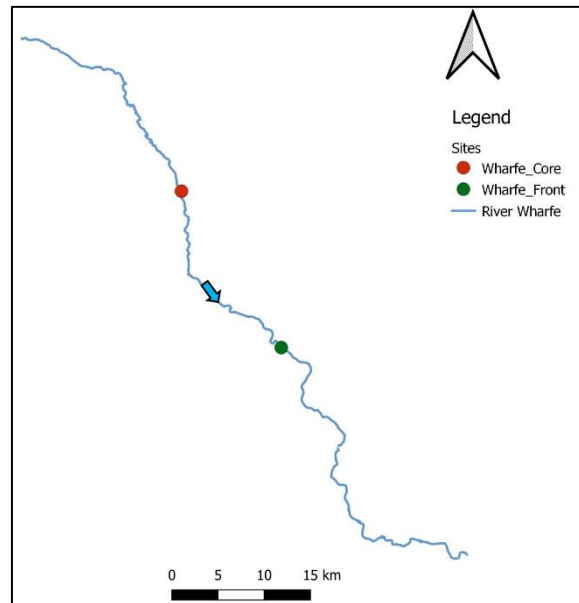


Figure 4.5: Map of the stretch of River Wharfe with invasion-core (red circle) and invasion-front (green circle) sites. Arrow shows the direction of the flow of water.

River Tees

The River Tees is one of the largest rivers in the northeast of England, discharging approximately $17\text{m}^3\text{s}^{-1}$ into the North Sea (Davies et al., 1991). The catchment of the Tees is largely rural in its upper sections, whereas its lower part contains some extremely heavily urbanised and industrialised areas (Davies et al., 1991). Although historically the River Tees catchment has been inhabited by native white-clawed crayfish, signal crayfish also have a relatively long history in the area, being introduced in the 1980s and spreading throughout the catchment thereafter (Galib et al., 2022). The invasion-core in the River Tees catchment was located on Westholme Beck just downstream of Little Newsham, County Durham. On the other hand, the invasion-front site was on the Thorsgill Beck, a tributary further upstream on the River Tees catchment. These two sites are the locations of Galib et al.

(2022). For this study, the invasion-front was updated to reflect the movement since that study took place (**Figure 4.6**).

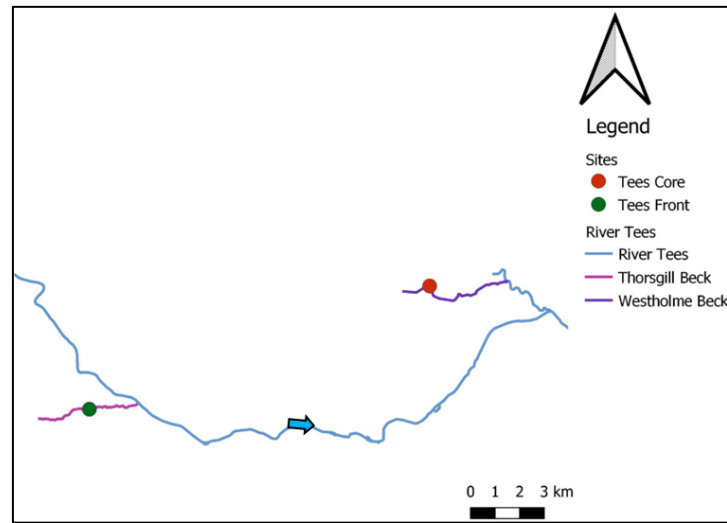


Figure 4.6: Map of the stretch of River Tees with invasion-core (red circle) and invasion-front (green circle) sites. Main River Tees channel shown by light blue line, whilst the purple line shows Westholme Beck, and pink line shows Thorsgill Beck. Arrow shows the direction of the flow of water.

Table 4.2: Key characteristics of the five rivers used in this study.

River	Dominant Substrate	Invasion Date	Land Use	Average pH
Darent	Gravel	2006	Woodland	7.9
Nene	Silt	2000	Woodland	7.5
Soar	Gravel	2004	Farmland	7.7
Wharfe	Cobble	1983	Woodland	8.8
Tees	Gravel	1980	Woodland	8.2

4.3.2. Collection of crayfish

Signal crayfish required for the morphological and behavioural assays were collected from the 100m stretches of river that made up each invasion-front and invasion-core site. At each site, crayfish were collected by two surveyors using hand-net searching throughout the

100m stretch of each site. Manual hand-net searching was used in this investigation as it does not have as strong a bias towards the collection of certain size classes and/or sex as other approaches such as baited funnel traps (Green et al., 2018). To maintain a consistent level of effort in searching and collecting crayfish, the two surveyors spent three hours at each site. Crayfish larger than 20mm in carapace length (CL) were used for assays, however, all crayfish (including those smaller than this and young of the year) were collected to determine crayfish density at the sites. To collect sufficient crayfish for the analyses, two visits on separate days were conducted to each site, meaning a total of 12 hours of crayfish searching per site (6 hours per visit). This allowed the collection of between 18 (Wharfe Front) and 27 (Soar Core) crayfish per site. All crayfish collection occurred during daylight hours and the time of day was held as consistent as possible between sites. Most crayfish were collected from instream refuges, particularly under large non-embedded boulders, as well as in burrows found on the riverbank. Some crayfish were also collected outside of these refuges, but these tended to be adult crayfish of larger size (although not exclusively). After collection crayfish were placed in a 15L plastic holding container with 5 L of river water that was periodically refreshed. At the end of the assays, it was legally necessary to euthanise invasive crayfish following Natural England protocols.



Figure 4.7: Collection of photographs from fieldwork associated with this study (during summer 2022). Principle investigator with caught signal crayfish in River Darent (top left), signal crayfish walking on riverbed in River Soar (top right), crayfish burrow in River Soar (bottom left) and tributary of River Wharfe (bottom right).

4.3.3. Assessment of morphological traits

Carapace length (CL) was measured as this is the most commonly used method to understand overall body size in crayfish (Hepper, 1966). CL was measured following the methodology outlined by Hepper (1966) as the distance from the tip of the rostrum to the end of the carapace. Carapace width was also measured as it is another common measurement to dictate the overall body size of crayfish. Relative pereopod length was also calculated using the ratio of the total leg length (established by measuring the 4th pair of legs [pereiopods]) to the CL of the individual (**Figure 4.8**). As well as enabling individuals to walk on the riverbed or over land (Cruse and Saavedra, 1996), the legs of crayfish play an important role in reducing the force of drag during tail flips, a typical escape behaviour (Pond, 1975; Cooke and Macmillan,

1985). The relative size of signal crayfish claws is another important morphological trait. Like other crustaceans, crayfish claws have evolved to perform a variety of key activities, including food habits, sexual display and agonistic behaviour (Gherardi, 2002; Levenbach and Hazlett, 1996). Large chelipeds may in turn increase their chance of acquiring and defending resources (Levenbach and Hazlett, 1996), as well as asserting dominance (Levenbach and Hazlett, 1996). The relative claw (cheliped) length of individuals was established following Bovbjerg (1956), where the total claw length was divided by CL. All measurements were established to the nearest millimetre using manual callipers. As well as these morphological measurements, crayfish mass was recorded using an electronic scale (Fisherbrand, Loughborough, United Kingdom) to the nearest 0.1mg. Studies have found a significant increase in stride length with increasing body mass, resulting in greater overall speed (Claussen et al., 2000).

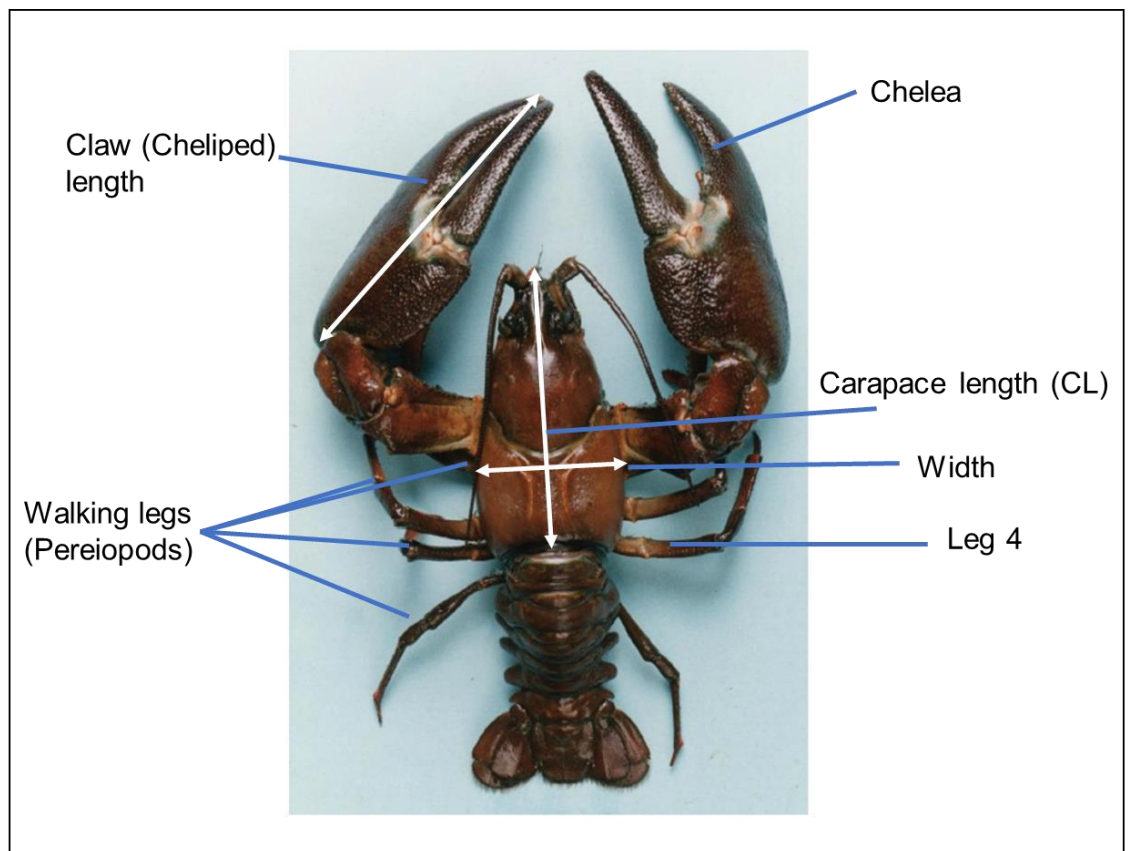


Figure 4.8: Image showing the top-view of signal crayfish (*Pascifastacus leniusculus*) and the morphological features that this study will focus on (modified from Holdich et al., 2014).

4.3.4. Assessment of behavioural traits

As already covered, activity and exploration are important behavioural traits that have been found to vary at invasion fronts (**Table 4.1**). This study will also look at another key behavioural trait in signal crayfish, climbing tendency. We analyse this trait as variations along the invasion continuum could have important implications on the effectiveness of physical barriers as a management approach for signal crayfish (Frings et al., 2013; Krieg and Zenker, 2020). However, crayfish are able to climb over certain obstacles that block their advance (Daniels et al., 2023). As a result, a greater climbing tendency may allow signal crayfish to circumnavigate more/bigger barriers (be they natural or anthropogenic) and disperse further (Daniels and Kemp, 2022). Therefore, it is important to understand whether this behavioural trait varies between invasion-front and invasion-core populations.

The behavioural tests for this study generally follow those undertaken by Galib et al. (2022). All behavioural assays were conducted on the bank at each respective site and were performed during the daytime on the day of capture under natural light and temperature conditions (Závorka et al., 2020). Although crayfish are nocturnal, conducting all behavioural assays at the same time of day provides a standardised method of measuring individuals' traits (Galib et al., 2022). The experimental arena for the test was a rectangular plastic container (52 cm long, 34 cm wide, 25 cm high) that was marked with a 2 x 2 cm grid on the bottom, but empty of any other physical features. The container was wrapped with black opaque paper to minimise visual disturbance. All three behavioural traits (activity, exploration and climbing tendency) were measured simultaneously. Before the addition of each crayfish, the experimental arena was filled with 15 centimetres of fresh river water from the site. The crayfish were then placed inside a refuge (ceramic pot) and placed at the bottom right corner of the arena for one minute to allow for acclimatisation. After one minute, the refuge was removed, and the behavioural assay would begin. Signal crayfish

behaviour was recorded for 150 seconds by a camera (Apeman A80) that was suspended above the arena. Between tests, the tank was emptied and refilled with fresh river water to eliminate the potential for scents left by previous crayfish to influence the behaviour of subsequent individuals.

Videos were analysed after all the fieldwork was completed. Activity of crayfish was measured as the total number of seconds (out of 150) during which the individual was in motion. Exploration was quantified as the percentage of unique grid cells touched by the tip of the rostrum during each test. Climbing tendency was defined here as the number of seconds that a crayfish was active with its body against the walls of the arena at an angle of 45-90° from horizontal (out of 150).

4.3.5. Assessment of habitat conditions and population characteristics

Wetted width and water depth were measured at 10m intervals throughout the study reach at each site (total of 11 measurements), giving a mean value of these characteristics for each site. Substrate composition (a key factor for crayfish; (Nyström, 2002), was also recorded following the River Habitat Survey approach (Raven et al., 1998). This approach was also used to determine additional factors such as the type of dominant vegetation present, adjacent land use type and shade percentage. Water quality data (water temperature, dissolved oxygen percentage and pH) were also collected using a YSI DSS Pro water quality sonde.

Relative crayfish density was determined by dividing the total number of crayfish collected by hand-net searching, by the wetted surface of the site. As each site was sampled twice, the site relative crayfish density was defined as the average of these two visits. Finally, the ratio of females to males at each site was determined by recording the sex of all captured individuals.

Table 4.3: Number of crayfish by sex in the invasion-core and front sites in each river.

River	Core/Front	Female	Male	Total
Darent	Core	15	11	26
	Front	13	12	25
Nene	Core	15	10	25
	Front	10	9	19
Soar	Core	14	13	27
	Front	14	12	26
Wharfe	Core	12	14	26
	Front	9	9	18
Tees	Core	12	15	27
	Front	10	12	22

4.3.6. Statistical analysis

Before statistical analysis, data were inspected to ensure compliance with the assumptions of normal distribution and homoscedasticity (Verma and Abdel-Salam, 2019); Box-Cox transformations were applied to normalise non-normally distributed data (Osborne, 2010) using the R package 'MASS' (Ripley et al., 2013). Because of one particularly higher value (outlier), the only variable that was not normally distributed following transformation was the climbing tendency. However, we retained this outlier as it represented a real data point.

Other variables (ie., time of day, surrounding land-use, average water depth, pH, temperature, dissolved oxygen) were inspected for significant differences between the front and core sites within the rivers. As these did not differ markedly within rivers, they were not included in any further analyses to understand core-front differences.

We used 2-way ANOVA tests to analyse i) the effect of location along the invasion continuum (invasion-core versus invasion-front) and ii) river (Darent-Nene-Soar-Wharfe-Tees) had on the traits of signal crayfish using the R package 'Car' (Fox et al., 2007). 2-way ANOVA

Type II tests were applied when there was no interaction between the two variables while 2-way ANOVA Type III tests were used when an interaction was detected (Littell et al., 2002). All analyses took place in R Studio (R Studio, 2023) considering an α significance level of 0.05.

4.4. Results

In total, 555 crayfish were caught at the pair of invasion-front and invasion-core sites within the five rivers. Of these, 241 (female: 124, male: 117) were larger than 20mm CL and took part in the morphological and behavioural essays.

4.4.1. Population characteristics

Within all five rivers, the invasion-core sites had greater density of signal crayfish than in the invasion-front sites. Whilst in the River Soar the difference in population density between the two sites was relatively small (65% greater in invasion-core than invasion-front), there was a much larger difference (359% greater in invasion-core than invasion-front) in the River Darent (**Figure 4.9A**). In the three other rivers, the difference in population density between the invasion-front and invasion-core sites ranged from 82% (River Tees) and 130% (River Wharfe). Between the five rivers, there were also some differences in population density, with some consistently having higher or lower densities across both sites compared to others.

In contrast, there were no large differences in sex ratios between populations of signal crayfish in invasion-core and invasion-front in each river (**Figure 4.9B**). Within the rivers, the largest difference was in the River Darent where the invasion-core site had a higher percentage of females (62.96%) than the invasion-core site (52.00%). Within all rivers, the same sex tended to dominate both the invasion-core and invasion-front sites. The only exception to this was in the River Wharfe, where there were more males in the invasion-core sites and an even

split of gender in the invasion-front site. Among the invasion-front sites, females outnumbered males in three of the rivers.

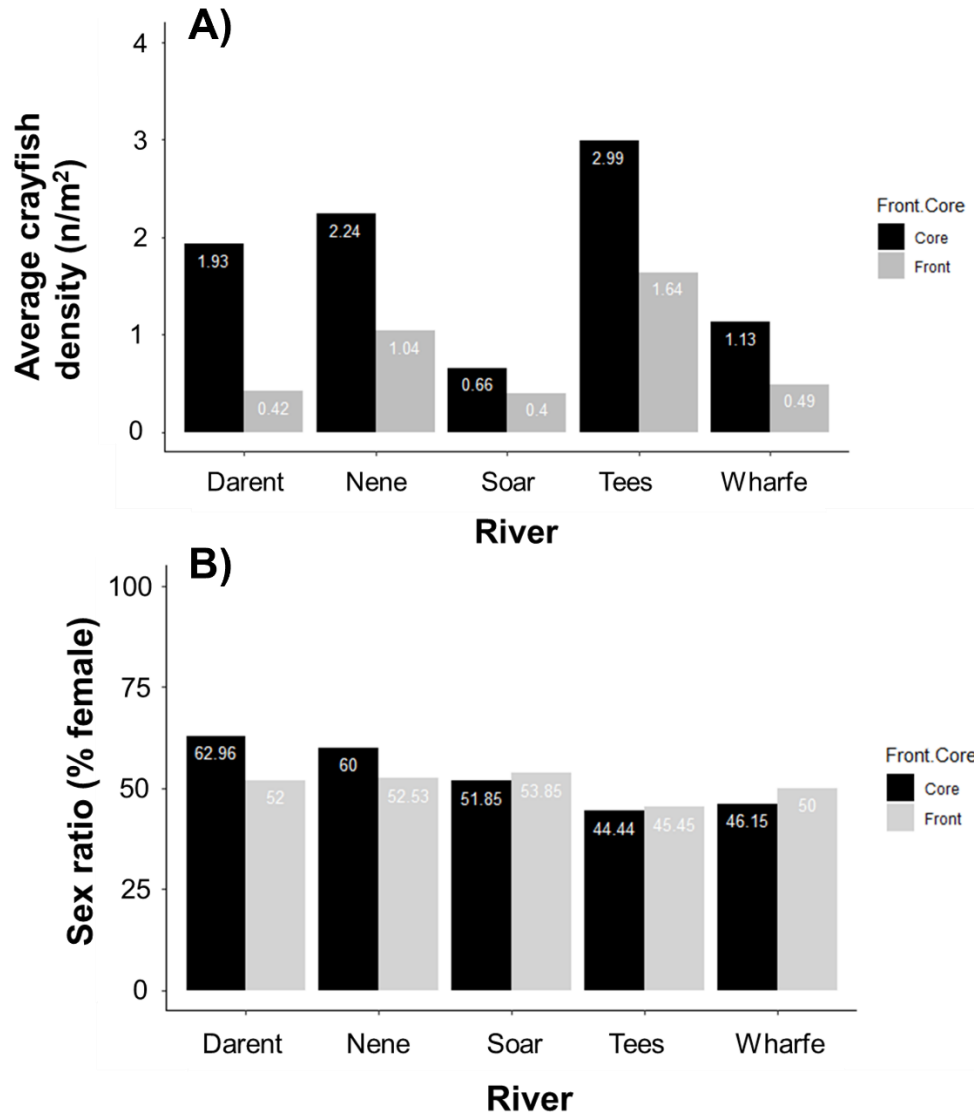


Figure 4.9: Graph showing crayfish population characteristics for the invasion-core and invasion-front sites in the five rivers. A) shows average crayfish density (individuals per m²) and B) shows sex ratio (% of females).

4.4.2. Morphological traits

The location along the invasion continuum (invasion-front versus invasion-core) had a significant effect on the carapace length (CL; $F=21.61$, $P < 0.001$), mass ($F=19.57$, $P < 0.001$), and width ($F=13.87$,

$P = <0.001$) of signal crayfish (**Table 4.5**). Individuals from the invasion-front sites were smaller, in terms of CL and width, and weighed less than those of the invasion-core sites in all five rivers (**Figure 4.10**). In the River Darent, the average CL of signal crayfish at the invasion-front site was 26.6mm and 33.4mm at the invasion-core site (**Figure 4.10A**). The location along the invasion continuum did not affect relative claw ($F = 0.61$, $P = 0.43$), and relative leg length of signal crayfish ($F = 1.39$, $P = 0.24$). The river from which signal crayfish were caught did have a significant effect on all five morphological traits that were analysed in this study (**Table 4.5**). For example, signal crayfish on the River Soar tended to, on average, have greater CL (38.6mm) compared to those on the River Darent (30.1mm), whereas signal crayfish on the River Darent had greater relative leg length (0.8) than those on the River Nene (0.77).

4.4.3. Behavioural traits

The location along the invasion continuum alone had no significant effect on any of the three behavioural traits analysed in this study (**Table 4.5**). Whereas in some rivers (e.g., River Darent), the signal crayfish at the invasion-front site were more active, bolder, and climbed more than those at the invasion-core, in others (e.g., River Soar) the pattern was completely different (**Figure 4.11**).

As with the morphological traits, the river that signal crayfish were caught in had a significant effect on all the behavioural traits that were analysed (**Table 4.2**). For example, crayfish from the two sites (invasion-core and invasion-front) on the River Tees exhibited higher exploration values than those from any other sites studied here. Furthermore, we also found a significant interactive effect between river and location along the invasion continuum on the activity ($F = 11.79$, $P = <0.001$) and climbing tendency ($F = 4.5029$, $P = 0.001$) of signal crayfish (**Table 4.2**).

Table 4.4: Effect of location along the invasion continuum (Invasion-core vs Invasion-front) and river (Darent-Nene-Soar-Wharfe-Tees) on the morphological (weight, carapace width, relative claw length, relative leg length) and behavioural (activity, exploration and climbing tendency) traits of signal crayfish. Statistically significant values ($p < 0.05$) are highlighted in bold. Star (*) indicates that there is a significant interaction between the location along the invasion continuum and the river terms (linear Model type III tests were used in these circumstances).

Trait	Location P-value	River P-value	Interaction
Carapace Length (CL)	<0.001	<0.001	
Weight	<0.001	<0.001	
Width	<0.001	<0.001	
Relative claw length	0.43	0.002	
Relative leg length	0.24	<0.001	
Activity	0.98	<0.001	*
Exploration	0.11	<0.001	
Climbing tendency	0.16	0.001	*

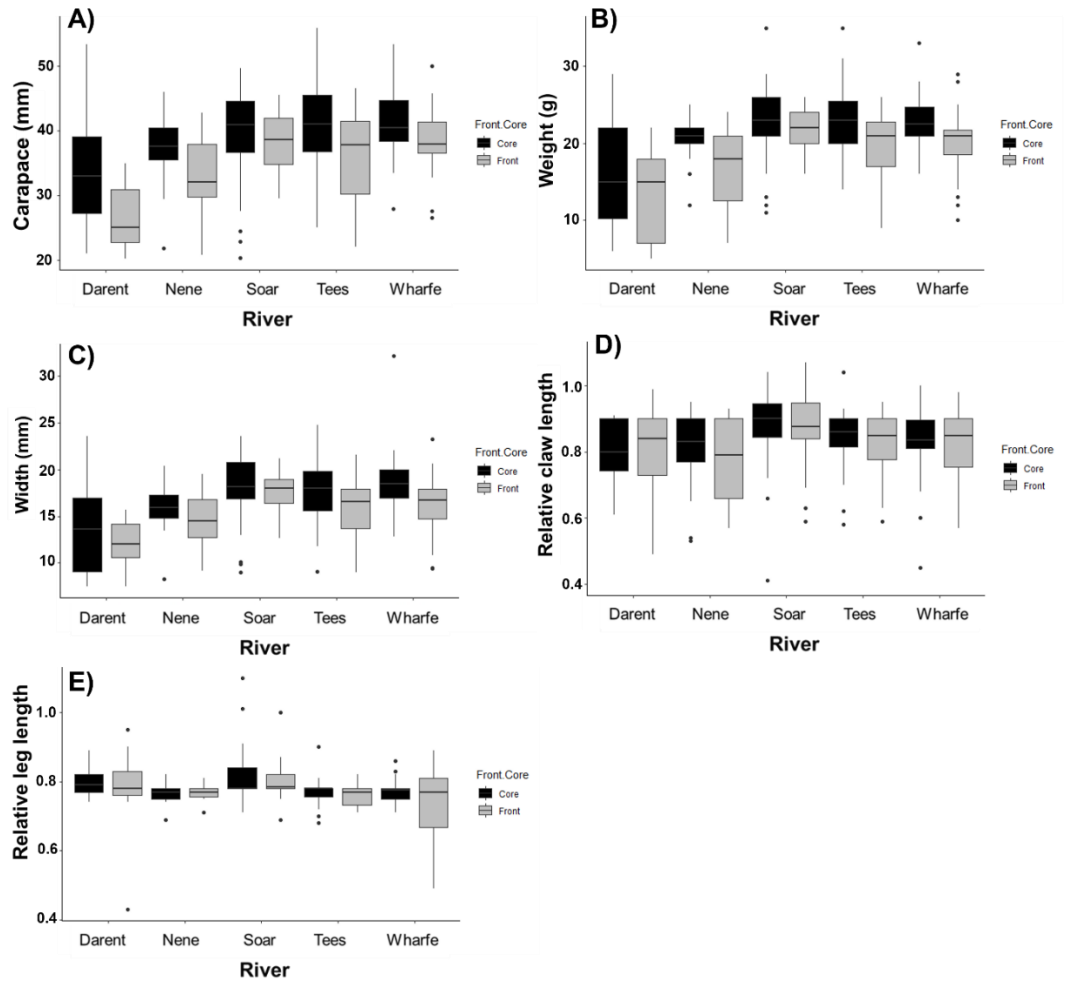


Figure 4.10: Boxplot showing the difference in morphological traits between the invasion-front and invasion-core sites in the five different rivers. **A)** shows carapace length (mm), **B)** weight (g), **C)** width (mm), **D)** relative claw length (claw length/ carapace length), and **E)** relative leg length (leg length/ carapace length).

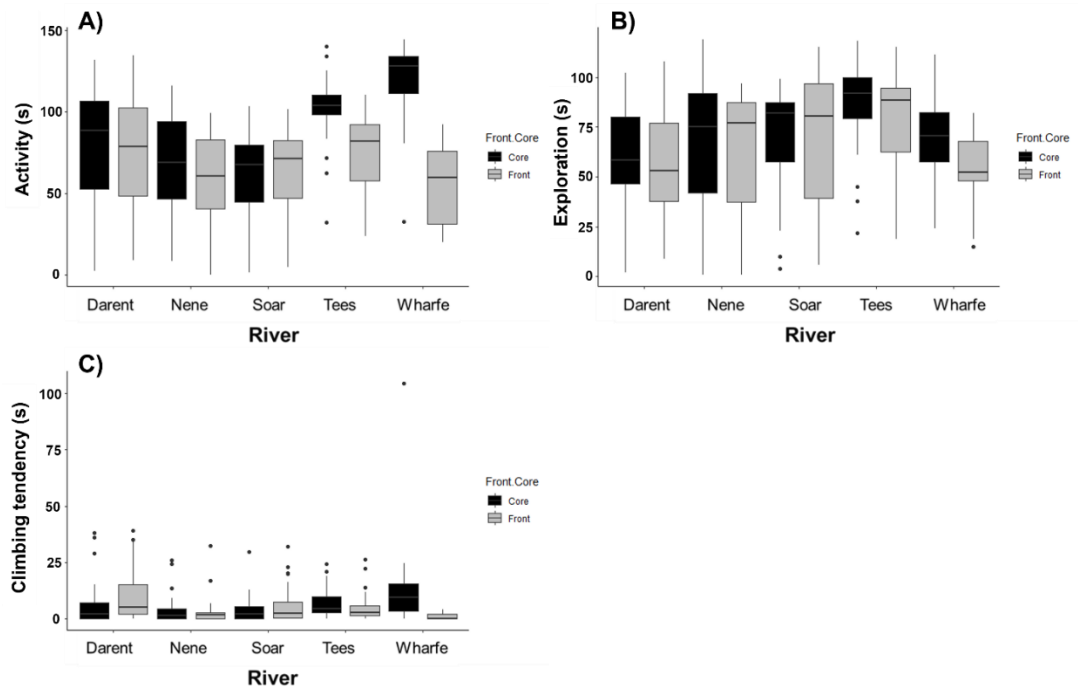


Figure 4.11: Boxplot showing the difference in behavioural traits between the invasion-front and invasion-core sites in the five different rivers. **A)** activity (seconds), **B)** exploration (seconds), and **C)** climbing tendency (seconds).

4.5. Discussion

In this study, we found that the location along the invasion continuum (invasion-core versus invasion-front) does affect some, although not all, key traits in signal crayfish in the UK. (**Objective 3**). We also found that some population characteristics seem to vary between invasion-front and invasion-core sites.

We found that in all five rivers, signal crayfish tend to be smaller (CL and width) and weigh less at the invasion-front than at the invasion-core site. This shift towards smaller body size at the invasion-front in signal crayfish has been previously seen in other countries (Hudina et al., 2012), and here we show for the first time that it is a pattern that also occurs in the UK. Importantly, we show that this pattern of smaller signal crayfish at the invasion-front sites appears to be geographically consistent, as we find it across the five rivers that we analysed in this study. While the finding that CL, width and weight all varied similarly is to be expected, as the growth pattern of crayfish means that these

three traits tend to be correlated; (Holdich, 2002), the fact that they were significantly different between invasion-core and front sites across all sampled rivers is an important finding and requires interpretation. A possible explanation for this shift towards smaller individuals at the invasion-front may be linked to the social hierarchy of crayfish and the effect this has on dispersal. In crayfish social structures, larger crayfish are typically dominant and are victorious in most antagonistic encounters (Bovbjerg, 1956; Pavey and Fielder, 1996). Therefore, these larger individuals can exclude smaller individuals from the more favourable habitats, forcing smaller crayfish to seek refuge elsewhere (Harrison et al., 2006). This process may in turn lead to smaller and/or younger signal crayfish, who have been excluded by larger individuals, to be overrepresented at the expanding front of the invasion.

These dynamics would correspond with the theory of a 'pushed' population expansion (Dahirel et al., 2021). 'Pushed' expansion are particularly likely to occur in populations where dispersal is greater at higher densities, due to the desire to escape from the high levels of competition (Harman et al., 2020). Previous work has shown that signal crayfish dispersal rates do increase with population density (Galib et al., 2022). Like previous work in other countries (Hudina et al., 2015; Rebrina et al., 2015), we found that the density of signal crayfish was higher at the invasion-core sites in all five rivers in the UK. This further supports our argument that the exclusion of smaller signal crayfish from the core sites 'pushes' them out towards the invasion-front, which has been previously suggested (Hudina et al., 2015).

Previous research looking at signal crayfish morphological differences between invasion-core and invasion-front sites in other countries has found mixed results, with some finding larger (Hudina et al., 2017) and others finding smaller individuals at the leading edge (Hudina et al., 2012). Our result suggests that a general pattern, at least in the UK, is that signal crayfish tend to be smaller in size at the invasion-front. These results also run contrary to other studies suggesting that larger and heavier individuals at the invasion-front may be preferentially

selected due to competitive and dispersal advantages, an idea referred to as the “bigger is always better” theory (Brandner et al., 2013). The finding of smaller individuals at the invasion-front sites suggests that there may be less/no benefits of larger body size at the invasion front. Likewise, it may also suggest that the benefit of larger size is greater at the invasion-core. Studies on invasive red swamp crayfish (*Procambarus clarkii*) have found positive correlations between larger body size and increased survival probability (Edeline et al., 2023). However, this correlation was only found in the high-density invasion-core sites (Edeline et al., 2023). This is thought to be linked to the fact that greater size provides advantages for competition between conspecifics, which tends to occur more frequently in high-density conditions (Edeline and Loeuille, 2021). Therefore, it may be that a greater selective pressure for larger body size at the invasion-core could explain why we found larger individuals at these sites. This again would suggest a ‘push’ model for signal crayfish expansion, where processes at the invasion-core dictate dynamics at the expanding front.

Whilst this study found that the location along invasion continuum in UK rivers had a significant effect on signal crayfish body size, we found that there was not a significant effect on claw and leg length. This finding contradicts those of previous studies in Croatia that have found that signal crayfish have larger relative claw length at an invasion-front site (Hudina et al., 2012). Likewise, that same study also found an increase in male bias towards the invasion-front (Hudina et al., 2012). On the other hand, in the current study we found no consistent bias towards males at invasion-front sites. It is possible that the different observations (ie. longer claw/leg lengths and male-biased populations) between the studies is linked. A common aspect of sexual dimorphism in crayfish is that males typically have larger relative claw sizes compared to females (Holdich, 2002). Therefore, it is possible that the lack of male bias found towards invasion-front sites in our study contributed to the lack of increase in relative claw length. Relative leg length has been found to increase at the invasion-front in some INNS,

with cane toads in Australia being a prominent example (Phillips et al., 2006). However, this well-established case study is a famous example of a 'pulled' wave, where higher dispersal at the front results in rapid phenotypic variation at the invasion-front (spatial sorting theory – Shine et al., 2010). As the evidence here suggests that the invasion of signal crayfish in the UK has the characteristics of 'pushed' expansion, it may be that the dynamics of this population do not stimulate the rapid variation phenotypic variation seen in other INNS.

The location along the invasion continuum alone did not have any effect on the behavioural traits analysed here, namely activity, exploration and climbing tendency. Studies on other INNS have previously found high levels of activity and exploration at the invasion-front (Gruber et al., 2017a; Lindstrom et al., 2013). As the authors are not aware of any previous study to test for differences in signal crayfish activity, exploration and climbing tendency between invasion-core and invasion-front sites, we are unable to compare our results to others. However, although not tested statistically, Galib et al. (2022) noted that climbing tendency and activity tended to be higher towards invasion-front sites in signal crayfish.

Similarly, while not significant, the results in our study also indicated that activity was higher at the invasion-front sites in four out of the five rivers. This similarity in findings suggests that perhaps location along the invasion continuum may have some weak effect on this behavioural trait. Certain limitations in our approach may mean that we were unable to determine whether there was any significant difference in these behavioural traits between invasion-core and invasion-front sites. Firstly, signal crayfish are considered to be mainly nocturnal species, therefore it is conceivable that the behaviour of captured individuals would have been different were the assays conducted during the night instead of during the day. However, as crayfish collection was done in the daytime via hand-net searching, we did not want to keep individuals for elongated periods to wait for nightfall (as prolonged time in captivity is known to also influence animal behaviour; (Saré et al., 2021).

Additionally, all assays were conducted during two months between summer and autumn (August and September 2022), and it is possible that the behaviour might have been different during different periods of the year. This is particularly the case as the activity of signal crayfish is known to differ seasonally (Johnson et al., 2014). While this period was chosen because it represents when signal crayfish are most active (Johnson et al., 2014), and thus there is a greater chance to catch them, it would nonetheless be beneficial for future studies to conduct similar experiments at different points in the year to see whether this influences the results obtained in this study.

Interestingly, the study found that there was a significant interactive effect between the river that crayfish were in and the location along the invasion continuum on the activity and climbing tendency. This suggests that any difference in these behavioural traits in signal crayfish between invasion-core and invasion-front sites is mediated by the river condition and/or vice versa. Explaining behavioural traits in animals is notoriously difficult (Pruitt, 2014). In crayfish, multiple external factors are known to influence behaviour, including water level (Johnson et al., 2014), temperature (Zhao and Feng, 2015), refuge availability (Galib et al., 2022), lighting (Thomas et al., 2016) and many more. Likewise, crayfish behaviour is also influenced by complex social interaction with conspecifics (Edeline and Loeuille, 2021; Graham and Angilletta, 2020) and interspecific (Pintor et al., 2008), as well as the presence of disease (Thomas et al., 2020). These and other factors will vary between different rivers (Kelly et al., 2008; Vaughan et al., 2013). Therefore, it is possible that this variation in factors between rivers in turn influenced any impact that the location along the invasion continuum had on activity and climbing tendency in crayfish. For example, as body size is known to influence the likelihood that signal crayfish climb out of the water (Thomas et al., 2018), it is possible that the observed size variation along the invasion continuum and between rivers in this study both played a role in the tendency of individuals to climb. As has been previously suggested (Johnson et al., 2014), it may

also be possible that the behavioural decisions of signal crayfish are not strongly correlated to large-scale variation, such as river or location along the invasion continuum, because variations at smaller spatial scales that have more direct impacts on crayfish behaviour and activity mask the influence of larger-scale trends. Irrespective of the cause, the complex, nested and interactive effects of multiple factors on several of the behavioural traits analysed in this study demonstrate that signal crayfish behaviour is highly variable between sites.

One of the key advances of the current study is that, unlike previous attempts to study variations in signal crayfish along the invasion continuum (e.g. Gabib et al., 2021), we assessed multiple rivers. This allowed the current study to determine whether the effect that location along the invasion continuum had on traits was consistent across different rivers. However, it also allowed us to test whether the river that signal crayfish were found in had any impact on traits. We found that the river signal crayfish were caught in had a significant effect on all morphological and behavioural traits analysed in this study. There are large variations in environmental and ecological factors between rivers in the UK (Vaughan et al., 2013). As previously discussed, this may explain some of the variation we saw in signal crayfish behaviour between rivers. Indeed, previous studies have already shown that variation in general environmental conditions influences the morphology of signal crayfish (Ooué et al., 2019), with specific factors such as water depth known to influence the size class of crayfish that are found (Harrison et al., 2006). Therefore, the significant effect that the river had on the traits may be caused by variations in characteristics.

Furthermore, the invasion pattern of signal crayfish in the UK has been complex (see **Chapters 2 and 3**) with various environmental but also social factors influencing the location and timing of signal crayfish arrival in rivers (Holdich et al., 2014). Therefore, it is also possible that other factors such as time of arrival and genetic variations between populations could also explain the significant effect that the river signal crayfish were caught in had on their traits (Phillips et al., 2006). It would

be beneficial for future studies to assess the potential role of heritability and phenotypic plasticity in influencing trait variability between signal crayfish at different sites.

Management implications

The results of this study also have some important implications when it comes to the management of signal crayfish. First, it suggests that management approaches that preferentially target larger individuals, such as trapping (Green et al., 2018), may not be as effective in controlling numbers at invasion-front sites. Instead, any approaches conducted at these sites should be able to effectively target all size-classes to ensure maximum effect. Furthermore, the overrepresentation of smaller individuals that are harder to spot towards the invasion-front sites may mean that it may be years before environmental managers or others notice the arrival of signal crayfish at a site. The sentiment that it is difficult to detect the arrival of signal crayfish is often expressed by stakeholders (interviews in **Chapter 5**), and here we show the size distribution at the invasion-front sites may also be a contributing factor. This suggests that any management approach aimed at stopping or slowing the spread of signal crayfish in a river (e.g., physical barrier) should be placed with sufficient distance away from the last confirmed observations, to ensure that the population has not already expanded beyond it. The use of other approaches, such as environment DNA (eDNA) may be necessary to accurately detect the advancement of signal crayfish (King et al., 2022). This may be particularly important when ensuring that signal crayfish have not reached the ‘ark sites’ that aim to protect the remaining populations of white-clawed crayfish in the UK.

The differences in signal crayfish characteristics between invasion-core and invasion-front sites suggest that it is not possible to get an accurate assessment of a signal crayfish population in a river from only one site. As both the overall size (Claussen et al., 2000) and density (Galib et al., 2022) have been previously shown to influence the dispersal of

crayfish, any attempt to model their expansion must take into account how these factors vary along the invasion continuum. Furthermore, as we see that some crayfish traits may vary between rivers, it is necessary to take this factor into account.

4.6. Conclusion

The results from this study show that in UK rivers, the location along the continuum (invasion-core versus invasion-front) does influence certain important functional traits in invasive signal crayfish. Signal crayfish found in sites at the leading edge of their expansion tend to be smaller than those at the invasion-core in a river. Likewise, we also found that these invasion-front sites consistently have lower density than invasion-core sites. These observations, together with other aspects of crayfish social structure, appear to suggest that the expansion of this INNS represents a 'pushed' expansion wave where smaller individuals are excluded from the core and driven towards the invasion-front sites. While the location along the invasion continuum did not alone have a significant effect on behavioural traits, there was a significant interaction with the river on the activity and climbing tendency of signal crayfish.

The influence of the river on the traits we analyse in this study reveals how much variation there is in signal crayfish between sites. Specifically, it demonstrates that differences in environmental and ecological conditions between different rivers can in turn result in differences in the traits of the signal crayfish within it. When placed alongside the differences in size along the invasion continuum, these results suggest that managers and decision-makers must initially understand the characteristics of the signal crayfish at the site they are working with to ensure that they deploy the most effective solution. This study adds another example to the growing literature showing the variability in populations of INNS. Only through more research and understanding of the factors influencing the traits of INNS will we be able to effectively manage their impacts.

Chapter 5: Understanding the attitudes of stakeholders towards invasive signal crayfish (*Pascifastacus leniusculus*) in Great Britain.



There is no story that is not true, [...] The world has no end, and what is good among one people is an abomination with others...

- From “All things fall apart” by Chinua Achebe

5.1. Abstract

Aim

Humans play a critical role in all stages of a biological invasion. Whilst other aspects of the invasion of signal crayfish in GB have been studied, relatively little research exists on the stakeholders involved in the discussions around this invasive species. In this study, we looked at the attitudes of various stakeholders to understand their perspectives on different aspects of the invasion of signal crayfish and see whether these varied or were similar.

Methods

We conducted a mapping exercise with eight stakeholders to see the perceived power and interest of different stakeholder groups associated with signal crayfish in the UK. We also conducted semi-structured interviews with 12 stakeholders associated with signal crayfish in GB. These stakeholders belonged to different organisations, including governmental bodies, former politicians, anglers, and other relevant groups. We conducted a thematic analysis technique to analyse the interviews to find the major themes and attitudes shared by the stakeholders.

Results

The stakeholder mapping exercise showed that the stakeholders saw that governmental bodies such as the Environment Agency and Natural England and more local groups like Rivers Trust and Angling Clubs, were key players in the conversations around signal crayfish in the UK. However, Local Politicians and Local Businesses were perceived to not be very engaged in the discussions. There were similar attitudes between the stakeholders on some topics, such as the role of the government in the initial introduction and the need for stronger regulations and enforcement. However, there were also differences in attitudes between stakeholders on the significance of the illegal spread of the species and whether greater commercialisation of signal crayfish

was a good idea or not. Most stakeholders feel that the window for managing signal crayfish has already passed and that we need to learn to live with this invasive species.

Conclusion

These findings show how the attitudes of stakeholders on key aspects of an invasive species can vary. It also highlights the importance of understanding stakeholders' attitudes to effectively manage future biological invasions in GB.

5.2. Introduction

There is a growing appreciation of the intrinsic interconnectedness between nature and society (Ostrom, 2009). Whilst nature provides society with essential resources and ecosystem services for life, humans alter our environment and the processes within it (Díaz et al., 2015). Ecological changes due to, for example, over-exploitation, climate change, destruction of habitat, and the introduction of invasive species, are complex socio-environmental issues that draw a wide variety of attitudes amongst stakeholders due to widely differing economic, cultural, social, and political views (Bennett et al., 2017). Whilst a plurality of attitudes towards a topic can create productive discussion, highly conflicting views may also create conflict and prevent unilateral support for solutions to a given environmental issue (Reed, 2008).

The human-mediated introduction of invasive non-native species (hereafter INNS) beyond their natural range is one leading cause of ecological change and biodiversity loss globally (Bellard et al., 2016; Blackburn et al., 2019). Alongside biodiversity loss, the spread of INNS can have serious negative impacts on multiple sectors of the economy (Cuthbert et al., 2022; Diagne et al., 2021; Ahmed et al., 2022), cultural loss (Siegert et al., 2023), and human health (Mazza et al., 2014). Traditionally, research on INNS has focused on the ecological and

environmental impacts of invasion (Gallardo et al., 2016; Pyšek and Richardson, 2010). However, there is a growing awareness that INNS are also a social phenomenon, with important political, economic, and human dimensions (Bremner and Park, 2007). All phases of the invasion process contain human agency, from dispersal, colonisation, and ongoing spread of an INNS, to the decision of whether and how to best manage it (García-Llorente et al., 2008). As a result, there is growing awareness that the social element of invasion science is understudied, yet critical to form a comprehensive, holistic understanding of the invasion of an INNS (Shackleton et al., 2019).

The attitudes of stakeholders are a key concern in understanding the social dimensions of INNS and thus developing appropriate management strategies. In environmental management, stakeholders are typically defined as those individuals, groups, or organisations who can affect or are affected by an issue (Freeman, 1984). Whilst stakeholders can be further divided into primary (active) and secondary (passive) (McGrath and Whitty, 2017), the broader definition mentioned above is typically used as it encompasses all stakeholders and gives them equal importance (Bendtsen et al., 2021). The attitudes of stakeholders toward INNS can be highly variable, typically influenced by a myriad of factors including past experiences, views of nature, economic interest, political affiliation, and ecological knowledge (Novoa et al., 2016). Stakeholders can develop very strong attitudes towards INNS because of these factors and from the use of emotive terms, such as 'non-native', 'invasive' 'alien' 'exotic', and 'pest', which have deep social connotations (Davidson et al., 2013). For some stakeholders, the topic of INNS can even invoke deeply held values and attitudes about 'naturalness', culture, tradition, and how we see national borders (Dobson et al., 2013). The management of INNS can create complex ethical/animal welfare dilemmas that divide opinion, as demonstrated by conversations around the eradication of grey squirrels (*Sciurus carolinensis*) in the UK (Dunn et al., 2018), Reeves' muntjac deer (*Muntiacus reeves*) in the Netherlands (Verburg, 2007) and wild hogs

(*Sus scrofa*) in the USA (McClure et al., 2018). Likewise, attitudes towards INNS can also be shaped by the desire to protect impacted native species, particularly as these can have large cultural significance (Siegert et al., 2023). These emotive and complex factors mean that, even in the presence of empirical evidence, stakeholders typically construct their attitudes towards INNS based on subjective influences (e.g. past experience, cultural bias, scientific reasoning, ethical values) (Davidson et al., 2013).

Whilst the factors shaping attitudes are complex, developing an understanding of the attitudes that different stakeholders have towards an invasive species is crucial (Shackleton et al., 2019). This is particularly important in providing insight into perceptions of how/why INNS were introduced, how they spread, what actors were involved, and decisions around their management (Adams, 2016). Previous research in this area has analysed the attitudes of stakeholders towards various invasive species, including common Wall lizards (*Podarcis muralis*) in the UK (Williams et al., 2019), wild hogs in the USA, cacti in South Africa (Novoa et al., 2016), and invasive plants in Spain (Touza et al., 2014; Andreu et al., 2009). A common and important feature of many of these studies is that they look at multiple stakeholders to identify differences between them. For example, Novoa et al. (2016) compared attitudes towards cacti between stakeholders who want to promote their use (farmers, nursery owners) and those who want to reduce their presence in South Africa (invasive species researchers, land managers). This process allowed more stakeholders to get involved in the discussion of solutions and helped illuminate areas of consensus (Novoa et al., 2016). Understanding areas of consensus in opinions between stakeholders is crucial, as it guides the development of effective management strategies that have broad support (Bendtsen et al., 2021). Likewise, García-Llorente et al. (2008) evaluated the attitudes of different stakeholder groups to INNS and their management in the Doñana region in southwestern Spain. This study found that there were large differences in attitudes among the

stakeholders regarding the impacts of INNS in the region, as well as suggesting that more stakeholder engagement should be a priority (García-Llorente et al., 2008). Other research has focused on understanding the role of different stakeholders through a process referred to as stakeholder mapping (Reed and Curzon, 2015). Conducting stakeholder mapping exercises can provide insight into how best to engage with each stakeholder and increase collaboration (Liu and Cook, 2016; Liu et al., 2020).

Research on invasive signal crayfish has typically focused on understanding their ecological impacts and identifying management solutions. There has been little published work on the attitudes of stakeholders towards signal crayfish; the only known work in this area is Adams (2016) who identified conflicting attitudes between stakeholders towards control methods, legislation, and the extent of collaboration between stakeholder groups. However, this study did not examine stakeholder attitudes towards key aspects of the invasion of signal crayfish, such as their introduction and impacts. Such information is important to target action; for example, in creating public awareness campaigns that are effective in generating desired behavioural change (Banha et al., 2022).

In light of this important research need, this study aims to better understand stakeholders' attitudes towards invasive signal crayfish in the UK by conducting interviews with various participants, including staff at government agencies, academics, anglers, landowners, and former cabinet ministers. Our specific objectives are: 1) to provide an up-to-date understanding of the attitudes that these stakeholders have towards important aspects of the signal crayfish invasion, including their perceptions of how/why it has spread, important impacts of its invasion, and views about how to manage their ongoing impacts and spread; 2) to give insights into how participants perceive other stakeholders interested in signal crayfish in the UK and 3) to synthesise this information in an environmental management context, with implications

for future co-working, communication and strategy development around INNS.

5.3. Methods

5.3.1. Stakeholder interviews

The primary source of data for this chapter is 12 semi-structured interviews that took place between March and May 2023 with stakeholders identified to represent key groups in the discussion around signal crayfish in the UK (**Table 5.1**). This included current and former cabinet ministers and government agency personnel, as well as different local interest groups, anglers, estate owners, water companies and others. Some of the stakeholders were selected before the commencement of data collection, whilst others were identified during the interviews via a snowballing approach (Farquharson, 2005). For this chapter, it was deemed important to include stakeholders from many different groups/ types of organizations influenced by signal crayfish in the UK to identify differences and/or similarities in attitudes and opinions. An interesting note is that there were instances of stakeholders who did not want to take part in the interviews, but who did communicate their strong opinions (generally negative) towards the current debate around the management of signal crayfish in the UK.

Table 5.1: Description of the participants that took part in the interview section of this study. Note that names of specific groups/organisations have been anonymised to protect interviewees' identities.

Participant	Group	Role
Estate Owner	Individuals	Owner of an estate that contains signal crayfish
Former cabinet minister	Individuals/ ex-politicians	Previous UK politician with an interest in signal crayfish and their management
Chair of a river association	Angling Community	Leader of a community of anglers in a river
Chair of fisheries group	Angling Community	Leader of a community of anglers in a river

Rivers trust staff	Non-governmental charities	Working in rivers trust to manage rivers in a region in the UK.
Academic	Academic community	Researches aquatic environments and invasive signal crayfish
Invasive manager at a water company	Environmental Manager	Leads the management of invasive species for a UK water company
Environmental manager	Environmental Manager	Manages the environment (including invasive species) at a site.
Environmental consultant	Environmental Manager	Conducts work/research for clients on managing invasive species in the UK.
Staff at government body A	Governmental Bodies	Works in a government body whose remit is the management of the environment and conservation.
Staff at government body B	Governmental Bodies	Works in a government body whose remit is the management of the environment and conservation.
Staff 2 at government body B	Governmental Bodies	Works in a government body whose remit is the management of the environment and conservation.

Interviews were semi-structured, consisting of primarily open questions that invited participants to talk and express their opinions on different aspects of the debate around signal crayfish in the UK. However, two questions in the interview applied a Likert 5-point scale to gather the participant's views of invasive species and signal crayfish in general (**questions 5** and **7** respectively in **Appendix B**). The time taken for each interview varied depending on the participants, ranging from 19 to 70 minutes in duration. Most of the interviews were conducted orally in real time using video-conferencing software. However, one of the participants, *Former cabinet minister*, preferred to respond to the interview questions via email, and whilst they did answer most questions, the length of the responses were much shorter than the oral

interviews. The responses were analysed along with the other interviews due to the unique and important perspective of this interviewee in the analysis.

The analysis of the interviews followed the methodology for thematic analysis as described in Braun and Clarke (2006). Initial first impressions and notes were created describing some of the attitudes and opinions of the participants after the completion of each interview. After all the interviews were transcribed using automatic transcription software (powered by Microsoft's Azure Cognitive Services), the transcriptions were checked, and errors were corrected manually. Following a process of anonymisation, the interviews were analysed qualitatively using NVivo 12 (Lumivero, 2017). The data analysis in NVivo consisted of the creation of initial codes using a predominantly inductive approach that followed closely the responses from participants (Horangic et al., 2016). After an initial pass, these codes were then analysed using a more deductive approach that focused on key attitudes and feelings that were expressed by the participants. This mixed inductive and deductive approach enabled the identification of themes relating to attitudes and opinions of stakeholders towards signal crayfish in the UK without sacrificing nuances present in the participant's responses (Braun and Clarke, 2006).

5.3.2. Stakeholder Mapping Exercise

As well as taking part in the semi-structured interviews, participants were also asked to complete a short computer-based task in their own time. This involved placing stakeholders in a power vs interest graph, according to their relative levels of power and interest in the conversation on signal crayfish in the UK (Reed and Curzon, 2015). Although some pre-specified stakeholders were already present for the stakeholders to map (**Appendix C**), they were also advised to include any other stakeholders they deemed relevant. This was important so participants were not restricted by *a-priori* selection. In total, eight

participants completed the stakeholder mapping exercise, including seven who took part in the interviews, and one who did not want to be interviewed.

5.3.3. Positionality and ethics

As a PhD student who was researching invasive signal crayfish for over three years, my previous experiences and/or personal opinions may have had some influence on the analysis. This issue of positionality arises commonly for postgraduate researchers conducting qualitative analysis in their field and it must be acknowledged (Bourke, 2014; Holmes, 2020). In light of this, relevant approaches were conducted during this study to minimise the amount of bias present (Fadnes et al., 2009). In particular, the wording of questions in the interview was carefully selected to remove as much bias as possible and allow respondents to provide their honest opinions on the topics.

This research received ethical approval from the School of Geography at the University of Nottingham Ethics Committee before the commencement of data collection.

5.4. Results and Discussion

5.4.1. Stakeholder Map

The results of the participatory mapping exercise highlighted that interview participants consistently placed the two government bodies, Natural England and the Environment Agency (EA), as having the highest power and high interest in signal crayfish in the UK (**Figure 5.1**). The placement of Natural England and the EA as stakeholders that are both powerful and interested in the topic is not surprising as both are Arm's Length Bodies (ALBs), which operate under the UK government (HMG, 2019). These two ALBs operate throughout England and have some legislative power when it comes to dealing with INNS, such as signal crayfish, and their impacts. For example, one

of Natural England's key purposes is "*promoting nature conservation and protecting biodiversity*" (DEFRA, 2022). This sentiment was emphasised by a staff member at Natural England who was interviewed for this study, "*to be honest, our focus is of course on white-clawed crayfish*"; the native crayfish in the UK which is currently threatened by the spread of the signal crayfish. The EA's involvement in signal crayfish in the UK comes from its role as the government's ALB responsible for fisheries and ecology in England. For example, any individual or organisation that wishes to trap signal crayfish, be it for management or scientific purposes, must apply for a licence from the EA. Both Natural England and the EA were placed very close to each other in the stakeholder map (**Figure 5.1**), and this suggestion of similarity between the two organisations was also alluded to by participants in the interview, with a *Chair of river association* stating "*you've got the Environment Agency who sets the rules and you've got Natural England... they sort of tend to overlap*".

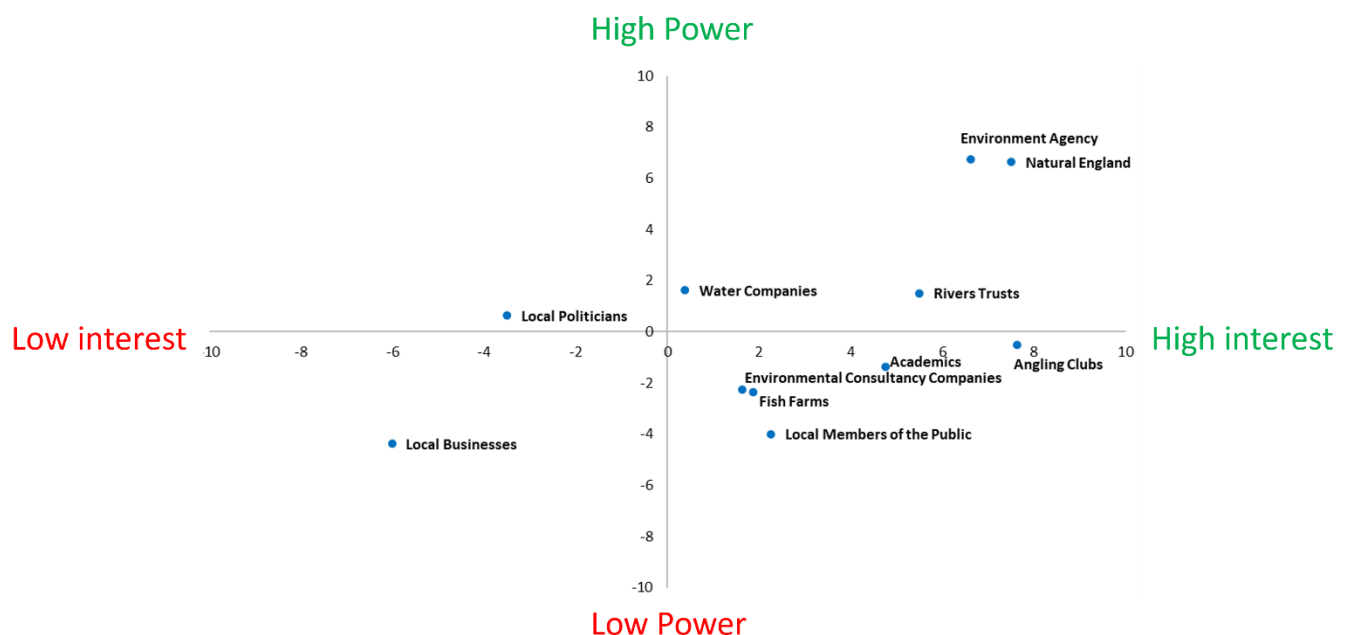


Figure 5.1: Stakeholder Map showing the average 'Power' and 'Interest' scores that the participants assigned to each stakeholder.

Whilst Natural England and the EA were positioned consistently in similar positions of power and interest by participants, other organisations were positioned in more variable positions (**Figure 5.1**). Other organisations generally perceived as having high interest were the Rivers Trusts and Angling Clubs. Rivers Trusts are independent community-led charitable organisations that typically focus on the conservation and improvement of waterways (e.g., Trent Rivers Trust) or a region (e.g., Norfolk Rivers Trust) (Rolston et al., 2017). Angling Clubs are typically volunteer-run organisations that are made up of anglers who manage recreational fishing in a specific area (Williams and Moss, 2001). In the stakeholder mapping exercise, both rivers' trusts and angling clubs were given 'interest' scores greater than 5 by the participants but relatively neutral 'power' scores (**Figure 5.1**). The perception of relatively low power for both Rivers Trusts and Angling Clubs may be due to their lack of regulatory power and independence from government entities. As pointed out by Newson (2011, p. 1), Rivers Trusts occupy a "*niche between national regulators and the regulated*". The high interest scores emphasise that these organisations are perceived to be engaged in managing stressors that threaten their local rivers, and that signal crayfish represent one of those key stressors. Angling clubs, whose principal focus is its members' ability to fish their local areas, have a keen interest in signal crayfish due to their perceived impacts on recreational fishers and fishing stocks; for example, one participant stated:

"as an angler who often likes fishing in ponds... it's incredibly infuriating if your float's just about to go under and you think, oh, tension and it goes under...And you pull up the signal crayfish that's been munching" (Academic).

Additionally, the geographical scope of both Rivers Trusts and Angling Clubs may contribute to the high interest score they received by many participants. Both Rivers Trusts and Angling Clubs have areas of focus much smaller and precisely defined than other stakeholders (e.g., academics), but within the context of nationwide organisations.

Participants indicated that Local Businesses had the lowest relative interest (-6.0) and power scores (-4.38) of all groups, which is not entirely surprising. The other stakeholder groups included have a known tendency to be directly involved in the topic of signal crayfish, either because of the conflict they present to their activities or because of responsibility. In contrast, Local Businesses (excluding fish farms that were ranked separately) are more indirectly impacted (e.g. use of corporate tax to fund bodies such as the EA that aim to manage signal crayfish) and have not yet been major participants in discussions around invasive crayfish in the UK. Whether this is the result of a lack of desire to participate or the exclusion of this group from discussions, is currently unknown. Low engagement from local businesses to environmental issues is recognised, including the impacts of climate change (Williams and Schaefer, 2013). Whilst Local Businesses are perceived to be a minor stakeholder by the participants here, businesses and their infrastructure in general are still impacted by signal crayfish; for example, the *Chair of a fisheries group* mentioned “*Network Rail just had... massive works on underpinning the stanchions of the bridge types across the river*” due to crayfish burrowing. Statements such as this demonstrate how the connection between businesses and signal crayfish revolves around their economic impact.

Other stakeholder groups were generally perceived by the participants as having medium levels of both interest and power when related to signal crayfish in the exercise (**Figure 5.1**). This includes Water Companies, Fish Farms, Environmental Consultancies, and Academics. Alongside Local Businesses, the other stakeholder group that was consistently given low interest scores were Local Politicians. The low interest given to Local Politicians may be because of a perceived lack of involvement by the political class in discussions around signal crayfish. The topic of invasive signal crayfish is not typically discussed by Members of Parliament (MPs) in the UK. However, one participant in the interviews did mention talking to a politician in parliament about signal crayfish, saying they are “*as exercised about this issue as I am*.”

Well, we talked about it in [Parliament] once or twice. There's a river in [city] where he lives, where a similar problem has arisen" (Estate owner), referring to the impacts of this invasive species. The low interest score may also reflect frustration that the political class is not acting on signal crayfish to the extent that they would like to seem, as mentioned by participants in the interview, with one saying:

"unfortunately the way our government works have, and I'm not blaming one government, but they tend to [focus on] longer term problems, they tend to ignore and let them become critical. And when [it] becomes critical they, throw their hands up in horror and say there's a crisis here."

5.4.2. Interviews

Analysis of interviews conducted with the 12 different participants provided a rich dataset of attitudes and opinions towards different aspects of signal crayfish. Following on from the coding process of the interviews, four key talking points synthesising attitudes the stakeholders had towards signal crayfish in the UK were selected for further interpretation and discussion. These were: i) the introduction and spread of Signal Crayfish, ii) the impact of signal crayfish, iii) their management, regulations and government response, and iv) the outlook for the future. Below we analyse each of these four areas in more detail.

signal crayfish were promoted by the UK government because they believed that they could be harvested and sold to international markets because “*there was this market ready in the Scandinavian countries for more crayfish after the Noble crayfish was decimated, by crayfish plague*” (*environmental consultant*). However, the same stakeholders mentioned that a market for British signal crayfish “*was never there*” (*interview with invasives manager at a water company*) and that the whole experiment was doomed to fail from the beginning as crayfish were being “*produced cheaper from Spain [and] China*” (*environmental consultant*). Several different stakeholders used the phrase “*cash crop*” when describing the introduction of signal crayfish in the UK. The use of this term by stakeholders is interesting, as this is a value-laden phrase that is typically associated with the harvest of products that have high economic value but can result in negative social and environmental costs (Maxwell and Fernando, 1989). The use of this phrase reiterates that these stakeholders perceive the introduction of signal crayfish as a flawed decision driven predominantly by economic incentives.

Another criticism that stakeholders labelled at the government was that they did not properly consider the dangers and/or listen to the opinion of experts before introducing signal crayfish. One stakeholder believed that the Ministry of Agriculture, Fish and Food (MAFF), the government ministry at the time who “*encouraged*” the introduction of signal crayfish in the 1970s, “*still [had] a Victorian attitude to what the risks actually were*” (*Academic*). Another argued that the government did not properly listen, even when experts and those in the “*aquatic community*” expressed “*concern*” at the introduction of signal crayfish (*staff 2 at government body B*). This same stakeholder likened the situation to the recent Covid-19 “*pandemic*”, stating that in both instances “*the role of experts*” was questioned by certain influential politicians who believed they did not “*need experts*” or their input (Bennett, 2020). Drawing similarities to the government’s response to the Covid-19 pandemic demonstrates this stakeholder’s opinion that disregarding expert opinion on the introduction of signal crayfish has caused dire impacts. A

related criticism shared by all stakeholders was that the government is that it was slow to react when it became clear that there was a problem. Excessive and slow bureaucratic processes in government can make it difficult and slow to pass appropriate regulations on environmental issues (Mitchell et al., 2014). This sentiment was expressed here by some of the stakeholders, with one participant adding that when river managers began to notify the government that these INNS had negative impacts, it “*wasn’t acted on early enough*” (Academic).

An additional criticism that most stakeholders mentioned is poor enforcement of necessary regulations. UK regulations that have been designed to control invasive species (including signal crayfish) are the Wildlife and Countryside Act (HMSO, 1981), which made the release or intentional spread of any invasive species illegal, and The Prohibition of Keeping of Live Fish (Crayfish) Order 1996, which banned the import of signal crayfish for the aquarium trade (Peay et al., 2010). However, many stakeholders interviewed believe that regulations aimed at controlling signal crayfish in the UK such as these have “*never been properly enforced*” (environmental consultant). This lack of enforcement means that many of the regulations are frequently broken, leading to further signal crayfish spread.

As well as infrequent enforcement, the stakeholders believe that those who are found breaking the regulations are given soft punishments: “*they probably get smacked in the wrist and maybe a £50 fine*” (rivers trust staff). The enforcement of invasive species regulations has been difficult for many countries around the world (Martin and Choy, 2016), but many of the stakeholders interviewed in this study believe that this is made more complicated by the complexity of the regulations. This perception of weak enforcement of regulations around signal crayfish was also mentioned by stakeholders in Adams (2016), suggesting it is a widespread opinion. Those stakeholders who believed that the government response to signal crayfish has been too weak attribute this to “*pander[ing] to certain interest pressure*” (Environmental consultant) or “*bending to some politically influential people*” (Invasives

manager at a water company) “*because they don’t want to lose votes*” (*Environmental consultant*). The Prohibition Order introduced in 1996 includes an exception whereby its ruling does not apply to restaurants and fish markets that use crayfish for human consumption (Alderman and Wickins, 1996). Stakeholders criticise exceptions such as this because they argue they have allowed a market for signal crayfish to exist, which ultimately provides the “*financial incentive for illegal activity*”, i.e., the continued harvest of the INNS (*Staff at government body B*).

In contrast, another smaller group of stakeholders were similarly critical of the government because they believed there was too much regulation. One of the stakeholders mentioned that the current regulations were too restrictive and that instead, the government could allow “*major private landlords*” and “*private operators who have a real interest in reducing numbers*” to make money by selling caught crayfish (*Former cabinet minister*). Another stakeholder added that it would “*be better to tell people to try to exploit the species, which may reduce its numbers*” as it is a “*very tasty form of food*” (*Estate owner*). This opinion was also shared by the rivers trust staff, who mentioned that they had planned a “*sustainable way*” whereby they could sell caught crayfish to “*chefs and fishmongers*” to “*pay for the volunteers time*”. The opinion of managing signal crayfish through consumption has received lots of attention, with popular TV chefs and scientific articles exploring the control of INNS such as signal crayfish through human consumption (Nuñez et al., 2012; Pritchard, 2020; Barnes et al., 2022).

All stakeholders, including those who currently work in government bodies, criticised the UK government for its role in the introduction of signal crayfish. In particular, stakeholders mentioned that the government was slow to react to the threat posed by these INNS and that they failed to properly listen to the concerns of experts. Whilst there is a consensus that there needs to be improvements in the government’s response to signal crayfish, there was disagreement on what these steps should be. Most stakeholders directly involved in the

management of signal crayfish believe that there must be stronger regulations, whereas other, more local stakeholders and/or those less involved in the daily management of crayfish and their habitats, believe that the government should relax its regulations and allow signal crayfish to be harvested sustainably.

Role of humans in the introduction and spread of signal crayfish

There is consensus that humans have played a pivotal role in the initial introduction of signal crayfish into the UK in the 1970s. However, there are differences of opinion on the relative importance of humans to the subsequent spread of signal crayfish. Humans are known to have contributed to the spread of signal crayfish through legal introductions (Holdich et al., 2014). One of the stakeholders mentioned how his own family were persuaded to stock signal crayfish when it was legal:

“in the 1970s when there was a legal encouragement to put them in ponds... And I think my father may have done that to a pond near here, which may be why how they got into the [River name]” (Estate owner).

As exemplified by this comment, various stakeholders feel that the legal introduction of signal crayfish subsequently led to their spread through releases and escapees. The stakeholders believed that signal crayfish also escaped from large fish farms as *“the early physical security on those sites was probably a bit woeful” (Staff 2 at government body B)*. Crayfish escaping from ponds and fish farms is not unique to the UK, with similar experiences in other European countries (Gutierrez-Yurrita et al., 1999; Gherardi et al., 1999).

Additionally, these stakeholders also believed that another important way that humans contributed to the spread of signal crayfish is through intentional illegal introductions. Although regulations were added to criminalise the movement of signal crayfish (see previous section), practically all stakeholders mentioned how certain actors have nevertheless moved this INNS illegally. One stakeholder mentioned they knew of *“stories of people deliberately spreading them so that they*

could come back and trap them at some point in the future” (chair of river association). Another stakeholder had a more personal experience, mentioning that a commercial trapper had “*admitted to [him] that they*” had illegally introduced signal crayfish into a river (*Chair of fisheries group*). Many of the stakeholders commented that this illegal movement was driven by the “*black market that goes on for them*” (*Chair of fisheries group*). Although the spread and catching of invasive signal crayfish in the UK without a license is illegal, the human consumption of invasive species is still legal (Peay et al., 2010), meaning there is still an economic value for caught signal crayfish.

Finally, some of the same stakeholders also professed an agreement that humans have contributed to the spread of signal crayfish by unintentionally introducing them in new areas. Recreational activities such as angling can result in the unintentional spread of aquatic INNS (Smith et al., 2020). The *Check Clean Dry* campaign was launched by the Department for the Environment, Food and Rural Affairs (DEFRA) in 2010 (NNSS, 2023), to improve awareness of INNS in water bodies and minimise unintentional spread (Anderson et al., 2015). Although many stakeholders welcomed campaigns such as *Check Clean Dry*, they felt they did not represent a panacea as there are still many instances of people unintentionally spreading signal crayfish. This is exemplified by various stakeholders who mentioned how “*juvenile crayfish can get caught up with angling equipment*” (*Environmental consultant*). Another stakeholder mentioned that “*there is always a risk of the public or anybody fishermen or whatever accidentally or deliberately, unwittingly moving them around*” (*Academic*). Comments such as this portray the stakeholders’ attitude of acceptance, as they acknowledge that any human activity in aquatic environments has the potential to spread signal crayfish. This comment also highlights their opinion on the role of awareness, as several other stakeholders (*Environmental consultant, Invasive manager at a water company and Environmental ranger*) also commented on people spreading signal crayfish as they were not aware that they were an INNS.

As a result of these potential pathways, most stakeholders felt strongly that humans had been the principal driver behind the spread of signal crayfish in the UK, with some commenting that the “*anthropogenic pathways that have probably had a greater impact*” (Environmental consultant). Several of these stakeholders felt even more strongly about this, adding that “*anthropogenic spread*” is “*absolutely the number one [cause of signal crayfish spread], no matter what anyone says*” (Staff at government body B). All stakeholders from organisations involved in managing signal crayfish at a national level and/or creating regulation felt that humans had been the most important driver for signal crayfish spread. However, a subgroup of stakeholders who belong to local organisations (the majority of whom are not directly involved in their management), felt that the natural dispersal of signal crayfish had been more important in driving their spread. Signal crayfish are highly mobile creatures, able to travel long distances both upstream and downstream along rivers (Bubb et al., 2004), as well as travelling considerable distances over land when conditions are favourable (Thomas et al., 2018). Studies have found that the range of populations of signal crayfish can expand by 2.4 km per year (Bubb et al., 2005), with individual crayfish having been observed moving hundreds of meters per day (Bubb et al., 2004). One stakeholder mentioned that whilst they had “*heard from the Environment Agency*” about the deliberate and illegal spread of signal crayfish in the UK, they had “*seen no evidence of that*” (Estate owner). Instead, this stakeholder felt that the natural dispersal of signal crayfish had been the most important pathway as “*they spread naturally from river to river quite easily*” (Estate owner). A similar opinion was shared by the chair of the fisheries group who commented that “*in the majority of cases, it’s simply a case of the crayfish [being] able to migrate from one water to another*” (Chair of fisheries group). These types of comments portray the belief of these stakeholders that the high dispersal ability of signal crayfish allows them to quickly invade new waterbodies. Finally, the rivers trust staff had similar attitudes to these other stakeholders, adding that they believed “*most*” of the spread of signal crayfish was because of their

“natural march” and not driven by humans. Interestingly, these stakeholders who believed that human activity was not the biggest factor driving the spread of signal crayfish were also some of those who felt that regulation around signal crayfish and their use should be relaxed. Previous investigations have found there to be correlations between certain attitudes when it comes to environmental issues (Liu et al., 2010). Although the small sample size in this study does not allow us to test whether these two viewpoints are correlated more generally between stakeholders, the correspondence between them here suggests that they may be related.

Impact of Signal Crayfish

Signal crayfish are known to have numerous deleterious effects in the invasive ranges that they occupy (Holdich et al., 2014). These include various ecological (Galib et al., 2020; James et al., 2017), environmental (Mathers et al., 2020a; Faller et al., 2016) and social impacts (Williams et al., 2010). However, perhaps their most notorious impact of signal crayfish in the UK has been on the native white-clawed crayfish populations. Stakeholders mentioned that the *“loss of the native crayfish”* was their biggest concern (Staff at government body A) and another mentioned that they had *“watched the decline of the native crayfish”* because of *“the massive advance of signal crayfish”* (Staff at government body B). The stakeholders believed that one mechanism by which signal crayfish pose a threat to white-clawed populations is through competition, stating:

“they share broadly similar niches to our own native crayfish, the difference being that they are much more fecund, they grow larger and they have higher standing stocks or biomasses”
(Academic).

This narrative of the larger and more aggressive American INNS ‘dominating’ its native British counterpart can be seen in other examples, including the American mink (*Neovison vison*) (Fraser et al., 2017) and the infamous grey squirrel (*Sciurus carolinensis*; (Coates,

2015). Whilst competition was mentioned, the majority of stakeholders mentioned that the biggest impact on native crayfish populations by signal crayfish was as a vector of crayfish plague (*Aphanomyces astaci*). One participant mentioned:

“our focus, of course, is on white-clawed [crayfish], but [we work with signal crayfish as] signals [carry] Aphanomyces, [which is] the principal driver behind [the white-clawed crayfish] demise” (Staff 2 at government body B).

Although many invasive crayfish species from North America, including signal crayfish, are typically asymptomatic to crayfish plague, it is usually fatal to European species, including white-clawed crayfish (James et al., 2017). James et al. (2017) found that over 50% of signal crayfish populations were infected with crayfish plague, meaning that white-clawed crayfish populations that come into contact with signal are at high risk of being lost. Some of the stakeholders shared their personal experiences of having seen “*plague outbreaks*”, mentioning that “*all of the white claws die essentially overnight*” leaving “*hundreds of dead crayfish on the riverbed*” (Staff at government body B). This participant went on to compare the impact of crayfish plague to “*someone*” tipping “*pesticides*” such as “*synthetic pyrethroids*” into the water (Staff at government body B). This graphic description of the effect of crayfish plague on white-clawed crayfish populations demonstrates just how strongly many stakeholders feel about this certain impact of signal crayfish.

Whilst the impact of signal crayfish on white-clawed crayfish was noted, their large size (>100mm), high population density (>100 per m²) and omnivorous nature results in them having many other detrimental impacts on freshwater ecosystems (Lodge et al., 2012; Chadwick et al., 2020). Signal crayfish in their invasive range are capable of reducing the biodiversity of freshwater flora (Nystrom and Strand, 1996) and fauna (Mathers et al., 2020b; Beatty et al., 2020), as well as impacting economically significant salmonid populations (Stenroth and Nystrom,

2003; Findlay et al., 2015). Various stakeholders interviewed in this study mentioned these wider impacts on the whole freshwater ecosystem:

“most [people] probably... would...immediately go to the white-clawed crayfish situation. But I don't think that's the biggest impact they have at all. I mean I think that the way that they change whole ecosystems most probably has a much greater impact” (Environmental consultant).

Some of the reasons the stakeholders gave to why they believe this wider trophic effect is their greatest impact included that they “simplified” ecosystems because they “eat everything” (Estate owner), referring to their omnivorous nature (Lodge et al., 2012). Others also pointed to the fact that they are “a threat not only to the indigenous crayfish population, but also to the wildlife and ecological well-being of our streams, rivers and ponds” (former cabinet minister), including their impact on “salmonids” (Staff 2 at government body B). Some stakeholders also mentioned how they believe that signal crayfish populations are altering the presence of species that predate on crayfish; “Otter populations are spreading, probably as a result of the profusion of crayfish, because they [form a] principal part of their diet” (chair of a river association), whilst another added that “the impact on predators” will “change the mix of our rivers markedly” (Rivers trust staff). Research in the UK has shown that European otters (*Lutra lutra*) feed on invasive signal crayfish (Britton et al., 2017) and that otter populations have markedly recovered from near extinction in the 1980s (Sainsbury et al., 2019). Likewise, research has found that signal crayfish are key prey for native fish populations like chub (*Squalius cephalus*), with the presence of this INNS able to influence the growth rate of the latter (Wood et al., 2017). Interestingly, when the participants were asked about any positive impacts that signal crayfish have had in the UK, those who responded tended to mention their potential as a food source for predators such as “otter[s] and heron[s]” (Academic).

As well as their ecological impacts, signal crayfish in the UK are notorious for the geomorphic modification of riverine environments, including causing bank collapse and increasing the transport of both coarse and fine sediments (Mathers et al., 2022; Johnson et al., 2011; Sanders et al., 2021). A few stakeholders interviewed in this study believed that this environmental influence, and the associated economic implications, was the greatest impact of signal crayfish in the UK. This can be seen in several comments: “*The degradation of banks [is the worst impact] because [it creates] knock-on impacts*” (Chair of river association), and; “*The burrowing without a doubt [is the worst impact] because that leads to the degradation of spawning habitats, bank collapse*” (Chair of fisheries group). This last comment makes reference to how increased fine sediment transport associated with signal crayfish activity degrades the quality spawning habitat for many salmonid fish species, which typically need to be free of fine sediment to allow for the unrestricted flow of oxygenated water to the eggs (Greig et al., 2005). These stakeholders believe that it is not only fish species that are affected by the knock-on impact of signal crayfish burrowing, but also “*invertebrates*”, stating that increased transport of sediment is “*changing the overall quality of the river*” (Chair of river association). Such comments link back to the ideas previously mentioned about the trophic change associated with the introduction of signal crayfish (Lodge et al., 2012). However, they also reveal that these stakeholders see signal crayfish firmly as ecosystem engineers, organisms that are capable of altering the very physical properties and structures of their habitat (Emery-Butcher et al., 2020). This point was echoed by another participant: “*I don’t think... the state of the water encourages them or anything... they change the state of the water*” (Estate owner). These stakeholders also felt passionate in their belief that the geomorphic impact of signal crayfish is having significant social and economic impacts. They commented on the destruction of important “*infrastructure*”, the danger of “*bridge collapse*” (Chair of river association) and the damage to “*properties*” (chair of fisheries group). One of these stakeholders exemplified this last point by stating they

believed that structural damage caused by signal crayfish burrowing had already led “*Magdalen College in Oxford*” to spend “£800 grand [*thousand*]” in repairs. This story received wide media coverage, including an article in one of the largest newspapers in the UK (Hughes, 2016).

All stakeholders agreed that the negative impacts of signal crayfish far outweigh any positive impact (if any) that they may have. Interestingly, however, there were differences in opinion between certain groups over which impacts they perceived to be the most important. Those in government bodies were clear in their belief that the threat posed to native white-clawed crayfish populations was the biggest impact of signal crayfish. This may be explained by the particular focus and interest these bodies have towards the conservation of native species (DEFRA, 2022). On the other hand, members of the angling community saw the geomorphic impact of signal crayfish, and the associated economic and social consequences of this, as their biggest concern. Once again, the particular interest of these stakeholders may provide some ideas as to why they hold this belief. In particular, the geomorphic activity of signal crayfish can impact recreational angling by decreasing the habitat quality for many important fish species (Galib et al., 2020).

Another interesting point is that, when asked to rate how much of a problem signal crayfish were for rivers in the UK, participants from government bodies tended to provide lower scores than the other participants. This may be because their roles also bring them into contact with the impacts of other environmental issues, including climate change, and habitat modification, whereas other stakeholders have a greater focus on invasive species (e.g., invasives manager at a water company). The low number of participants in this study means that we cannot say that the differences in attitudes between these groups can be applied to all that belong to these organisations, they only tell us the attitudes of the individuals interviewed. However, the difference in perception between the groups again suggests that there

could be some ideological differences when it comes to signal crayfish in the UK between key groups.

Management approaches

The management of signal crayfish in the UK is a topic that has received lots of attention (Sibley et al., 2009; Stebbing et al., 2014; Freeman et al., 2010). Different approaches have been suggested to control invasive crayfish and their impacts (Frings et al., 2013; Johović et al., 2020; Peay et al., 2019). The most popular approach to managing signal crayfish in the UK has been trapping, where baited containers are used to lure and subsequently remove individuals (Ulikowski et al., 2017). Many of the stakeholders interviewed, including those from the angling community and from non-governmental associations, mentioned how they had previously removed “*thousands*” of signal crayfish via trapping as a means of controlling their impacts (*environmental ranger*). However, one of the stakeholders mentioned that they had noticed the number of crayfish trapping applications being sent to the EA for “*fisheries management*” purposes have fallen in recent years (*Chair of fisheries group*). This shift decline appears to have coincided with new research that brings into doubt the effectiveness of trapping as a management approach for signal crayfish (Chadwick et al., 2020). Crayfish trapping has been found to be biased towards selectively removing large males (Green et al., 2018). Because large male crayfish typically control population size through their predation of smaller individuals, there is concern that trapping may be promoting the spread of signal crayfish (Moorhouse and Macdonald, 2011; Chadwick et al., 2020). This worry was expressed by a government official:

“the harder you trap them, the more you change the size structure...when people talk about trapping them to manage them, they're not managing them” (Staff at government body B).

New trap designs have been developed to remove signal crayfish from different size classes (Green et al., 2018). However, the opinion of those in government roles is that the increased risk of accidentally spreading signal crayfish associated with trapping, either through modification of size class or poor biosecurity, outweighs its benefit. These government stakeholders mentioned how they believe that trapping is a highly intensive approach that, even when done correctly, may only work in “*certain areas*” to potentially “*cause less interference with anglers*” (Staff at government body B). This sentiment of trapping only being effective in reducing the impacts of signal crayfish, rather than being able to control their population, is also expressed in the recommendations from the UK’s Non-Native Species Secretariat (NNSS, 2011).

Another popular management approach that was mentioned by the participants during the interviews in the use of genetic modification. This management approach typically involves spreading a genetic trait that causes a decline in the population of the target INNS (Phelps et al., 2020). Whilst gene editing may circumvent some of the drawbacks of other approaches, this management technique is generally seen as controversial and fraught with unknown risks (Macdonald et al., 2020). A popular example of the use of this approach is the use of the Myxoma virus to control invasive European rabbits (*Oryctolagus cuniculus*) in Chile and Australia (Correa-Cuadros et al., 2023). Studies show that stakeholders generally have mixed opinions towards the use of gene editing approaches to manage INNS, with some being staunch advocates for the technology whilst others are wary of its consequences (Bernos et al., 2022; Macdonald et al., 2020). In this study, there was a similar mix of opinions towards gene editing approaches from the stakeholders. Many of the stakeholders who are part of more local, on the ground, organisations tended to be positive about the use of genetic modification approaches. Some of these stakeholders mentioned that it was “*an extraordinary opportunity*” (Estate owner), whilst another even added that they thought “*the best*

way forward is, is a biotech solution" (Rivers trust staff). Whilst many of those who supported genetic modification approaches were part of smaller and more local organisation, one participant within a government body also shared their support, mentioning that "*some form of biocontrol to get the population of biomasses down is the only option we have*" (Staff at government body B). However, not all the stakeholders were so positive about genetic modification approaches. One participant expressed their fear of these approaches, adding that "*it terrifies me, it feels like it is playing God*" (invasives manager at a water company). This concern was echoed by another stakeholder, adding that there is "*a lot of public unease about deliberately spreading a disease*" to control an INNS (Academic). This type of concern is common when it comes to dealing with genetic modification, be it for the control of invasive species or other applications (Devos et al., 2022).

Another potential management approach that has been piloted for the control of signal crayfish is the use of chemical treatments such as biocide (Sandodden, 2019). Although not commonly used in the UK, investigations testing the effectiveness of biocide treatment have found it can be highly successful in eradicating signal crayfish populations in small enclosed water bodies such as ponds (Peay et al., 2019). The use of biocide is currently perceived to be the only viable approach for the complete eradication of signal crayfish from a site (NNSS, 2011). Whilst one stakeholder mentioned the mixed success of biocide approaches (*environmental consultant*), other stakeholders were more apprehensive. One of the stakeholders mentioned how they could not approve of its use as they believe it involves "*just poisoning the whole river and killing everything in it*" (Chair of a river association). This is a common criticism of biocides, as they generally cannot be targeted to affect a single species (e.g. signal crayfish) and result in a negative impact on all organisms present in the water body (Ballantyne et al., 2019). This sentiment was also expressed by another stakeholder, who referred to the use of biocide as the "*nuclear*" option (Staff 2 at

government body B), referring to it being an unfortunate last resort approach with lots of drawbacks.

Finally, another approach that was mentioned by several of the participants in the interviews is the use of 'ark sites' to protect the remaining population of native white-clawed crayfish. The use of 'ark sites' has gained popularity in conservation circles and involves the translocation of the remaining white-clawed crayfish populations, and/or those from captive breeding programs (Nightingale et al., 2017), to suitable sites where they may be at a lower risk of exposure to signal crayfish and the crayfish plague (Kozák et al., 2011). These 'ark sites' need to be carefully selected to ensure that they are not only suitable habitats for the native species but also that they are sufficiently isolated to ensure the future safety of the population from the advance of signal crayfish (Peay, 2009). The Great Britain Non-Native Species Secretariat (NNSS), a key figure responsible for deciding the UK's strategy towards INNS, argues that ark sites may be the best option we have to conserve white-clawed crayfish (NNSS, 2011). Many of the stakeholders from government bodies also believe that ark sites may be the best options we have to manage the impacts of signal crayfish: "*the main solution is ark sites*" (*Staff at government body A*). Many stakeholders outside the government who are also focused on conserving the white-clawed crayfish have also started using ark sites: "*We're trapping and moving our white-clawed to a site up the other side of [Town]... super site... we moved 200 last year [and we're] hoping to move as many as we can again this year*" (*Environmental ranger*). Research evaluating the success of ark sites in south-west England appears to show promise, with around 75% of the sites appearing to have successfully established populations of white-clawed crayfish (Nightingale et al., 2017). The popularity of ark sites among stakeholders in the government is not surprising, as stakeholders tend to favour non-lethal management solutions to INNS (Shackleton et al., 2019). Furthermore, ark sites might be the most popular management approach among those in governmental positions as it aligns with their

attitudes on the impacts of signal crayfish. As already mentioned, those in government positions all ranked the threat to native, white-clawed crayfish as the biggest impact of signal crayfish. Therefore, it appears logical that they would favour a management solution that focuses on preserving the remaining populations of this native species. In contrast, whilst ark sites appear to be popular within those in government roles, other stakeholders interviewed here also see it as an “*interim*” management approach (*Academic*). This opinion from these other stakeholders may stem from the fact that ark sites do not actively manage the advance of invasive signal crayfish or their other impacts.

As in Adams (2016), there was a mix of opinions towards the different management solutions from the stakeholders in this study. Although various stakeholders, particularly from local groups, were keen to see new approaches such as genetic modification being tested, the majority of those in governmental positions and more focused on conservation efforts were apprehensive about the ethics of its use. Likewise, there were also contrasting opinions when it came to the effectiveness of trapping. Stakeholders from local groups were keen to continue trapping, whereas those in government bodies felt that it may be counterproductive to stopping the spread of signal crayfish. Instead, stakeholders in government bodies tended to favour the use of ark sites to protect the remaining white-clawed populations from the advance of signal crayfish.

Outlook for the Future

Some of the stakeholders interviewed shared a level of optimism for the future. Although they consistently believed the initial response to the crayfish invasion was slow, they feel there has been some improvement in the way the government is set up to deal with INNS: “*where we are now compared to... where we were 20-30 years ago... we’re in a much better place now*” (*Academic*). Some of the improvements that this stakeholder was referring to are improved regulations that have a more species-specific focus:

“You know, we’ve got stronger legal controls now. We have staff in CEFAS [Centre for Environment, Fisheries and Aquaculture Science] now responsible for trying to identify and stop the spread” (Academic).

As well as dedicated staff overseeing aquatic invasive species, CEFAS have also developed tools such as the Aquatic Species Invasiveness Screening Kit (AS-ISK) to help decision makers identify possible threats (Copp et al., 2016). Another stakeholder also shared some optimism, describing how their organisation has begun “*novel*” management approaches including “*using detection dogs to survey large areas and look for them [signal crayfish]*” (*Invasives manager at a water company*).

However, whilst some stakeholders shared positive developments and improvements, most were generally pessimistic about what the future holds. One source of pessimism came from the bureaucracy that they felt still hampers the search for viable management solutions. For example, one environmental ranger mentioned their attempts to implement the use of barriers to halt the advance of signal crayfish but that this was discontinued as they “*couldn’t get permission from the local landowner to install it*” (*Environmental ranger*). Likewise, another stakeholder whose organisation translocated native white-clawed crayfish to ark sites felt frustrated by the bureaucracy:

“There’s a lot of red tape involved and... we’re trying to help a species survive and yet we’re having to follow red tape” and “if an organisation like a rivers trust wants to try and save an iconic little species like a white-clawed crayfish, try and help them from six or seven permits [they need] to fill” (Rivers trust staff).

Adams (2016) also noted that many stakeholders are frustrated with the perceived high level of bureaucracy surrounding signal crayfish management efforts.

As well as bureaucracy, many stakeholders feel that there is little hope of finding a viable solution to the problem of signal crayfish because of government inactivity:

“We need to do something about it, and it feels frustrating that some of the big organisations like the Environment Agency and Natural England really seem to be taking a back seat in this” (Rivers trust staff).

Many of the non-governmental stakeholders expressed a belief that the government seems to be acting in a “defeatist” manner (*Chair of river association*). Interestingly, all the government officials interviewed here shared a pessimistic outlook for the future crayfish in the UK:

“Basically there’s not a lot we can do about it [signal crayfish]... I’m an optimist, so I hope they [white-clawed crayfish] will survive. Yes. But I don’t know that they will” (Staff at government body A).

Stakeholders acknowledge that research into whether gene editing or other technologies could act as viable management approaches requires “massive amounts of investments” (*Academic*), and they believe that currently there is a lack of “funding and political will” from the government (*Environmental consultant*).

One approach that can be used to increase political will is collaboration between stakeholders and engagement with the public (Irvin and Stansbury, 2004). There have been some efforts to collaborate, with the *Invasive manager at a water company* stating how they had various forums, including “*regional Invasives Forum and the National Water Company Forum*” to increase regional collaboration between water companies, NGOs and local groups in the management of signal crayfish and other INNS. Another example of collaborative working in the UK is the South West Crayfish Partnership (SWCP), which involves the EA, Bristol Zoo, and a host of different trusts including Buglife (Robbins et al., 2013). This group have set up white-clawed crayfish captive breeding programs at Bristol Zoo Gardens, as well as

translocated crayfish from here to ark sites across the Southwest England and Wales (Nightingale et al., 2017). Although some collaborative approaches like this have been set up, most stakeholders agree that we need more collaboration: “*we need a broad collegiate of stakeholders... Rivers trusts have a fundamental role... the environment agency... maybe wildlife groups*” (Academic).

Although collaboration seems to offer many solutions, the stakeholders alluded to the fact that there appears to also exist a lot of conflict and fractured relationships in the crayfish community in the UK. Effective management of INNS requires close co-operation between relevant stakeholders (Perrings et al., 2010). Some of individuals interviewed expressed negative experience with governmental bodies, describing some officials as being “*sat behind a desk and [with] not the first clue what they’re talking about*” (Chair of fisheries group) or labelling the EA as a “*very bossy regulator that tries to control everything that happens in rivers*” (Estate owner). On the other hand, another stakeholder commented how working in crayfish management is “*a difficult arena to work in*” because it’s a “*world [that] is small and high[ly] political*” and mentioned how “*individuals have verbally attacked me and tried to discredit work I’ve done*” (Environmental consultant). The stakeholders interviewed in Adams (2016) also shared their belief that there was conflict between different groups, particularly between more local groups (anglers, crayfish trappers) and government officials. This sense of strained relationship between regulators and the regulated was also expressed in various of the interviews in this study. As one stakeholder put it, this may be because the conversation around crayfish in the UK is “*quite emotive*” (Environmental consultant). Many stakeholders are very passionate about the topic of signal crayfish and have strong opinions on the different aspects of the conversation, be it how they were introduced, what are their major impacts and how we should manage them. As well as costing the UK at least £2.6 million a year (Williams et al., 2010), signal crayfish threatens the hobby of many anglers and are also driving the only native crayfish species close to

extinction (Chadwick, 2019), therefore this passion and vested interest can be understood. Whilst this passion may sometimes make collaboration between groups difficult, example such as the SWCP project (Nightingale et al., 2017) shows that it can lead to impressive results when the communication between stakeholders is effective, and their goals align.

As well as greater collaboration between all parties, stakeholders mentioned how there is a clear need for far greater awareness when it comes to signal crayfish in the UK. Studies have shown that increasing public awareness of INNS and their impacts can lead to greater support for management (Novoa et al., 2017). Stakeholders from all different groups mentioned how, although there is more awareness than there was previously, there should be a greater effort to increase the awareness of signal crayfish in the UK: *“I think [there’s] been complete unawareness of what a bad thing they are” (Invasives manager at a water company)*. The stakeholders mentioned how that greater awareness could be enhanced by using new approaches, such as *“social media”, “TV”, “Newspapers” (academic)* or via high profile figures like sports personalities (*“Alan Shearer or Gary Lineker”*) and famous wildlife presenters (*“David Attenborough” (Rivers trust staff)*). Media attention on the use of signal crayfish for consumption has previously been shown to increase interest in the topic (NNSS, 2011), thus coverage on its impacts and management may likewise raise awareness on these aspects. Many stakeholders stressed that awareness building should be *“local as well... not just... national scale” (Academic)* and how local stakeholder groups such as Rivers Trusts are perhaps best placed for this type of work because they have *“better trust relationships [with] landowners... local communities... [and] anglers”* than larger organisations like the EA (*Academic*).

Synthesis: Towards an improved management of the invasion of signal crayfish

In this study, we explored the role and attitudes of stakeholders associated with signal crayfish in the UK. The aim of this was to gain a

better understanding of these stakeholders and provide actionable recommendations. Through the stakeholder mapping exercise, this study has demonstrated that stakeholders perceive that different groups have varying levels of interest and power in the discussion around signal crayfish. Government bodies such as the Environment Agency and Natural England unsurprisingly were perceived to have both lots of power and interest. Interestingly, stakeholders also felt that more local groups such as river trusts and angling clubs were also important players because of their high interest in signal crayfish in the UK. Greater collaboration between these varied groups of stakeholders with differing levels of perceived power would allow a diverse range of opinions, knowledge and experiences to contribute (Shackleton et al., 2019). For example, greater dialogue between government staff and local anglers may provide more accurate collective knowledge of the state of signal crayfish in local areas. Greater collaboration could also enable government bodies to engage more effectively with the public, as many of the stakeholders interviewed here felt that the local groups generally had better relationships with local communities.

The mapping exercise also revealed the opinion of the stakeholders that key groups such as Local Businesses and Local Politicians seemed to be currently disinterested in the debates around signal crayfish and its impacts. Increased engagement with these currently disinterested groups through dialogue and partnerships would enable them to be more engaged in discussion around signal crayfish, particularly if it is clearly explained how they are also impacted by this INNS (Novoa et al., 2018). This will be critical as greater buy-in from a wide range of stakeholders increases the chance of successfully controlling invasive species (Irvin and Stansbury, 2004).

The interviews that were conducted also shed light on the attitudes of stakeholders on different aspects of the debate around signal crayfish. They also provided insight into where there is consensus between the stakeholders and where there are conflicting attitudes. The stakeholders shared similar attitudes when it came to certain topics. For

example, all stakeholders agreed that the government has made various mistakes when it came to dealing with signal crayfish in the UK. This includes not adequately responding to the advice of experts prior to their introduction and overestimating the size of the market there was for it. Many stakeholders accept that there has been some improvement in the government's handling of signal crayfish. However, whilst some collaborative efforts such as the South West Crayfish Partnership (SWCP) (Robbins et al., 2013) have taken place and had success, all stakeholders felt that there needs to be much more collaboration and awareness to effectively manage signal crayfish. Whilst these points create a sense of optimism, practically all the stakeholders are pessimistic about the future (with regards to the signal crayfish invasion) and feel that it may already be too little and too late. Those in non-governmental roles felt that the government agencies were acting defeatist and that they did not have the political will or funding to create an effective management solution to control signal crayfish. Likewise, those in governmental roles believe that there is little that can be done to stop the spread of signal crayfish and instead are trying to protect the remaining populations of native white-clawed through ark sites.

The difference in attitudes between the stakeholders around certain topics highlight the plurality of opinions when it comes to signal crayfish in the UK. Many of the differences in attitudes were between those stakeholders in government bodies or working at a national level and those more local groups on the ground. Although there were exceptions, the attitudes of these stakeholders appeared to fall under certain themes. Those in government roles and/or part of national organizations tended to favour stronger regulation that limited the spread of signal crayfish by human activity, were against greater commodification, tended to prioritise the impacts of signal crayfish on white-clawed crayfish and focused on management solutions that enabled their conservation. On the other hand, those in local groups tended to be open to some deregulation that allowed for the exploration of more experimental management solutions to eradicate signal

crayfish and were open to their use as a resource to fund this. With the small number of participants interviewed in the study, we cannot say that these general attitudes are representative of all stakeholders from these groups. Particularly as people within the same organization or role can have very different attitudes towards environmental issues (Wolf and Moser, 2011). Therefore, it would be useful for future research to explore these topics with a greater number of participants to see whether these trends are widespread among stakeholders in these groups. However, this perceived dichotomy in attitudes suggests that there may be some fundamental differences in perspectives between these two camps when it comes to signal crayfish in the UK. Differences in attitudes between local groups and national-level organisations when it comes to INNS can be common (Novoa et al., 2016). This is particularly the case when there are also differences in their power and role (i.e. regulated vs regulator) that may alter their experiences and interests (Adams, 2016).

5.5. Conclusion

This investigation highlights varied attitudes and perceptions of multiple stakeholders to the UK's ongoing signal crayfish invasion. Whilst the contrast in attitudes between stakeholders may provide challenges, this is to be expected when dealing with an environmental issue that impacts so many different groups of people. It is clear from the study that there must be greater collaboration of dialogue between stakeholders, particularly those with different roles, power, and perspectives when it comes to signal crayfish in the UK. Powerful outcomes can be created through well-designed collaboration that emphasises the sharing and respecting of perspectives, experiences, and ideas from different groups. Projects such as the SWCP showcase the power of schemes that benefit from involving multiple stakeholders to achieve a desired outcome (Robbins et al., 2013). A criticism that various stakeholders shared was that the crayfish "*world is small and high[ly] political*" (*environmental consultant*). It is important that future

work also explores further the attitudes of the public as increasing the general population's awareness of signal crayfish and their impact can allow more people to be part of these important discussions.

Furthermore, allowing academics, regulators and other groups to openly discuss their attitudes and the facts enables science to be translated into action (Cash et al., 2003).

Although this study focuses on signal crayfish in GB, the issues, opinions, and ideas outlined here can be applied to the management of INNS more generally. There are other invasive crayfish species starting to spread throughout the UK (Peay et al., 2010). Relevant stakeholders must begin to work towards shared goals respectfully and collaboratively despite the presence of certain differences in opinions. Whether it is for invasive signal crayfish or for other INNS that are "coming down the line" (*Chair of fisheries group*).

Chapter 6: General synthesis and conclusion



6.1. Testing of hypotheses

This thesis set out to investigate the invasion of signal crayfish by testing three key hypotheses:

- **Hypothesis 1:** Signal crayfish are found in more diverse environmental conditions than white-clawed crayfish
- **Hypothesis 2:** Signal crayfish in GB are bigger, more active and have higher exploration at invasion-front compared to those invasion-core sites.
- **Hypothesis 3:** Those who create and enforce environmental regulation have different attitudes towards the invasion of signal crayfish compared to those whose activities are impacted by the regulation (i.e. ‘the regulated’)

Hypothesis 1: Signal crayfish are found in more diverse environmental conditions than white-clawed crayfish

Chapter 2 tested this hypothesis using different data sources to determine the conditions where signal and white-clawed crayfish have been observed in Great Britain. The variables that were part of the analysis included topographic, land cover, geological and water quality parameters, as well as the density of physical barriers. The study also utilised relatively new citizen science platforms to provide an updated map showing the distribution of both species and highlighted the pattern of spread of the INNS.

Results showed that signal crayfish and white-clawed crayfish have generally been observed in very similar environmental conditions in Great Britain. The similar environmental ranges of both species also support another finding, namely that signal crayfish are continuing their rapid expansion into areas around Wales and northern England where only white-clawed crayfish are currently found. Whilst most of the

catchments where signal crayfish were initially introduced were in the south of England, representing a core of its invasive range in Great Britain, the species has quickly spread outwards, occupying vast swathes of the island that previously only contained white-clawed crayfish.

The inclusion of water quality variables in the analysis did not alter the generally nested distribution of white-clawed crayfish inside the range of conditions where signal crayfish have been found. A small difference in their distribution was found to be driven by one sub-catchment where only white-clawed crayfish are found and that has a much stronger association with high oxygen concentration and elevation than the other sites. When this was analysed further, it was noted that this sub-catchment is at the northern edge of where signal crayfish have currently expanded. Therefore, with the currently available information and the findings in this study, it appears that it is likely only a matter of time before signal crayfish reach this sub-catchment as well.

Hypothesis 2: Signal crayfish in GB are bigger, more active and have higher exploration at invasion-front compared to those invasion-core sites.

Chapter 3 tested this hypothesis by comparing the traits of signal crayfish in locations where they have only recently arrived (invasion-front) and those in areas that have been colonized for a longer period (invasion-core). Importantly, this study represented the first known attempt to compare signal crayfish between the invasion-front and invasion-core in multiple rivers. This pairwise comparison in five different river systems allowed testing of whether differences in traits between these locations were generalisable or not.

The study found that locations along the invasion continuum did have an impact on several key traits of signal crayfish, with individuals at invasion-

front sites generally being smaller than those at the invasion-core within a river. Likewise, the study found that the density of signal crayfish at invasion-front sites is consistently lower than the corresponding invasion-core sites. Previous research has shown that large individuals are highly territorial and exclude smaller signal crayfish from highly suitable areas (Edeline and Loeuille, 2021). The exclusion of smaller and younger individuals from more suitable conditions appears to provide a likely explanation as to why smaller crayfish were overrepresented at the invasion-front sites. If true, this would mean that the expansion of signal crayfish is primarily through 'pushing' outwards from the core, rather than it being 'pulled' by dynamics at the front. Likewise, the finding that signal crayfish density was also lower at invasion-front sites further supports the idea that this population is driven by 'pushed' processes. This is because 'pushed' expansions are thought to be particularly prominent in species where dispersal is greater at higher densities (Dahirel et al., 2021), and previous work has shown that this is the case for signal crayfish (Galib et al., 2022). Whilst the existence of 'pushed' expansions has previously been described (Dahirel et al., 2021), this feature of signal crayfish dynamics would set it apart from other infamous examples of species whose traits also differ at the invasion front but who present the characteristics of a 'pulled' expansion (Phillips et al., 2006). Likewise, it also suggests that processes such as spatial sorting, a popular theory to explain why differences in traits may arise at the invasion-front, does not apply to signal crayfish in Great Britain.

Whilst the location along the invasion continuum had an impact on the size of signal crayfish, this study found that it did not have a significant impact on the behavioural traits that were analysed, namely activity, exploration and climbing tendency. However, it appears that the individual rivers that signal crayfish were caught from can have a significant impact on these traits, regardless of whether it was from an invasion-core or front site. The interaction between location along the invasion continuum and study site (ie. a given river) had a significant impact on two of the signal crayfish traits (activity and climbing tendency).

Likewise, the river that signal crayfish were caught in had a significant impact on all the traits that were looked at in this study. In combination, this demonstrates that traits of signal crayfish, be they morphological or behavioural, can vary greatly between different locations.

Hypothesis 3: Those who create and enforce environmental regulation have different attitudes towards the invasion of signal crayfish compared to those whose activities are impacted by the regulation (i.e. ‘the regulated’)

Chapter 4 tested this hypothesis by analysing semi-structured interviews with a range of different stakeholders that have a connection with signal crayfish in the UK. This study subsequently analysed the interviews using a thematic analysis (Braun and Clarke, 2006) to present the attitudes of different stakeholders in several key areas.

A consensus of opinions from stakeholders was found in some areas. For example, all stakeholders that were interviewed agreed that the government had historically made some serious errors that led to the initial introduction and subsequent spread of signal crayfish throughout Great Britain. Likewise, all the stakeholders felt that there are currently issues with the current legislation around the use and management of signal crayfish. Stakeholders from government bodies who operate at a national level tended to feel that the current legislation, such as The Prohibition of Keeping of Live Fish (Crayfish) Order 1996 (Peay et al., 2010), is too weak and has troublesome ambiguity. On the other hand, those participants who are part of smaller, more local organizations feel that current legislation is too heavy-handed and that it limits the management work that local organizations can do. These two groups tended to also have conflicting attitudes towards other important issues. For example, the stakeholders from local groups tended to believe that the natural dispersal ability of signal crayfish has been the dominant driver behind the spread of signal crayfish in Great Britain. In contrast,

stakeholders from government bodies and other large organisations felt that anthropogenic activity had played a greater role in the spread of this INNS. The two groups also differed in their preferred management solution, with those from government bodies favouring the use of 'ark sites' to protect the remaining native white-clawed crayfish populations, but others preferring a more proactive approach of trying to control populations of signal crayfish. One attitude shared by practically all stakeholders is that the window for managing signal crayfish has likely already passed, that we need to learn to live with this INNS, and that we must learn lessons from mistakes and apply them to future biological invasions. Variations in stakeholder opinion towards signal crayfish have been explored previously (Adams, 2016), but here we demonstrate that contrasting opinions persist and expand beyond just the preferred management approach.

6.2. Discussion and implications of the thesis

In testing these hypotheses, this thesis has, among other things, provided new information on the invasion of signal crayfish, the variability in their traits between sites, and how stakeholders feel about how they have been managed. In the remaining section of this chapter, we discuss in more details these findings and their wider implications, focusing on several key themes:

Signal crayfish, their invasion and impact on white-clawed crayfish

Previous studies have shown that the range of signal crayfish has increased since their initial arrival in 1970s (Sibley, 2003; Rogers and Watson, 2010; Holdich et al., 2014; Chadwick, 2019). The current thesis has demonstrated that signal crayfish in Great Britain are still expanding

their range into new areas (Chapter 3). Furthermore, the maps in Chapter 3 highlight areas where signal crayfish have most recently colonized, including sub-catchments in Wales and northern England, both of which contain the remaining sizeable populations of native, white-clawed crayfish. Whilst demonstrating that this pattern of signal crayfish advance and white-clawed crayfish retreat is still taking place is useful information, this thesis goes beyond this and discovers some possible explanations behind these trends.

First, in Chapter 3, we used principal components analysis (PCA) to demonstrate that signal crayfish are capable for thriving wherever the native species is found. Previous studies have suggested that the INNS appear to have wider tolerance than the native species (Holdich and Rogers, 2000) and this study does not rule this out. Future research should expand on this and include a greater number of factors and sites in the analysis to be able to provide a more definitive answer to this. A novel aspect of the thesis that separates it from other previous investigations (Chadwick, 2019), is the inclusion of observational data from a citizen-science repository called iNaturalist. In this chapter, we discuss some of the exciting benefits that citizen-science data has already and can provide for managing INNS such as signal crayfish. However, we also discuss some of the challenges that are still associated with this type of data. Overall, the analysis carried out in this chapter indicates that signal crayfish can thrive wherever white-clawed crayfish are found, as well as in other areas where the native species cannot sustain a population.

Another factor that might be contributing to the advance of signal crayfish and retreat of native white-clawed crayfish, is the difficulty in detecting the advance of the former. Chapter 4 of the thesis used primary field data collected from five rivers to provide the first known demonstration that signal crayfish at invasion-front sites in Great Britain tend to be smaller in size than those at the invasion-core. Although smaller in size of crayfish at the front does not by itself equate to a faster spread, it may allow the species to expand its territory without detection/removal by

local environmental managers or other organizations. This sentiment was echoed in some of the interviews that took place in Chapter 5 of the thesis, where two stakeholders mentioned how it may be several years after signal crayfish have arrived at a site before they are detected. Without early detection, it is very difficult for relevant organizations to establish adequate control measures to halt crayfish advance (NNSS, 2011). Future research could replicate the fieldwork conducted in Chapter 4 by looking at additional factors to see whether there are other differences between signal crayfish at invasion-front and invasion-core sites. Furthermore, future work could also conduct a common-garden experiment using crayfish from invasion-front and invasion-core sites to investigate whether differences in size and other possible traits have any genetic component.

Related to this, the analysis of stakeholder attitudes that took place in Chapter 5 also provides several findings that can help explain the advance of signal crayfish. Firstly, the interviews with the stakeholders show that many of them believe that, as well as signal crayfish being able to naturally spread at a high rate, humans have aided the expansion of the species in Great Britain. Many of the stakeholders interviewed from large organizations feel that people have intentionally and unintentionally spread signal crayfish into new areas. The chapter demonstrates how humans have illegally planted individuals into new rivers to harvest them at a later point for profit. Although several stakeholders from more local organizations question the importance of anthropogenic activity in the spread of signal crayfish, these modes of anthropogenic expansion have been noted by previous authors (NNSS, 2011; NNSS, 2023; Holdich et al., 2014). Additionally, this chapter also uncovers the overwhelming belief of stakeholders that there is a lack of adequate regulation or management to control the spread of the species. A wide variety of stakeholders, except those in governmental bodies, were eager for the development of new approaches to manage signal crayfish, including genetic modification, which has been used to control other INNS (Correa-Cuadros et al., 2023; Devos et al., 2022). In the absence of these or other

new management approaches, there is limited capacity to control the expansion of signal crayfish in Great Britain.

When we take into account all the contributing factors discussed above, as well as the general competitive advantage of signal crayfish over white-clawed crayfish (Dunn et al., 2009), it is of little surprise that we see the INNS continuing to expand their territory and replace the remaining native crayfish populations in Great Britain. Most of the stakeholders interviewed in Chapter 5 felt all these factors indicate that it might be already too late to save wild populations of native, white-clawed crayfish in Great Britain. The UK government and the relevant agencies are prioritising the use of 'ark sites' to protect the remaining native crayfish populations. However, as has been seen from projects such as the South West Crayfish Partnership (SWCP) (Nightingale et al., 2017), many of these projects already rely partially on implanting captive-hatched white-clawed crayfish. The findings in Chapter 3 that signal crayfish can thrive in any location where white-clawed crayfish are found, coupled with the finding that signal crayfish are smaller at invasion-front sites (Chapter 4), puts extra pressure on the managers of ark sites to ensure that they deploy extra measures, such as the use of eDNA sampling or barriers, to ensure that the INNS does not threaten the survival of native white-clawed crayfish at these locations.

Role of humans in the invasion of signal crayfish

Another prominent contribution of this thesis is the demonstration of the influence humans have on the invasion of signal crayfish. The findings of the thesis present how humans have not only played a prominent role in the introduction and expansion of signal crayfish but that the social aspect of the invasion is key to decision-making, as it provides us with a look at the interplay between politics, stakeholder relationships and science. As Chapter 5 focuses on the human factors in the invasion of signal crayfish, that content will not be repeated here; however, some

more general aspects and areas that cut across the whole thesis are explored below.

The role of humans in the introduction of signal crayfish has been covered extensively in previous studies (Sibley, 2003; Sibley et al., 2009; Holdich et al., 2014; Peay et al., 2010). By analysing interviews with different relevant stakeholders, Chapter 5 of this thesis provides key insight into how humans have influenced crayfish in Great Britain. As mentioned above, the chapter explores the attitude of many stakeholders that anthropogenic activity has been the primary driver behind the rapid and constant expansion of signal crayfish in Great Britain. Throughout the other chapters in this thesis (Chapter 3 and 4), the human influence on the expansion of signal crayfish has also had an influence. In Chapter 3, the map showing the progression of signal crayfish expansion through time (**Figure 2.3**) demonstrates large 'jumps', where signal crayfish have been observed in areas very far from previous observations. It is possible that these 'jumps' may be an artefact of the incomplete nature of the dataset (Barry and Elith, 2006). However, when combined with the attitudes of the stakeholders, this may very well be evidence of human activity, either, intentionally or unintentionally, spreading signal crayfish across Great Britain. Likewise, when conducting the fieldwork for Chapter 4, the author and his field assistants came across children searching for crayfish near rivers and streams. Whilst it is heartening to see this type of engagement from young people with rivers and their ecology, it is these exact situations that the stakeholders interviewed in Chapter 5 and previous authors have mentioned can lead to the unintentional spread of signal crayfish (NNSS, 2011; NNSS, 2023). The characteristics of signal crayfish allow them to generally have naturally higher dispersal ability than the native white-clawed crayfish, particularly when paired with the deleterious impact that crayfish plague has had on the population of the latter. The findings in Chapter 4 that individuals at invasion-front sites may in some scenarios contribute to this, particularly as high-flow events may be able to move smaller signal crayfish a large distance in the downstream direction (Bubb et al., 2004). However, the

discussions with the stakeholders, several of whom mentioned that they had known of individuals intentionally stocking waterbodies with signal crayfish, and the observations in the other chapters appear to support the conclusion that anthropogenic activity has played a key role in the spread of signal crayfish in the UK.

Another important theme in the thesis is the idea that the issue of signal crayfish, and perhaps INNS more generally, has not received the appropriate attention or funding it merits. These sentiments were expressed loudly by almost all stakeholders interviewed in Chapter 5. However, examples of this were seen across the other chapters that make up this thesis. For example, most of the limitations of Chapter 3 result from the lack of access to or collection of relevant crayfish data in Great Britain, be this observational or environmental data. For example, the low spatial coverage of water quality data meant that we had to use a lower number of sub-catchments for our analyses. Similarly, the incomplete nature of the observation datasets and the low number of points in more rural locations complicated the analysis in Chapter 3, but also the location of adequate sites for Chapter 4.

Although signal crayfish are a particularly well-known INNS in Great Britain, these issues with data still impede research and make it more difficult to analyse their spread, their impact, or the development of effective management solutions. As expressed by most stakeholders in Chapter 5, it appears that these issues stem from a lack of political will or urgency when it comes to tackling the issue. One stakeholder even contrasted the pace of action, legislation, and funding for the COVID-19 pandemic and the lack thereof when it comes to INNS. The study and management of signal crayfish (and other INNS) in Great Britain, would be hugely boosted by access to reliable data representing the location of the species and other environmental factors that can impact their presence. In addition to higher quality data, the management of invasive species like signal crayfish may also benefit from a review of the governance practices and policies that interact with our ecosystem. Clement (2020) argues that anthropogenic activity, including the

movement of invasive species, is creating novel ecosystems. She argues that the intrinsic influence of humans on these ecosystems means that we need to modernise our approach to managing and regulating these ecosystems to account for this anthropogenic influence. The frustration felt by many stakeholders interviewed in this thesis, including those creating and enforcing environmental policy, suggests that many share Clement's views that how we govern invasive species and their impacts requires modernisation.

Whilst revealing an important issue, this sentiment that anthropogenic activity (and inactivity in some cases) has impacted the invasion of signal crayfish perhaps offers a glimmer of hope that we can also play an important role in managing the signal crayfish and other INNs in Great Britain. Chapter 3 used data collected through citizen science and demonstrates that this is becoming increasingly important in shaping our understanding of where signal crayfish are in Great Britain. As discussed in that Chapter, missing or incomplete datasets remain an important barrier to answering important questions about the ecology of crayfish, as well as their presence and absence from different locations. As well as contributing data, a greater number of initiatives that leverage citizen science may also allow a wider range of people to engage with the topic of signal crayfish, just as it has in other case studies (Potgieter et al., 2024; Earp and Liconti, 2020). This may have the positive impact of raising awareness of signal crayfish, which may ultimately result in policymakers and politicians paying greater attention to this important topic. The author believes that we are only just scratching the surface of the contribution that citizen science can to the study of invasive species and other environmental threats. In the future, we may see citizen science playing an even greater role in what questions ecologists ask, how data is collected, and the wider impact of scientific research.

6.3. Final remarks

Throughout the different chapters, this thesis has tried to address important questions surrounding the invasion of signal crayfish in Great Britain. From the advance of this INNS across the island, the factors that influence their spread and the population dynamics result in variations in ecologically important traits. Whilst this thesis has contributed to our understanding of signal crayfish in Great Britain, there are still important questions that remain unanswered. It would be highly beneficial for future research to continue investigating this INNS. From an ecological standpoint, future research must investigate whether there are other traits (not identified here) that vary between invasion-core and invasion-front sites. Likewise, it would be beneficial to understand whether there are any other environmental variables (again, further to those examined here) that may influence where and where not signal crayfish can persist. Previous research has shown that warming rivers may increase the performance of signal crayfish (Rodríguez Valido et al., 2021), but it would be interesting to understand more clearly how the impact of climate change and altered flow regimes may impact this INNS. We have also seen throughout this study how there are currently limited approaches to managing signal crayfish. Therefore, it would be beneficial to develop future management solutions that may provide us with a better chance of managing signal crayfish.

This thesis has demonstrated that signal crayfish are highly adaptable INNS that, because of their naturally wide environmental tolerance, high dispersal ability and human activity/inactivity, pose a very serious threat to native species. The thesis also demonstrates that the invasion of signal crayfish is a complex situation, with population and individual-level processes influencing their wider ecology. Whilst this thesis focuses on signal crayfish, many of the issues here also apply to other INNS.

Through the holistic approach taken, this thesis does not restrict itself to a single discipline and has the freedom to look at the interactions between different aspects of the invasion of signal crayfish. It is within

these interspaces between often siloed disciplines that subtleties and nuances are discovered. Additionally, by looking across these different disciplines, this thesis has the opportunity to observe and comment on how an array of different factors, some physical and others social, have come together to create a complex biological invasion. With the number of INNS expected to increase in the future (Bailey et al., 2020; Pyšek et al., 2020), it is paramount that we develop robust and effective approaches to dealing with these scenarios. We must develop a sound understanding of the ecology of INNS but also create effective policy that places adequate urgency to deal with their impacts. A more holistic approach to researching environmental threats, one that does not only focus on the physical aspects but also respects the social and political nature of the problem, may provide the best approach to managing the novel ecosystems humans have created. It may be that we are already too late to control the spread of signal crayfish in Great Britain, but we need to be prepared for the INNS that are on their way.

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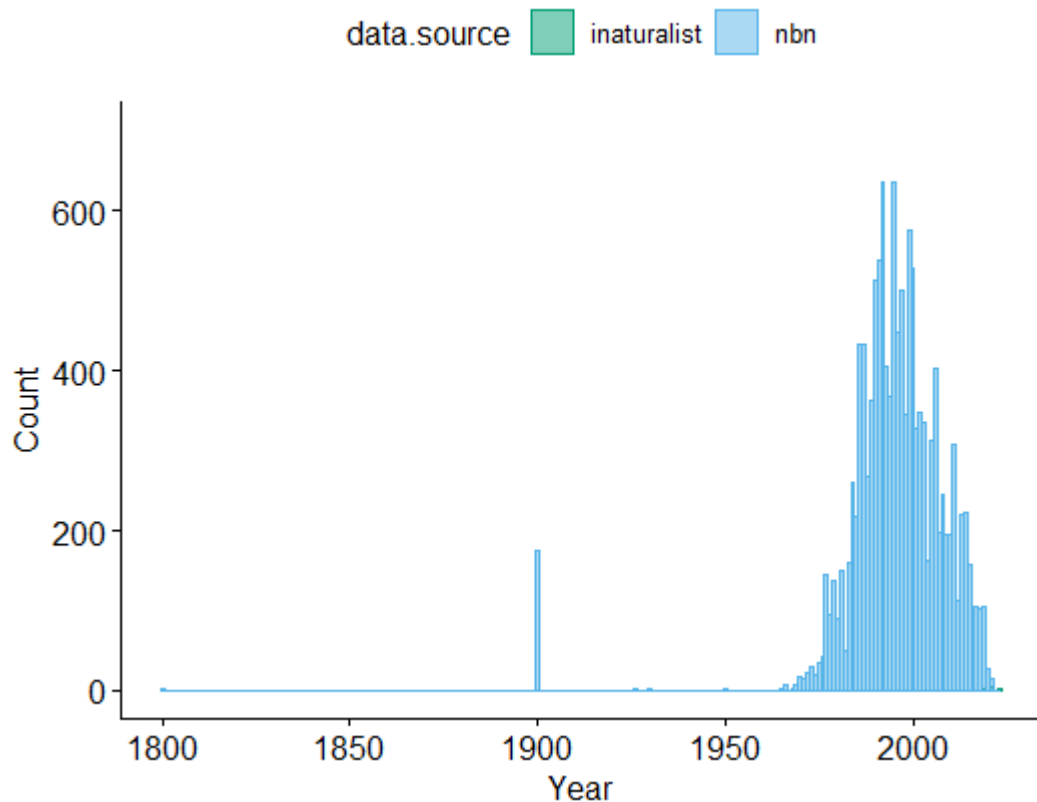
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Appendix 1: Histogram showing the histogram for all the observations of white-clawed crayfish.

Appendix 2: Sample of interview questions

Context	1. Could you briefly introduce yourself and what you do? 2. What do signal crayfish represent for you? 3. What is your connection to Signal Crayfish? 4. How long have you known about signal crayfish? 5. On a scale of 1-5, how much of a problem would you say Invasive species are? (with 1 being not at all and 5 being a very serious problem)
Attitude toward signal crayfish	6. Do you think that signal crayfish are a problem in the UK? 7. On a scale of 1-5, how much of a problem would you say signal crayfish are? (with 1 being not at all and 5 being is a very serious problem) 8. In your opinion, what (if any) are some of the negative effects of signal crayfish? a. [If multiple effects provided] Can you put them in order from worst to least bad in your opinion? 9. In your opinion, what (if any) are some of the positive effects of signal crayfish?
Invasion Process	10. How were signal crayfish introduced to your area?

	11. What factors do you think led to the current state of signal crayfish invasion in the UK? 12. Do think there is any difference in crayfish depending on whether they recently arrived or have been there for a longer period?
Management	13. Are you aware of any laws regarding signal crayfish? Open question 14. What are your opinions on these laws? 15. Do you think that signal crayfish should be managed (yes/no) a. [If Yes] What do you think would be the best approach to manage them? b. [Also if yes] Who do you think should be involved in this management? c. [If no] Why do you think this? 16. Which people or organizations should finance the management of signal crayfish? 17. Do you think there should be more collaborations in the management of signal crayfish?

Appendix C: Sample of blank stakeholder map provided to participants

