Review of methods for the control of invasive crayfish in Great Britain

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Executive summary

• Invasive species of crayfish are some of the most damaging aquatic invasive species currently present in Great Britain (GB), causing massive environmental and economic damage and there is therefore a need to control and potentially eradicate these species from GB.

• A review of current methods used to control and/or eradicate invasive species of crayfish was conducted. Prevention of spread was also covered. Suggestions for novel methods and modifications of current methods were made. The areas reviewed were:
  o Mechanical control (trapping)
  o Physical control (electrocution, draining, habitat modification and barriers)
  o Biological control (predation and pathogens)
  o Biocidal control (the use of chemical pesticides)
  o Autocidal control (male sterilisation and semiochemical and pheromone control)
  o Legislative control

• A population model describing a signal crayfish population was used to underpin recommendations and suggestions made as part of the review.

Main conclusions and recommendations

Mechanical control

• Targeting all life stages equally (unbiased trapping) is the most successful strategy, and could result in eradication. Otherwise types of trapping (size biased, sex biased) are unlikely to eradicate crayfish populations.

• Unbiased trapping would require new traps designs or a combination of different designs used simultaneously, and would be fairly labour intensive.

• The most effective trap design, bait and trapping regime for the removal of different life stages of crayfish should be established, preferably a regime that is easily followed and applied by stakeholders and the voluntary sector, under guidance from experts.

• A method of calculating maximum sustainable yield for crayfish populations should be developed to aid more effective management.

• The effects of exploitation at varying degrees on crayfish population dynamics should be determined.

• The crayfish trapping industry should be engaged with to discuss control mechanisms, trapping regimes and trap design.

• An economic analysis of the value of the crayfish industry in GB should be conducted.
Physical control

- A combined approach of electrocution and water draining has the potential to be successful in eradicating crayfish populations but only if treatment is intensive and occurs frequently and over a long enough time period (e.g. every six months for several years at typical culling rates achieved).
- However, there are issues in terms of the damage caused to other organisms.
- Draining, habitat modification and barriers should be examined as potential methods of control and prevention of spread on an ad hoc basis e.g. obtain information from British Waterways on the habitat modifications they have undertaken as well as the barrier installed in Scotland.

Biological control

- Eels may be successful in controlling signal crayfish (suppressing population size), but for eradication to be achieved this may have to be used in conjunction with other methods.
- Several pathogen candidates were suggested for consideration as biological control agents:
  - The signal crayfish virus, PVBV shows promise as it is geographically isolated, may be host specific, may be associated with crayfish mortalities, and signal crayfish in GB are likely to not currently be resistant
  - The most promising bacterial group is the spiroplasmas, which affect male fertility.
  - A fungus, *Thelohania contejeani*, may have potential as a control agent but much research would be needed as little is known about it.
- These have potential for long term suppression of crayfish but need further development.
- A major issue is host specificity; this needs to be confirmed before release, and information is require on the life cycle and requirements of the pathogen.
- In addition, efforts may be required to understand the geographical spread of the selected pathogens and ensure that methods are available to neutralise these agents once the target host has been eradicated.

Biocidal control

- A total of six chemicals not previously considered for the control of invasive crayfish have been suggested for further development: Pyriproxifen, Fenoxycarb, Lufenuron, Cyromazine, Methoxyfenozide, and Chlorantraniliprole.
- It is recommended that the compounds are administered as bait, capitalising on their ingested activity.
- The intrinsic activity of these six chemicals should be tested on signal crayfish in the laboratory. Levels of efficacy can then be determined for each molecule.
• If a chemical is selected as a control agent, the HSE needs to be approached for emergency licensing of the compound as a biocide. The manufacturers should also be approached to discuss the new potential use of their product.

• The main concerns relating to biocidal control are the evolution of resistance, bioaccumulation, biomagnification and damage to non-target species.

• A combined approach of biocide application and trapping could be modelled in future work.

Autocidal control

• Irradiation reduces male fertility without affecting survival or mating, but there are significant logistical challenges surrounding the catching or rearing of sufficient numbers of males, so male sterilisation alone by this method is unlikely to be effective.

• An alternative approach would be to combine male sterilisation with trapping over an extended period. This could lead to long term population suppression, or potentially eradication if intensity is fairly high. As with trapping alone, this is labour intensive.

• The effects of 1st and 2nd pleopod (appendages used by male crayfish for fertilisation) removal on male behaviour, including mating and effectiveness to compete, and fecundity should be examined in the laboratory, as this may be a more feasible method.

• Small scale field trials should be conducted to determine the impact of treatment at the population level.

Legislation

• We recommend the introduction of new controls under Article 14 of the Wildlife and Countryside Act 1981, to regulate the sale and advertisement of non-native crayfish.

• We also recommend the Prohibition of keeping of Live Fish (Crayfish) Order 1996 is amended, to regulate crayfish imports and suppliers of signal crayfish.

Data gaps

• Additional information is required to enhance our understanding of crayfish biology and assist in the creation of a population model that more realistically represents a crayfish population.
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1. Introduction

The overall aim of this document is to provide information to assist in the development of a control programme to alleviate the impact that non-native crayfish have on invaded habitats in Great Britain (GB). Non-native species of crayfish have been present in GB for over 30 years: initially introduced for aquaculture, the ornamental trade, and live for human consumption, they have subsequently escaped, or been released into natural waters. There are six species of non-native crayfish currently established in British waterways: signal crayfish (*Pacifastacus leniusculus*), Turkish or narrow-clawed crayfish (*Astacus leptodactylus*), noble crayfish (*Astacus astacus*), red swamp crayfish (*Procambarus clarkii*), spiny-cheeked crayfish (*Orconectes limosus*), and virile crayfish (*Orconectes virilis*). Considerable differences exist between the species in terms of their distributions, population dynamics, physiology, behaviour, ecology and impact. Some species are present only in a few localised populations (e.g. the noble crayfish), with others being found extensively throughout much of GB (e.g. the signal crayfish).

Of the non-native species of crayfish currently present in GB, the signal crayfish poses the most significant threat. This is not just due to the threat posed to the native white clawed crayfish (*Austopotamobius pallipes*) through disease transmission and competitive exclusion, but also due to the influence the species has on the wider ecosystems through: a) negative effects on wider invertebrate communities; b) competitive interactions with native fish; and c) impacts on river morphology through burrowing and sediment mobilisation. Any of these impacts might compromise progress towards good ecological status under the terms of the Water Framework Directive (WFD). The presence of non-native crayfish is therefore a contributing factor to water bodies failing to meet WFD targets, and the implementation of mitigation measures to alleviate the impact of non-native crayfish is of high importance in meeting these targets.

The four objectives of this study are as follows:

**Objective 1. Literature review**

- To provide a detailed review of current techniques that could be applied to the control and eradication of invasive non-native species of crayfish; this will identify potential approaches to applied research
- To provide information by which different control measures can be tested for effectiveness using the population model developed in this report
**Objective 2. Legislative Review**
- To provide a comprehensive critique of legislation relating to the control of invasive non-native species of crayfish

**Objective 3. Modelling the effects of control mechanisms**
- To develop models that describe the key life characteristics of crayfish
- To provide an assessment of the various control mechanisms covered by the literature review and their potential effectiveness at controlling and/or eradicating the mathematical population of crayfish developed
- To test the effectiveness of control strategies, including multiple control mechanisms applied simultaneously, using the model
- To assess the effects on the modelled population of the long term application of these control mechanisms

**Objective 4. Recommendations**
- Based on the outcome from the mathematical model studies, to recommend control strategies that show the greatest potential for controlling invasive species of crayfish
- To recommend the most cost effective control strategy based on a basic assessment of the techniques involved, and discuss how these strategies could be adopted in a national strategy incorporating the 3rd sector
- To recommend future research to build on the understanding developed during this process
- To recommend potential adjustments to current legislation to prevent the further introduction and spread of invasive species of crayfish

This review considers mechanisms that are applicable to all of the non-native crayfish species currently present in GB. Where possible the relevance of the control mechanisms is discussed in relation to the different species. However, the development of a population model requires specific information relating to the population dynamics of a specific species. Therefore, for the population model and subsequent virtual testing of control mechanisms, the signal crayfish was used, as the most problematic of the non-native crayfish species.

**1.1. The development of control mechanisms**

When developing programmes for the control of invasive species, there are several factors that need to be considered. The IUCN (2000) identifies four key areas essential to the development of control programmes:
This document focuses on methods for developing mechanisms for eradication and control (3). Bomford and O’Brien (1995) suggested 6 criteria for deciding if eradication is technically possible:

1. **Rate of removal exceeds rate of increase at all population densities.** Any control method needs to remove the population more quickly than the rate of replacement (migration or reproduction). A density threshold (Keitt et al. 2001) is the point at which the population will cease to be self-sustaining. It is important to note that populations subject to exploitation usually compensate with high breeding and survival rates due to an increased availability of resources. In addition, as control measures progress it takes more time and expense to locate and remove animals. Hence removal rates are lower at low population densities. Clearly, if the rate of removal falls below that of the rate of increase then the population will not decline further. It is important therefore to maintain the rate of removal despite very low numbers being caught. The complete removal of a population may not be required as some species will become extirpated. Unfortunately minimum viable population size is unknown for most species.

2. **Immigration is prevented.** If animals can migrate or be released from captivity into the control area, eradication will be transient, and it is for this reason that many eradication success stories are on remote off-shore islands. It is therefore important to ensure that there is zero immigration either by using natural borders or erecting artificial barriers.

3. **All reproductive animals must be at risk.** All reproductive or potentially reproductive animals must be potentially susceptible to the control mechanism. In some cases trap shyness or resistance to poisoned bait has resulted in a subset of a population persisting above the density threshold.

4. **Animals can be detected at low densities.** Without a successful mechanism by which the target species can be detected at low densities, there is no way to determine the level of success of eradication efforts or if it has been achieved.

5. **Discounted benefit-cost analysis in favour of eradication.** The overall cost of the eradication programme needs to be carefully compared to costs incurred by the presence of the species, including damage to resources, remediation and control. In theory eradication requires a large initial outlay, but if successful, there are no further costs and benefits accumulate indefinitely. However, even if eradication is the most cost effective solution, the benefits still need to be weighed
against other alternatives. The benefit of retaining the species also needs to be considered. Those who lose income as a result of eradication may seek compensation for loss of revenue.

6. **Suitable socio-political environment.** Social and political factors can play an important role in determining if eradication programmes should proceed, even when technical and economic criteria are met. Clear and reliable information on the impacts of a species assists in developing strong support needed from the community. There are also moral, emotional and cultural responses to the termination of a large number of animals that require consideration.
2. Life history and ecology of the signal crayfish

Of all of the non-native crayfish species present in Britain it is the signal crayfish, *P. leniusculus* that has had the most significant impact. Originally from North America (west of the Rocky Mountains, including the Canadian province of British Columbia, and the U.S. states of Washington, Oregon, and Idaho) it is considered to be the most successful invasive crayfish species (Hogger 1988), being found throughout much of Europe. Originally bought into Britain during the 1970s to subsidise farming, it was soon found not to be well suited to intensive farming. Crayfish stocks were released into the wild or allowed to escape, resulting in the establishment of wild populations. It has subsequently spread throughout much of England and is now found in parts of Wales and increasingly in Scotland. The Republic of Ireland and Northern Ireland remain free of non-native crayfish (Sibley 2002).

2.1 Habitat preference

Signal crayfish are found in many freshwater habitats, including streams, rivers, lakes, ponds, and tidal areas (Goldman and Rundquist 1977; Goldman 1973; Shimizu and Goldman 1983). It has been found to be tolerant of saline conditions (Holdich *et al.* 1999) and tolerate a wide temperature range (Hogger 1988), having been reported to thrive in temperatures up to 33°C (Becker *et al.* 1975) and as low as 4-5°C (Shimizu and Goldman 1970). The species prefers temperatures below 25°C (Hogger 1988), with optimal growth occurring at 22.8°C (Firkins and Holdich 1993; Westman *et al.* 1993). They prefer high levels of dissolved oxygen (Nystrom 2002). Like most crustacea, signal crayfish are sensitive to calcium and pH levels (Lodge and Hill 1994; Kirjavainen and Westman 1999). Despite preferring certain conditions the species is very robust and can tolerate a wide range of environmental extremes.

Substrate heterogeneity strongly influences both the density and size of populations. Substratum is considered to be the single most important variable related to population size (Kirjavainen and Westman 1999). Signal crayfish generally prefer a rocky substrate (Flint 1977; Klosterman and Goldman 1983; Shimizu and Goldman 1983; Lewis and Horton 1997), avoiding flat, soft or silty bottoms (Goldman and Rundquist 1977; Elser *et al.* 1994). Higher densities are therefore normally found around areas of prime habitat (Lowery and Holdich 1988; Guan and Wiles 1996; Kirjavainen and Westman 1999). Signal crayfish have been found to burrow extensively (Kirjavainen and Westman 1999; Guan 1994) especially in areas where habitat is limited. There is a clear ontogenic shift in spatial distribution with juveniles preferring margins where the substrate is finer and more complex; adults populating deeper waters and less fractal complex habitat (Lewis and Horton 1997). Light levels (effecting resource availability) and temperature will limit distribution in lakes (Abrahamsson and Goldman 1970). Populations of signal crayfish in lakes have been recorded as
being larger than those found in rivers and streams, but animals may congregate around favourable habitat which affects population estimates (Hogger 1988).

2.2 Dietary preferences

_Pacifastacus leniusculus_ is omnivorous, feeding on a wide variety of items including algae, benthic insects, other crayfish, vascular detritus, woody detritus as well as fish and their eggs (Mason 1974; Guan and Wiles 1998). There is an ontogenetic shift in diet in signal crayfish (Mason 1975; Guan and Wiles 1998), with adults preferring vascular detritus, and juveniles showing a preference for benthic insects (Guan and Wiles 1998). Cannibalism increases with size, specifically during and immediately after ecdysis. Diet is highly influenced by availability; as signal crayfish are omnivorous and highly adaptable, they will feed on the most easily exploited food source available.

2.3 Maturation, reproduction, and fecundity

There is considerable variation in the age of maturation within populations (e.g. Mason 1975; Abrahamsson and Goldman 1970; Hogger 1988). Maturation has been recorded to occur as early as 1 year, but most studies have reported a maturation age of 2+. Females have been found to normally mature 1 year after males (e.g. Abrahamsson and Goldman 1970), which may be due to the higher growth rate of males. Size at maturation also varies considerably, from between 25mm and 47mm carapace length (Abrahamsson 1971; Abrahamsson and Goldman 1970). A polygynous system of sexual relations are observed (Guan and Wiles 1999). Males may forms harems, guarding females after mating (Stebbing _et al._ 2003) to prevent other males from copulating with them, thereby ensuring the continuation of their genetic line. It has been found that in many species of crayfish, males will consume the spermatophores of other males from the females that they encounter, and guarding would prevent this occurring (Mason 1975). This helps to explain the hierarchy observed in many populations. However, there is a lack of evidence for this occurring and how it may affect reproductive success rates.

The mating behaviour of signal crayfish has been detailed in Stebbing _et al._ (2003). Copulation usually occurs in October (Svardson 1965; Abrahamsson 1971; Flint 1975; Mason 1975, 1977; Shimizu and Goldman 1983; Soderback 1995; Lewis and Horton 1997). Lotic populations have been reported to occur slightly later by about 3 weeks (Lewis 2002). It has been suggested that reproduction is triggered by a drop in temperature (Mason 1975; Shimizu and Goldman 1983; Westin and Gydemo 1986; Reynolds _et al._ 1992), while others have suggested that it is a change in photoperiod (Lewis and Horton 1997). Mating will continue until November (e.g. Hogger 1988; Guan
and Wiles 1999), but again this varies massively between populations. Spawning occurs a few weeks after mating.

Despite the sex ratio of populations being considered 1:1 (see Lewis 2002), the ratio of males and females involved in reproduction differs. Abrahamsson and Goldman (1970) state that “almost all adult individuals of both sexes take part in reproduction every year” which concurs with Westman et al. (1995) who found that over 90% of mature females reproduce every year. Mason (1975) claims females spawn a total of 3-4 times during their lifespan, which is supported by Westman et al. (1993) who showed that some females may mate only every other year.

Several studies have based estimates of fecundity on samples taken shortly after spawning (see Lewis 2002). This may provide inaccurate estimates as it has been identified that all adult females will spawn eggs whether mated or not (Guan and Wiles 1999), therefore providing an estimate of close to 100%. Studies have conservatively estimated that only 17-20% of females reproduce based on the proportion of females in catches carrying deposited spermatophores during the breeding season (Lewis and Horton 1997). This is likely to be an underestimate of the total proportion of adult females within a population that have been mated with. Females that spawn eggs that are not fertilised will lose those eggs within 3 months of spawning (Guan and Wiles 1999). Females will also lose eggs from disease, physical disturbance and failure to attach to the female (Lewis 2002). Therefore a clearer indication of the proportion of females that have mated within a population will be those that are still carrying eggs prior to hatching (Guan and Wiles 1999; Söderbäck 1995; Savolanien et al. 1996) and this is considered a more useful measure of a population’s reproductive capacity (Lewis 2002). Using this method, estimates of approximately 40% of the adult female population having been fertilised have been obtained. There is considerable variation in fecundity of signal crayfish, from 3-548 eggs per individual, one of the main contributing variables being the size of the animal (see Lewis 2002).

There is very little information on how the role that adult male _P. leniusculus_ plays in reproduction affects population dynamics, therefore parallels must be drawn from similar species such as _A. pallipes_ (from which information is still sparse). Given the limited breeding period, the number of receptive females, and competition from other males, it may be difficult for males to find even one mate (Gherardi 2002). Male crayfish show no preference based on female size, but receptive females are more selective, avoiding small males and preferring those with both chelipeds intact (see Gherardi 2002). Large males outcompete smaller males for females, suggesting the mating is dominated within a population by a limited few. In a laboratory trial, most males (52%) were only capable of mating with 1 female, and 20% of these did not deposit a spermatophore, therefore only
42.5% of males fertilised only 1 female (Rubolini et al. 2007). In the same study, some males did mate with up to 4 females, with a mean fertilisation rate of 1.35 per male.

2.4 Life history

Ovigerous females can be found for approximately seven months between October and April (Mason 1975). Hatching occurs in most populations around April-May (Miller 1960; Mason 1963; Abrahamsson and Goldman 1970; Shimizu and Goldman 1983; Söderbäck 1995; Lewis and Horton 1997). Approximately 2200 ‘degree days’ are required for hatching of P. leniusculus eggs (Mason 1977; Lewis and Horton 1997).

Immediately after hatching the juveniles feed from nutrients supplied from an egg sack (Lewis 2002). After 1-2 molts, stage II juveniles begin to forage away from the mother at increasing intervals, becoming more independent, but returning if threatened (see Lewis 2002). In their first year of life, juveniles moult 13-14 times (Mason 1974). In subsequent years the number of molts significantly decreases: 5-6 in the second year, 3 in the third year, and 1-2 in the fourth year. There are gender differences in moult frequency, with adult females often moulting only once per year (Kirjavainen and Westman 1999), resulting in a slightly lower growth rate for females. Of the two adult male molts, the first usually takes place in July, and the second takes place in mid-August to September, prior to the breeding season (Söderbäck 1995). Fecund females undergo one moult subsequent to the juvenile becoming fully independent, usually in July or August.

Estimates of the lifespan of P. leniusculus are varied, from 5-6 years (Mason 1974) to 9-10 years (Shimizu and Goldman 1983; Lowery and Holdich 1988; Huner and Lindquist 1995). A lipofuscin derived technique has been used to estimate a maximum lifespan in a British population of 16 years (Belchier et al. 1998). Survival of juveniles to maturity is estimated at 10-33%, and this percentage declines subsequent to maturation (Abrahamsson and Goldman 1970; Abrahamsson 1973). However, Lowery and Holdich (1988) note that it is very difficult to obtain estimates of survival rate in the field.

It is considered that the density of crayfish determines not only rate of growth, but also age and size at maturity, fecundity, and lifespan (Hogger 1988). Therefore, these density dependent variables are of great importance when modelling crayfish populations.
2.5 Population size and density

There is considerable variation in estimates of population size and density from both lentic and lotic systems. Table 1 provides an indication of some of the variability found in populations of *P. leniusculus*.

Table 1. Density and population estimates of *P. leniusculus* from lentic systems

<table>
<thead>
<tr>
<th>Location</th>
<th>Size of water (ha)</th>
<th>Adult density estimate (m²)</th>
<th>Population estimate (total number)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake Billy Chinook, USA</td>
<td>1,585</td>
<td>0.24 to 1.13</td>
<td>35,940,145 ±8,127,159</td>
<td>Lewis 1997</td>
</tr>
<tr>
<td>Kussharo, Japan</td>
<td>7,930</td>
<td>0.27 to 2.30</td>
<td>-</td>
<td>Kawai <em>et al.</em> 2002</td>
</tr>
<tr>
<td>Lake Karijärvi, Finland</td>
<td>10.8</td>
<td>0.08</td>
<td>462±162</td>
<td>Kirjavainen and Westman 1994</td>
</tr>
<tr>
<td>Stratfield Saye, England</td>
<td>1</td>
<td>1.8</td>
<td>2062±1397</td>
<td>Hogger 1986</td>
</tr>
<tr>
<td>Rögle, Sweden</td>
<td>20</td>
<td>-</td>
<td>9000 approx</td>
<td>Abrahamsson 1971</td>
</tr>
<tr>
<td>Lake Tahoe, USA</td>
<td>49,900</td>
<td>1.4</td>
<td>55,500,000</td>
<td>Abrahamsson and Goldman 1970</td>
</tr>
</tbody>
</table>
3. **Mechanical control**

Mechanical control includes the removal of crayfish from water bodies using traps, nets or hands searching. Trapping for crayfish is primarily conducted for exploitation for human consumption when considered on a global scale. The physical removal of crayfish as a food source has been undertaken around the globe for millennia. Currently management strategies are applied to maintain crayfish populations at harvestable levels for commercial purposes in a number of countries. The effects of exploitation on many economically valuable species have been well documented, and there is evidence to suggest that a number of species may be under threat from local and ultimately global extinction by the effects of mechanical removal (e.g. Cheung *et al.* 2005). It is therefore arguable that with the correct incentive and technology any population can be exploited to the point of extinction. By looking at management methods of both crayfish and other exploitation fisheries this section aims to examine physical removal as potential means to control and/or eradicate invasive non-native species of crayfish. We define eradication as removal of 99% of the population.

3.1. **Crayfish population management**

The primary objective of managing commercial fisheries is to ensure that the populations continue through time while still allowing a sustainable harvest. The principles of sustainable harvesting provide a useful insight into how to maintain healthy populations, and therefore an indication on how to create an ‘unhealthy’ one. The cornerstone of crayfish management (and most fishery policies) has been the concept of maximum sustainable yield (MSY), which is the largest catch that can be removed over an indefinite period of time while maintaining population equilibrium. The concept of MSY aims to maintain the population size at the point of maximum growth rate by harvesting the individuals that would normally be added to the population, allowing the population to continue to be productive indefinitely. At low levels of effort the harvest consist of a yield of larger animals, while at high levels of effort the yield is the same in weight, but composed of smaller animals. We may be able to use the concept of MSY in reverse to suppress or potentially eradicate invasive non-native crayfish populations. One of the main issues with applying this to crayfish management is that due to the wide variation between crayfish species, and even between populations of the same species, a single line of approach does not work. To fully implement MSY management effectively, detailed information is required on the biology and dynamics of the population to be managed. This is demonstrated where incorrect application of MSY has resulted in the collapse of a number of important marine fisheries.
Overharvesting can occur when the mean size of the animals in a population is reduced over time ("growth overharvest") or where the mean age of the population drops below that of the mean age at maturity ("recruitment overharvest"). A common strategy to avoid overharvesting is to put into place management methods such as size limits, equipment restrictions, sex limits, total harvest size quotas and seasonal restrictions. Size limits for example will allow a cohort to reproduce once or twice before they come legally catchable. The most common fishery control techniques employed in relation to signal crayfish populations are size restrictions and closed seasons. In some states of the USA, gravid females caught have to be returned to the water. A recent study suggested that protecting the larger and more fecund animals from harvest, by introducing an upper capture size limit, can help to prevent gradual declines in harvested populations (Sadykova et al. 2011).

Recent discussions concerning the opening of Loch Ken as a signal crayfish fishery have been stopped due to concerns from Scottish National Heritage that it will result in the further spread of the species to other water bodies. However, the on-going economic impact that the species is having on the local tourism, and the potential for a growth industry to be established in the area, is a significant driver for local politicians. If a commercial fishery is established with a capital outlay on creating jobs and infrastructure to support the fishery then it would seem unlikely that there would much drive to eradicate the population.

3.2. Trapping and its effects on population

The effect of trapping on crayfish population depends on several factors, including environmental variables. Seasonal changes have been reported in the distribution and abundance of crayfish caught in traps (Miller and Van Hyning 1970; Klosterman and Goldman 1983). Fluctuation in trap catches (kg/trap) is a result of temperature fluctuations as well as the effect of the moulting period (Shimizu and Goldman 1983; Lowery and Holdich 1988). In Oregon, it has been found that catches in winter are generally low due to the decrease in feeding rate with decreased water temperature (Miller and Van Hyning 1970). Although *P. leniusculus* populations generally have a stable sex ratio of 1:1, there are seasonal differences in the catches based on sex (Miller 1960). Spring catches are more biased towards males, but total catch may be generally low because the males are in their moulting period. Berried females are reluctant to enter traps (Abrahamsson 1971; Mason 1975; Kirjavainen and Westman 1999), but are often caught subsequent to the hatching period, when they aggressively seek food to replenish reserves lost while carrying eggs (Lewis 1997). Both genders are caught in increasing numbers during summer months and the breeding period when both sexes are more active. Despite this catches consist of between 0 and 50% females (Cullen et al. 2003), but rarely exceed more than 20% females.
Trapping is often considered to be inherently biased to the removal of dominant large adult males (Holdich et al. 2006). However, this bias may not be a function of trapping per se, but the type of traps used, and the use of traps with smaller entrances may be biased in the opposite direction. The removal of the dominant (large) males from a population may lead to reduced pressure on juveniles giving rise to even larger populations (Gherardi et al. 2011). This was observed in populations of noble crayfish where the removal of larger animals reduced the level of competition on smaller animals resulting in the development of much denser populations (Skurdal and Qvenild 1986). This is observed when significant effort is placed on the harvest of crayfish populations (see above). The fact that some of these populations seem to be stunted in size may be a result of limited resources (Skurdal and Qvenild 1986). Several trapping programmes on riverine systems have found that removal of large adult males from one section of the river acts like a drain on neighbouring areas (both from up and down stream), with large adult males moving into the available space formed by the trapping. This results in enhancement of the population in the areas (Ibbotson et al. 1997; Holdich et al. 1999; Moorhouse and Macdonald 2010). It is thought that the removal of females may result in feedback mechanisms resulting in the production of more eggs and maturation at a lower size by remaining adult females (Holdich et al. 1999). A reduction in size of trapped animals has been observed on the river Clyde in Scotland (Freeman et al. 2010) but it is unclear if this is a result of a reduction of total population size or the number of females in the population.

There are several factors that need to be considered when assessing the effects of trapping on a population that are not always considered when conclusions are being drawn. Populations go through a period of establishment, followed by rapid growth and expansion before reaching equilibrium (see Herborg et al. 2003 for example in mitten crabs). It is even hypothesised (see modelling section) that this is followed by a period of decline and a new (lower) permanent equilibrium obtained. The potential effects of trapping on the total population may vary depending on at what stage the trapping survey has been conducted. This can ultimately impact on conclusions drawn in relation to control, fisheries management and population biology.

3.3. Trap design and bait type

The effect that trapping has on a population is influenced by the type of trap and the trapping regime used i.e. how many traps are laid, how often they are emptied, how much space is left between traps, and selectivity of placement. Usually trapping is conducted using cylindrical funnel traps, normally with a mesh size that allows the escape of smaller animals, these are commonly referred to as Swedish ‘Trappy’ traps (Figure 1a), and are the most common trap used in European crayfish fisheries (Fjälling 1995). Despite the popularity of these traps, West (2010) found them
ineffective when compared to minnow traps (Figure 1b). A number of other traps have been used and tested in a variety of different trials (Bean and Huner 1979; Westman et al. 1979; Fjälling 1995; Campbell and Whisson, 2000). One of the main drawbacks of most of these trials is that they are based primarily around the commercial exploitation of populations rather than their control/eradication. One common feature of traps used in commercial fisheries is that the mesh size is big enough to allow the escape of animals that are below a commercial size. The smaller mesh and entrance size of minnow traps compared to that of commercial designed Trappy traps, may help to explain the observation made by West (2010).

Figure 1. (a) “Trappy” trap, (b) Minnow trap, (c) Opera house trap, (d) Refuge trap, and (e) Fyke net
One key factor affecting total catch (and catch composition) may be the initial residence of the trap. Peay and Hiley (2001) suggested that smaller adults may enter traps if they find them first, but may be discouraged if occupied by a larger animal; this was also observed by West (2010) where groups of smaller animals avoided traps that contained larger animals. This is found in other species of decapod crustaceans, such as lobsters, where traps are occupied and defended by dominant males (Jury et al. 2001). The result from a study by Stuecheli (1991) suggested that the size of males entering a trap may also affect the sex ratio of final catches, with a more equal sex ratio being observed in traps where the entrance diameter was smaller.

Trap retention is a key feature of trap functionality. Retention was an issue with the majority of traps tested, with animals being able to enter and exit some trap designs at will (Westman 1991). Modification of the entrance to crayfish traps to a slit-like aperture was reported to increase retention considerably (Westman 1991). These findings have been refuted by Kozak and Policar (2003) who found that up to 90% of crayfish escaped from traps, even with modified entrances. Morgan et al. (2001) modified funnel traps by introducing a ‘T’ junction that animals have to enter the trap through. This modification improved trap efficiency and reduced the number of fish caught. The retention rate of traps can also be improved by decreasing the mesh size of the traps (Peay and Hiley 2001). This could explain the increase in catch observed by West (2010) when Trappy traps were replaced with minnow traps (which have a small mesh size). This also means that the traps catch a wider size range of animals (Wright and Williams 2000). While normal Trappy traps will catch animals of 35-70mm carapace length, traps that have a reduced mesh size will trap considerably smaller animals (minimum 18mm according to Wright and Williams).

Traps with a large internal ‘volume’ (e.g. opera house traps (Figure 1c) and tall cylindrical type traps) appeared to have both the best yield (catching the most animals in total) and the best retention (Bean and Huner 1979; Fjälling 1995; Campbell and Whisson 2000). The increased volume of the traps may negate the prior occupancy effect of deterring smaller animals from entering a trap as the additional volume makes encounters less frequent. This was also found to be the case by West (2010) during a 10-year trapping programme in the UK. The additional volume may also improve retention as it will make relocating entrances, once in the trap, more difficult. Trap colour has also been found to have an impact on yield, darker colours being more effective (Roqueplo et al. 1995).

Fyke nets (Figure 1e) are commonly considered to be the most effective trap at removing crayfish. There are no studies where their effectiveness is compared to other trap types to confirm this. However, Fyke nets are used extensively in Turkey to catch crayfish to great effect in a large commercial fishery (Balik et al. 2003). Fyke nets have been highlighted as a potential risk to other
species such as water voles and otters. Although un-baited traps are occasionally used as shelter by crayfish, baited traps are far more effective. Traps baited with parts of non-predatory fish species (Taugbøl et al. 1997) are consider more effective than those baited with predatory species. It is considered that the odour of predatory fish acts as a deterrent to the crayfish until there has been some degree of decay. Huner and Paret (1995) tested several formulated baits which did not show a significantly higher effectiveness compared to natural bait types. In some cases baits in traps were consumed so rapidly that the effectiveness of the bait as an attractant was short lived. Baits containing high levels of fish oil is considered by many to be the most effective bait types (Holdich et al. 1995).

A style of trap which is more focused towards stock surveys than commercial exploitation is the refuge trap (Figure 1d). The purpose of the trap is to use potential refuge rather than food as an attractant. By providing a range of refuge sizes a wider range of animal sizes can be trapped than in comparison to other trap types (Peay and Hiley 2001). One drawback of this type of trap is that it does not retain animals, the last animals entering the trap prior to ‘harvest’ being the only ones caught. The total yield from refuge traps is poor in comparison to normal food baited traps.

3.4. Trapping as a method of control

There have been several studies that have examined the potential use of trapping as a form of control and/or eradication with varying degrees of success and subsequent conclusions. Bills and Marking (1988) conducted intensive trapping in the USA on a population of *Orconectes rusticus* over a six week period. Although the trapping programme did fail to remove smaller animals, due to the design of traps used, the population was significantly suppressed. In a similar study, Roqueplo et al. (1995) trapped a population of *Procambarus clarkii* in France. Modified traps allowed the removal of a larger range of sizes, resulting in suppression of the population, but not eradication. Similarly Frutiger et al. (1999) conducted a trapping programme in 1997 on a population of *P. clarkii* in Switzerland. The programme resulted in the reduction of total population size; however evidence suggested that removed crayfish were replaced in a short time by young animals. Several studies have also been conducted in England with similar effects (see papers by Holdich). Rogers et al. (1997) reported a trapping exercise using Trappy traps where it was estimated that the population was reduced by more than half. However, despite a reduction in the number of larger animals, smaller animals were unaffected. The majority of these studies concluded that trapping is effective at reducing total population size, and therefore could be used to potentially control crayfish, but not eradicate. Another study (Peay and Hiley 2001) concluded that trapping was wholly ineffective as a control method. However, the study conducted by Peay and Hiley (2001) a) used a lower intensity of
trapping, b) was conducted over a shorter time period, and c) did not mitigate the effect of migration into the area being trapped when compared to other referenced studies. Peay and Hiley (2001) also examined other methods of control, including hand removal, modified kick samples, and dewatering, none of which they found to be effective at controlling or eradicating the target population.

Several studies have tried to address issues with trapping, such as intensity, duration and migration. West (2010) reports on a significant trapping exercise that has been conducted since 2001 and is still in progress on the River Lark, England. The project has: a) refined the types of traps used (from the commercial Trappy to modified traps with smaller mesh size and larger holding areas), b) used a range of trap styles to capture a wider range of sizes, c) undertaken trapping upstream of the control area to reduce migration, d) undertaken trapping for 9+ years. Although intensity of trapping has varied throughout the study, there has been a total reduction of 70% in the catches. This has resulted in observed recovery of the immediate ecosystem, such as river banks and fish populations.

Another long term trapping programme (1999 to present) on the River Clyde in Scotland has seen a significant reduction in total numbers caught (from 10,625 in 2001-2002 to 5335 in 2006-2007) with the same trapping intensity (Reeve 2004). This project has used Trappy traps for the whole period so may have been even more effective with other trap designs. However, the average size of the crayfish being caught is smaller and the animals are becoming sexually mature at a smaller size. This could be an important issue to consider when determining the trap type required to effectively control or eradicate a crayfish population.

One important issue to consider with trapping is the large number of live animals that are recovered. Given the demand for crayfish for human consumption, the most obvious solution is to sell them into the food chain. However, the assignment of a commercial value to invasive species almost inevitably results in further introductions of the species into previously un-invaded areas (Gherardi et al. 2011). Mechanisms by which would prevent further introduction should therefore considered. There is no doubt that trapping is a labour intensive mechanism of control, however if employed in a targeted manner, consistently over a prolonged period then it does seem to be an effective control method. However it does not seem to be a method of eradication, given existing trap designs. Trapping may contribute to eradication when combined with other methods.
4. Physical control

4.1. Draining and habitat modification

The principle behind draining and habitat modification is to remove suitable habitat for the crayfish exposing the animal to conditions that will cause mortality e.g. desiccation or predation. There is limited information in the literature in relation to this subject. However, there have been several occasions where still bodies of water have been drained and left to dry with the intention of culling crayfish. Holdich and Reeve (1991) reported a fish farm pond infested with crayfish being drained and left to dry, and refilled shortly after. Crayfish that had survived desiccation in burrows then reappeared the following year. Peay and Hiley (2001) reported that a lake in Wales containing a signal crayfish population was drained and dug out, not only to improve it as a fishery, but also to destroy crayfish habitats and removed burrowed animals. However, females carrying eggs were found 3 months after the process. A similar event occurred in a lake in Dorset, England, where animals were found despite an extensive drain down and digging out (author’s personal knowledge). Peay and Hiley (2001) also observed survival of animals in dried river beds for over 12 weeks. Holdich et al. (1999) suggested draining down stretches of river and then hand searching to remove crayfish. This method could potentially be effective at intensive removal over relatively short stretches, especially at certain times of year e.g. after breeding or before hatching. Kozak and Policar (2003) drained ponds in Poland containing signal crayfish, and despite over wintering at temperatures below -20°C crayfish still emerged the following spring when they ponds were refilled.

A project conducted by British Waterways on the Kennet and Avon Canal in Newbury, England in 2011, involved dredging the canal and using the material to stabilise banks that had become dangerous due to burrowing crayfish. The dredged material was then to be secured by a woven geo-technical material making the banks more stable while making the habitat less hospitable. However, no reports of this work have been released to determine how successful the project has been. Despite there being limited information on the success of these techniques, evidence would suggest that they can have significant short term impact on crayfish populations, and could be an effective control mechanism. However, the procedures can only be applied in limited circumstances due to the initial significant impact that they can have on the whole ecosystem, and the overall cost.

4.2. Barriers

While not a method for eradication of crayfish, barriers have been used successfully to prevent the spread of crayfish populations. Dana et al. (2011) effectively used dams to prevent the spread of red swamp crayfish in an upland stream in Spain. A series of 3 dams were used which were less than 3 metres high and constructed in a specific manner to prevent crayfish movement, with V-shaped
roofs and projecting rims. Kerby et al. (2005) observed similar results with the same species, finding reduced movement upstream in the presence of barriers. Peay and Hiley (2001) reported that 2 small weirs had prevented the upstream spread of a signal crayfish population in the River Rother, England. They also reported on the installation of a catch pit on the outflow of a lake containing crayfish which flows into a river devoid of crayfish, but there are no results on how successful the catch pit is at preventing movements.

A ‘crayfish barrier’ has recently (2011) been installed between the headwaters of the River Clyde and River Annan in Scotland in an attempt to control the spread of signal crayfish. The barrier, similar in design to that used by Dana et al. (2011) has been specially designed to stop the crayfish moving from one river catchment to another. No results of the effectiveness of the barrier have been released so far. Although barriers seem to be an effective mechanism by which the natural movement of crayfish can be halted (or at least delayed), there is still the potential for flooding, human activities or predators to result in the movement of the species beyond such barriers. The potential impact that the construction of barriers may have on other species (e.g. salmonids) and the ability of the waterway to be navigated would have to be considered. These potential issues limit the application of this method.

4.3. Electrocution

Electrocution has been used as a method of sampling fish for a number of years. While fish respond to an electric current by moving towards the anode by a process called galvanotaxis, this is not observed in crayfish. However, crayfish are stunned by the process, normally resulting in the animal appearing to leap a small distance into the water column before becoming completely motionless. This assists in capturing animals out in the open, but not those in cover or burrows at the time of treatment. Electrofishing equipment mounted on boats is sometimes used to harvest crayfish in the USA (Huner 1988). Westman et al. (1978) noted that electrofishing was effective at removing all sizes of crayfish. Laurent (1988) observed that catches using electrofishing equipment varied with time of day, suggesting that this technique is highly dependent on animals being out in the open, with Westman et al. (1978) suggesting electrofishing at night to increase catch rate.

Electrofishing was used on the River Clyde in Scotland (Sinclair and Ribbens 1999). In the treated areas of the stream, three consecutive runs were made each day for two days. Large numbers of animals were caught from a broad range of size classes during the exercise. However, there was no depletion in total catch numbers per run as would normally be expected, with between 24% and 35% of animals being removed in the second day of trials. This highlights an issue with the use of this
technique: animals that are in shelter may be stunned, but cannot be removed and will recover. A technique that may get around this issue is being developed in Northern Ireland by Robin McKimm. This is effectively a large electrofishing kit, with lengths of cathode spread across a river bed. These are used to send 96kW pulses through the water (in comparison to 0.5kW of a normal electrofishing kit). As with electrofishing this new approach is not size selective, but has the advantage that it will kill animals even if in cover, effectively removing all crayfish from a single treated stretch. In a recent study (2011), Peay and McKimm treated a small river in Yorkshire, demonstrating the effectiveness of the treatment. This technique has several significant drawbacks: it does not kill 100% of crayfish present, and it is not selective in what it kills, potentially killing any animal in the area that has not been previously removed, disadvantages shared with pesticides. McKimm has suggested several possible solutions, such as covering the stream bed with black plastic sheeting, generating a continual nocturnal condition encouraging more crayfish to leave their burrows during treatments. This should also insulate the water above the sheeting from the electrodes enabling several times more stream length to be treated at any one time from the one power source. Using steel tipped tubes filled with saline solution driven into the banks (to increase conductivity within the bank) could dramatically increase the impact of this method on burrowed animals. McKimm also suggests reducing the internal pH of the bank using a process known a electro kinetics. Again, this will have a significant negative impact on the flora and fauna of the banks. The other main drawback is that a power source is required, albeit at a low voltage.

There are several major drawbacks to the use of electricity and water. The most obvious is health and safety of those applying the method as well as members of the public, livestock, pets etc. The application of electricity is limited to shallow, clear water, with clement weather, therefore only small streams being treated during summer months. The system developed by McKimm would have to be coupled with fish removals and possibly a period of recovery to allow re-colonisation by macro-invertebrates.
5. Biological control

5.1. Predation

There are several studies that have examined the impact of fish predation on crayfish populations, and many suggest that fish predators can be used to reduce the size of crayfish populations (Westman 1991). The presence of predatory fish may also reduce growth and rate of sexual maturity in crayfish, and alter behaviour, for example increased utilisation of shelter (Blake and Hart 1995). Eels, burbot, perch, pike, chub, trout and carp are all recognised predators of crayfish. There is size selective predation depending on the species of fish, for example pike predate on all sizes whereas perch, carp and tench predate on smaller animals (see Gherardi et al. 2011 for review). Aquiloni et al. (2010) found that eel gape size limited the maximum size of the animals predated on. They also found that eels could enter into burrows, but were not found to be voracious feeders. However, they may have been the main contributor to the decline in crayfish populations in a study by Frutiger and Müller (2002). In concurrence, West (2010) concluded that the dramatic increase of signal crayfish in the River Lark was as a direct result of the removal of large numbers of eels from the river several years before. Other anecdotal evidence exists, where rivers (such as the Dorset Stour) with a strong population of eels have few signal crayfish, despite being considered suitable for the species, while the River Kennet has significant issues with signal crayfish, but is devoid of eels. The declining eel stocks in many GB rivers may help to explain the expansion of signal crayfish. This is illustrated by a study where fish were removed from a lake in Finland resulted in a dramatic increase in crayfish population, highlighting the natural control that the fish were having on the crayfish (Westman 1991).

Although the introduction of predatory fish does apply some level of control to invasive crayfish populations there are potential issues that need to be considered. The fish may predate on non-target species, a particular issue once the target population of crayfish has been reduced. In addition, the introduced fish may impact on the environment (e.g. carp causing turbidity), and may migrate away from the area of control if used in an open water system. Although stocking fish to artificially high levels may result in future issues, the enhancement of fish stocks may help in reducing crayfish numbers in the long term.

5.2. Pathogens

Invasive species can be successful in a new environment if they are introduced in the absence of constraints such as pathogens or predators that would normally keep population numbers under control. This idea is wholly ensconced in the enemy release hypothesis (ERH) (Clay 2003; Hilker et al. 2005) which states that the abundance or impact of a non-native species may be related to the
absence of natural enemies of these species in their introduced range compared with those occurring in their native range (Colautti et al. 2004). However, the premise of biological control is to utilise pathogens that are detrimental to host survival to control the population in question; these pathogens may in fact be absent in non-native species by virtue of the ERH. Whilst there are some success stories with regards to biological control of non-native species, particularly in plants, there are concerns that many biological control agents do not effectively control the target host (Colautti et al. 2004; Denoth et al. 2002). Most successes in the use of pathogens as control agents have been achieved in the terrestrial environment, for example the use of nematodes in the control of garden slugs, bacteria for controlling butterfly caterpillars, and the myxoma poxvirus for the control of rabbits in Australia. To date there do not appear to be any examples of successful commercial scale control of aquatic animals, although the utility of pathogens to control aquatic plants or their pests has been demonstrated (Freeman 1977; McFadyen 1998; Thanabalu et al. 1992). Furthermore, successful bio-control agents tend to have been derived from viruses, bacteria and fungi with occasional examples of higher taxa, such as nematodes, showing promise as a control agent. These are, however, relatively rare.

In principle, biological control may be viewed by the general public as a more “natural” approach to the control of pest species, particularly due to growing concerns surrounding over-reliance on harmful chemicals that may not be species specific, and issues surrounding resistance to these chemicals. In addition, the cost of development and production of some chemicals may be prohibitively expensive.

Successful biological agents should:

- be species specific,
- generally be directly transmitted without the need for a vector or intermediate host,
- be easily cultured,
- be readily released in large volumes and/or in a safe manner,
- be capable of survival in a new range or in the target environment long enough to infect a suitable host,
- be relatively fast acting,
- not alter host behaviour in such a way as to enhance or speed up release of progeny
- not enhance pathogenicity of other infections or lead to the release of other detrimental infections into the environment through host death,
- and if needed, be easily controlled itself.
One option available if the pathogen is not easily cultured is for the release of infected non-native individuals. This however would require special permission for the deliberate release of a non-native host into the environment and runs the potential risk of introducing hosts resistant to other factors or introduction of other pathogens that may be more harmful to indigenous species.

This review considers the pathogens of established non-native crayfish species and those with the potential to establish in Great Britain, including the noble crayfish, Turkish crayfish, signal crayfish, red swamp crayfish, marbled crayfish (Procambarus fallax), virile crayfish, spiny cheek crayfish and rusty crayfish (Orconectes rusticus). A particular focus of the review is on pathogens that have been shown to be mortality drivers, reduce fecundity or host survival and that appear to be host specific. In particular, this tends to be viruses, bacteria and fungi. Consideration is given to the possibility of mass culture and/or safe release of the potential pathogen. Finally, avenues for future research are suggested.

5.2.1. Pathogens of crayfish

Freshwater crayfish are widespread crustaceans that have been recorded on almost all continents. Through the anthropogenic movement of crayfish either for the aquaculture or aquarium trade, and the subsequent deliberate or accidental release into the environment, many have become established outside their native range. A particular focus of research has been the pathogens of Cherax spp. from Australia and Procambarus spp. in the USA, reflecting both the economic importance of these species and the location of the researchers involved in crayfish disease research. Diseases of crayfish have been extensively reviewed (Alderman and Polglase 1988; Edgerton et al. 2002; Longshaw 2011).

Viruses

The majority of viruses reported in crayfish have been described in antipodean Cherax spp. including Cherax albicus picorna-like virus (CaPV), Cherax destructor bacilliform virus (CdBV), Cherax destructor systemic parvo-like virus (CdSPV), Cherax quadricarinatus bacilliform virus (CqBV). Cherax quadricarinatus parvo-like virus (CqPlV) of Edgerton et al. (2000), Cherax quadricarinatus parvovirus of Bowater et al. (2002), Spawner-isolated mortality virus (SMV) in C. quadricarinatus, Penaeus merguiensis densovirus (PmergDVN) in C. quadricarinatus, Cherax quadricarinatus reovirus (CqRV) and Cherax quadricarinatus Giardia-like virus (CGV). Several of these have been shown to induce mortality in Cherax spp., particularly under farmed conditions, suggesting that other similar viruses may have some utility in biological control. Full details of the impact of these are described in (Longshaw 2011).
**Astacus astacus** bacilliform virus (AaBV) was reported from Finland at prevalences of up to 100% and was considered by Edgerton *et al.* (1996) to be intense in some individuals. Infection was restricted to the cells of the hepatopancreas and gut and in severe infections led to destruction of the tubules. Whilst (Edgerton *et al.* 1996) did not discuss reasons for the variability in intensity, it is clear from his paper that inter-site variability was marked. Furthermore, whilst not reported as a mortality driver in the populations surveyed, Edgerton *et al.* (1996) suggested that it may have a role in crayfish mortalities in Europe. *A. astacus* have also been shown to act as a mechanical reservoir for the fish pathogen Infectious Pancreatic Necrosis Virus (IPNV) although it did not appear to have any detrimental effect on crayfish (Halder and Ahne 1988a; Halder and Ahne 1988b). Thus any attempts to isolate AaBV from *A. astacus* would need to be mindful of the possibility of contamination by fish viruses. Furthermore, Edgerton *et al.* (2002) reported the presence of an unidentified virus of the gills of *A. astacus* with no further characterisation. The route of transmission, relationship to AaBV, impact, distribution and host range remains unknown and thus further characterisation of the virus and a full risk analysis would be required prior to isolation of AaBV as a control agent.

The other bacilliform virus reported in non-native crayfish species of concern to GB is *Pacifastacus leniusculus* bacilliform virus (PlBV). First reported in the USA by Hauck *et al.* (2011) and Hedrick *et al.* (1995), the virus, like AaBV, infects the hepatopancreas and midgut. Recently Longshaw *et al.* (2012) reported the presence of the virus in two established populations of *P. leniusculus* in mainland Britain; it was apparently absent in a further 14 sites sampled during a survey of signal crayfish. Longshaw *et al.* (2012) speculated, assuming that the virus was host-specific, that the virus must have been transferred with signal crayfish from California or Sweden. The apparent restricted geographical spread of the virus would support the view that the virus may have been imported in a small cohort of crayfish and represents a specific focus of release. In the samples examined by Longshaw *et al.* (2012) it was apparent that pathology was limited. Due to the nature of sampling, it is not clear if the limited pathology was due to prevailing environmental conditions, host susceptibility or as a result of examining survivors. Thus, the virus may have been more pathogenic than the authors considered, especially as mortalities had been reported in signal crayfish from one of the sites where the virus was recorded.

Whit spot virus syndrome (WSSV) is a notifiable virus with a wide host range, including crayfish; it is likely that the virus can infect all decapod crustaceans (Stentiford *et al.* 2009). The virus has been transmitted under experimental and field conditions to crayfish including *Procambarus* spp., *Orconectes virilis* and *Pacifastacus leniusculus* (Baumgartner *et al.* 2009; Claydon *et al.* 2004; Davidson *et al.* 2010; Du *et al.* 2008; Du *et al.* 2007; Edgerton 2004; Jiravanichpaisal *et al.* 2001; Shi
et al. 2000; Soowannayan and Phanthura 2011; Stentiford et al. 2009). Davidson et al. (2010) suggested that WSSV could be used as a biological control agent against invasive Orconectes virilis as it was considered to be highly pathogenic to the host and was readily transmitted between crayfish through cannibalisms. While the use of WSSV appears at first to show promise, it should be recognised that the virus is not specific and thus would readily infect non-target decapods. Secondly, it is currently absent from the UK and would therefore be unlikely to be considered as a suitable control mechanism in GB. Finally, Du et al. (2006), Xu et al. (2006) and Zhu et al., (2009) have shown that Procambarus clarkii are able to develop resistance to the virus. It is possible that release of the virus would rapidly lead to the untenable position of a pathogenic strain affecting native hosts at the same time as resistance building up in the target species.

It is highly probable that each virus described or reported from crayfish is host-specific, therefore if it were possible to culture sufficient amount of virus they may be useful as biocontrol agents. However, this may require development of specific crustacean cell lines. In addition, full characterisation of each crayfish virus would need to be conducted to confirm the apparent host specificity. Further work may be required to assess the impact of any viruses on host survival in conjunction with prevailing environmental conditions and confirm the host-specificity. The signal crayfish virus, PIBV, shows promise as a control agent. The virus may be associated with mortalities, appears geographically isolated and may well be host specific. Furthermore, at least in the short term, signal crayfish established in Great Britain may show no resistance to the virus given their limited exposure over time. This is based on an assumption that populations currently free of the virus were derived from crayfish imported into mainland Britain in the mid-1970s (Alderman 1993; Holdich et al. 2009).

Bacteria

Bacterial infections of crayfish tend to be opportunistic and non-specific with few infections leading to significant mortalities, particularly under wild conditions. Even then, mortalities are usually triggered by other underlying factors such as prevailing environmental conditions or other interacting pathogens (Alderman and Polglase 1988; Edgerton et al. 2002; Longshaw 2011). Furthermore, several of the bacteria isolated are known to be a source of gastroenteritis in humans (Edouard et al. 2009; Longshaw et al. 2012; Quaglio et al. 2006b; Reina et al. 1990; Thune et al. 1991) so caution would need to be exercised in the release of bacteria with the potential to cause problems for humans.

Mortalities associated with Coxiella cheraxi, an intracellular bacterium of Cherax quadricarinatus, have been reported (La Fauce and Owens 2007). Similar, but uncharacterised, infections have been
reported in *C. quadricarinatus* and marbled crayfish (Edgerton and Owens 1999; Jiménez and Romero 1997; Vogt *et al.* 2004). The infection of marbled crayfish was systemic and caused localised pathology in the host, particularly in the gonad of this parthenogenetic species. However, the authors did not consider that the infection was of sufficient density in the host or widespread enough to constitute a major issue for marbled crayfish.

One bacterial-like group that shows some promise as a biological control agent is the spiroplasmas. These are small helical bacteria normally associated with plants, arthropods and ticks where they have been shown to act as direct mortality drivers, as sex distorters or as male killing agents (Enigl and Schausberger 2007; Gazla and Carracedo 2009; Nienhaus and Sikora 1979; Özbek *et al.* 2003). Similar bacteria show promise as biological control agents in terrestrial systems (Floate *et al.* 2006). Most importantly, methods exist for the molecular and ultrastructural identification of the bacteria and for their culture (Ding *et al.* 2007; Nunan *et al.* 2005). Two spiroplasmas have been reported in crayfish. *Procambarus clarkii* are susceptible to “crayfish weakness disease”, which appears to be the same or very similar to tremor disease in mitten crabs (*Eriocheir sinensis*) caused by a *Spiroplasma* infection. However, attempts to transmit the infection from mitten crabs to crayfish has been unsuccessful (Wang *et al.* 2005), suggesting that the infection may in fact be host-specific, supported by reports of up to 4 different spiroplasmas in decapods (Bi *et al.* 2008; Heres and Lightner 2010; Nunan *et al.* 2005; Wang *et al.* 2005). More recently, Longshaw *et al.* (2012) described a *Spiroplasma* from the male gonads of signal crayfish. The infection occurred at six sites, out of 16 sites surveyed. The infection is restricted to the Sertoli cells of male gonads. Sperm production was markedly reduced or even absent in infected tubules and in latter stages of infection, degeneration and loss of epithelial cells in the tubules was noted. Due to the mode of collection, a full description or culture of the pathogens was not possible. This infection has not been previously reported in signal crayfish or in other crayfish species in GB. However, histological sections of male gonads of *Orconectes limosus* by Kozák *et al.* (2007) appear to show evidence of a similar pathology to that described by Longshaw *et al.* (2012) which Kozák *et al.* (2007) attributed to intersex. This would require further investigation. Otherwise there appear to be no records of an analogous infection in other crayfish species, despite a number of papers on crayfish gonadal development (Chybowski and Juchno 2002; Guan and Wiles 1999; Hobbs *et al.* 2007; Kozák *et al.* 2007; López Greco *et al.* 2007; Lucic *et al.* 2006). Therefore, the utility of the novel *Spiroplasma* described by Longshaw *et al.* (2012) as a suitable control agent should be further investigated. Studies would be required to be conducted on transmissibility, host specificity and impact on crayfish reproduction before release into the environment. Furthermore, methods for delivery of the pathogen and upscale production of the bacterium would need to be considered.
Mortalities in some *Cherax* spp. have been associated with *Vibrio* spp. In particular, *Vibrio mimicus* appears to be problematic for *Cherax* spp. in culture which may have been due to overcrowding (Eaves and Ketterer 1994; Wong *et al.* 1995). *Vibrio mimicus* and *V. cholerae* have also been isolated from a farmed *P. clarkii* population undergoing a mortality event (Thune *et al.* 1991). Affected animals were lethargic and up to 25% of crayfish died as a result of the infection which was exacerbated by elevated temperatures and lower dissolved oxygen. Thus, it appears at first glance that vibrios may have some utility as a control agent. However, *Vibrio mimicus* is transmissible to humans giving rise to gastroenteritis through the ingestion of raw or undercooked crayfish and thus caution would need to be exercised in any release of the bacteria into potable waterways (Eaves and Ketterer 1994). *Vibrio alginolyticus*, associated with necrotising fasciitis in humans (Gomez *et al.* 2003) has been isolated from the haemolymph of signal crayfish in GB (Longshaw *et al.* 2012) but its effect on naive crayfish is unknown.

*Aeromonas hydrophila* is ubiquitous in the freshwater environments and has been associated with disease outbreaks in fish, shellfish and humans (Grignard *et al.* 1996; Jiravanichpaisal *et al.* 2009; Tulisdas *et al.* 2008). The bacterium has been isolated from *P. leniusculus* and *A. pallipes* (Jiravanichpaisal *et al.* 2009; Longshaw *et al.* 2012; Quaglio *et al.* 2006a). *Aeromonas hydrophila* was isolated from unhealthy signal crayfish by Jiravanichpaisal *et al.* (2009) and subsequently injected into naive signals, leading to mortalities within 6 hours at 22°C. Whilst this may appear to have some utility as a biological control agent, its lack of host specificity gives cause for concern.

**Fungi**

Numerous fungi have been isolated from crayfish throughout their range, in some cases associated with disease and mortalities. However, many are opportunistic, invading crayfish tissues through breaches in the cuticle and may be poorly or incorrectly described or not ascribed to a species. Opportunistic infections by *Saprolegnia* spp. (Class Oomycetes) on dead eggs or moribund crayfish larvae have been noted (Royo *et al.* 2004; Vey 1981). Mortalities of *A. astacus*, *P. leniusculus* and *P. clarkii* exposed to *S. parasitica* zoospores via water was noted to be around 20%, rising to 60% if the epicuticle was breached (Diéguez-Uribeondo *et al.* 1994). No difference in susceptibility was noted between the three species. Furthermore, whilst Hirsch *et al.* (2008) reported the presence of several *Saprolegnia* spp. in a declining population of *O. limosus* in Germany, they were unable to unequivocally link the presence of the fungus with the mortality event. Thus the necessity of damaging epicuticle to enhance mortality as demonstrated by Diéguez-Uribeondo *et al.* 1994 and its lack of host specificity limit the usefulness of the fungus to control invasive species of crayfish.
The other main genus of oomycete fungi in or on crayfish is *Aphanomyces*, which includes the agent of so-called crayfish plague, *A. astaci*, as well as *A. reptans* and *A. frigidophilus* (Diéguez-Uribeondo *et al.* 2009; Royo *et al.* 2004). Approximately 35 species of *Aphanomyces* have been described, occurring in plants and animals as either saprophytic or opportunistic parasites (Diéguez-Uribeondo *et al.* 2009). *A. astaci* originated in North America and through the anthropogenic movements of crayfish, became established in numerous countries in Europe where it has been implicated in the decline of several native crayfish species (Alderman 1993; Bohman *et al.* 2006; Harlioglu 2008). There are at least two molecular clades of *A. astaci* (Huang *et al.* 1994; Lilley *et al.* 1997), with a recent report of a third genotype in *O. limosus* (Kozubíková *et al.* 2011). The possibility that different strains of *A. astaci* exist, each potentially being able to infect different hosts with different pathogenicity leads to the possibility of isolating strains that would specifically pathogenic to invasive crayfish (Kozubíková *et al.* 2011). However, until suitable experimental challenges are completed that demonstrate the host specificity and that they do not revert to the other clades, the use of *A. astaci* as a biological control agent should not be considered.

Another major group of filamentous fungi on or in crayfish are those in the class Sordariomycetes, with many reported under the generic name *Fusarium* (Quaglio *et al.* 2006a; Quaglio *et al.* 2006b). Longshaw (2011) provides a list of the different species isolated from crayfish and a discussion on the nomenclatural changes within the group following their original reports in crayfish. These are normally distributed in plants and/or soil, and in crayfish lead to melanised encapsulations in the gills and other external surfaces (Alderman and Polglase 1985; Chinain and Vey 1988; Fard *et al.* 2011; Maestracci and Vey 1987; Vey and Vago 1973). Moulting in infected animals can be delayed and in some cases, infections can be lethal (Chinain and Vey 1987; Chinain and Vey 1988). However, due to an apparent lack of host-specificity, the susceptibility of native crayfish, a lack of information on lethality and questions over the taxonomy of previous isolates, the use of *Fusarium* and *Fusarium*-like organisms appear to have limited utility as biological control agents.

Microsporidia were traditionally placed within the protistans, but recent molecular data has placed them as a sister group or as a clade within the fungi (Fischer and Palmer 2005; Gill and Fast 2006). One major genus, *Thelohania*, and several minor genera occur in crayfish. The caveat to this is that current taxonomic understanding of the genus *Thelohania* in crustacean hosts is confused and the possibility exists that members of the genus may be transferred to a different genus (Brown and Adamson 2006). *T. contejeani*, the causative agent of the chronic “porcelain disease” infects many different invasive and native crayfish species and is a recognised mortality driver in crayfish (Dunn *et al.* 2009; El-Matbouli and Soliman 2006). Morphologically similar, but undescribed microsporidians
have been reported from New Zealand (*Paranephrops zealandicus*) and Canada (*O. virilis*) (France and Graham 1985; Graham and France 1986; Quilter 1976). In both cases, mortalities were associated with the infections, although at low levels. Of particular interest is the form reported in *O. virilis* and although Graham and France (1986) were unable to transmit the infection to naive crayfish, it was shown to increase mortality in affected hosts. Its apparent absence in virile crayfish examined by Longshaw *et al.* (2012) and its impact on crayfish in its native range would suggest that it may prove useful as a control agent. This would require additional work however, to reisolate it from its type location and confirm its host specificity and lifecycle requirements as well understanding its taxonomic position.

**Mesomycetozoea**

Mesomycetozoea are a monophyletic group of organisms at the animal-fungi border that include *Dermocystidium*, rosette agent, *Ichthyophonus* and *Psorospermium* amongst others (Adl *et al.* 2005; Mendoza *et al.* 2002). *Psorospermium* spp. infect crayfish with several morphotypes existing in European, American and Australian crayfish species (Bangyeekhun *et al.* 2001; Edgerton and Owens 1999; Henttonen *et al.* 1997). Some authors consider that they can, under certain condition, be pathogenic to their host (Vey 1986). However, the triggers for the change in pathogenicity (if any) and questions over host specificity would need to be answered before they could be seriously considered as biological control agents.

**Protista**

Whilst ciliated protistans have been implicated in mortalities of crayfish, particularly under culture conditions (Alderman and Polglase 1988; Brown *et al.* 1993; Ninni 1864), these are generally rare. Furthermore, the apparent lack of host-specificity and the difficulties involved in mass culture of these sedentary parasites preclude their widespread use as biological control agents.

(Vogt *et al.* 2004) reported the presence of a putative coccidian infection in the ovarian tissues of a single marbled crayfish. Lesions in the hepatopancreas and connective tissues of the same animal were recorded by the authors but it is unclear of the association between these and the infection in the ovaries. Whilst they did not conduct additional studies on the parasite, Vogt *et al.* (2004) considered that the infection was likely to be lethal to the crayfish. Only one other report of a coccidian infection in crayfish has been made (Gousseff 1936) and thus the rarity of the infection in marbled crayfish and of coccidians in crayfish in general would suggest that they may not be ideal candidates for biological control in spite of their lethality. Furthermore, there is a lack of data on their transmission requirements (which may or may not include an additional host).
6. **Biocidal control**

Major concerns surround the use of chemicals as potential control mechanisms for any pest species. The evolution of resistance, bioaccumulation, biomagnifications and collateral damage of non-target species are some of the main concerns. To date no biocide has been found that is specific to crayfish (Peay and Hiley 2001). There have been several reviews conducted on potential biocides (e.g. Holdich *et al.* 1999), but recent changes in EU legislation have made parts of these outdated. Given the lack of specificity, focus has been given to chemicals that are not persistent in the environment, are readily available and inexpensive (Gherardi *et al.* 2011). This has resulted in 2 main chemicals having been used recently in field trials: Pyblast (3.0% pytherins plus piperonyl butoxide and alcohol ethoxylate), and BETAMAX VET (a synthetic pyrethroid).

Pyblast has most recently been used by Peay *et al.* (2006) in an attempt to eradicate a *P. leniusculus* population in ponds in Scotland. Pyblast is toxic to fish, crustaceans and insects, but has a low toxicity to mammals and birds and is harmless to plants. It was therefore necessary to remove the fish from the treatment site used by Peay and ensure good biosecurity during the treatment. The treatment resulted in effectively complete extermination of life in the treated pond, while Pyblast rapidly breaks down in sunlight and there is no harmful residue, meaning that treated waters will recover rapidly. There have been crayfish detected at the site subsequent to the treatment (see Gherardi *et al.* 2011) so further monitoring is ongoing. BETAMAX VET is highly toxic to aquatic crustaceans and so was selected to be used to treat *P. leniusculus* populations in Norway (Sandodden and Johnsen 2010). BETAMAX VET is a synthetic pyrethroid and therefore is very similar in its effects to Pyblast. Post treatment surveillance is still ongoing at the sites treated in Norway.

Other chemical pesticides do exist that have not been considered for the treatment of aquatic pests to date. These were included in a recent review of possible methods for controlling the invasive freshwater amphipod *Dikerogammarus villosus* by Cefas (contract code CS525). This review identified 6 chemicals which were short listed as candidates for the eradication of aquatic crustacea, namely Pyriproxyfen, fenoxycarb, lufenuron, cyromazine, methoxyfenozide, chlorantraniliprole. Many of these chemicals are very specific in their mode of actions, and there are options to further enhance their specificity to target species through targeted delivery. Cefas recommended further work on their use to control *D. villosus*, and this work may also be applicable to the control of invasive crayfish. It is hoped that it would be possible to deliver these chemicals in such a way that they could be deployed into systems in such a way so that there would be no need to remove susceptible high value non-target species (e.g. fish), and no or very little non-target collateral
damage. However the action of these chemicals on crayfish, and an effective mechanism of delivery, are still to be established.

**Pyriproxifen**

![Pyriproxifen molecule]

Toxicology: acute oral LD$_{50}$ (rats) $>$5000mg/kg. WHO acute hazard rating: “U” unlikely to be hazardous.

Environmental impact: Pyriproxyfen shows strong persistence in water (resistant to aqueous hydrolysis) and moderately fast aqueous photolysis at pH7. It has moderate toxicity to aquatic invertebrates but high toxicity to aquatic crustaceans but effects were sometimes reversible. (PPDB pyriproxifen).

Target specificity: There is not data on the activity of pyriproxyfen on crayfish but if laboratory tests showed the intrinsic activity of this molecule, one could envisage conferring selectivity by applying as bait. Application to mosquito larvae (also in the aquatic environment), provides control for 2 months duration. Active on some diptera, coleoptera and some homoptera (Tomlin 2000).

Availability: Pyriproxifen is Annex 1 listed under 1107/2009 and this exclusion expires on 31.12.2018. The product is not registered in the UK.

**Fenoxycarb**

![Fenoxycarb molecule]

Toxicity: WHO classification: U – unlikely to represent an acute hazard.

Environmental impact: water solubility 7.9mg/l with log$P$ of 4.07. Aqueous hydrolysis gives very persistent and aqueous photolysis is slow. The compound has moderate toxicity to fish and aquatic invertebrates. (PPDB Fenoxycarb)

Species specificity: active on Lepidoptera, homoptera, coleoptera, dictyoptera, diptera and hymenoptera. Conferring selectivity by the use of baits.

Availability: Annex 1 listed under 1107/2009 until 31.5.21. Registered for use in the UK.
Lufenuron

Toxicology: Rated as “unlisted” in WHO classification
Environmental impact: Classed as non persistent in soil, with fast aqueous photolysis at pH7. Classed as “very persistent” to aqueous hydrolysis with slow degradation in water sediment. The compound has low leachability potential because of its high lipophilicity. It has high toxicity to aquatic invertebrates but moderate toxicity to fish (PPDB Lufenuron).
Target specificity: There is not data on the activity of lufenuron on crayfish but if laboratory tests showed the intrinsic activity of this molecule, one could envisage conferring selectivity by applying as bait. Active on coleopteran, diptera, hemiptera, hymonoptera, lepidoptera and acari.
Availability: Lufenuron is Annex 1 listed under 1107/2009, with registration until 2019. Also has a registration as a veterinary medicine. It is not, however, registered as an insecticide in the UK.

Cyromazine

Toxicology: WHO classification 111 (slightly hazardous)
Environmental impact: It is stable and very persistent to aqueous hydrolysis and photolysis, showing persistence in sediment. Its low lipophilicity means it is moderately mobile in soil and its high water solubility (13g/l) would increase the risk of this molecule moving in the aquatic environment. It has moderate to low toxicity to aquatic invertebrates and crustaceans (PPDB Cyromazine).
Target specificity: Active on diptera in agricultural and veterinary applications (Tomlin 2009). There is not data on the activity of cyromazine on crayfish, but if laboratory tests showed the intrinsic activity of this molecule, one could envisage conferring selectivity by applying as a bait.
Availability: registered under Annex 1 until 31/12/2019 under 1107/2009. The product is not registered in the UK.
Methoxyfenozide

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**Toxicity:** WHO classification U (unlikely to present an acute hazard)

**Environmental profile:** compound is classed as very persistent in the aquatic environment. It has a high (calculated) logP and water solubility of 3.3 mg/l. It has moderate toxicity to fish, aquatic invertebrates and crustacea. (PPDB methoxyfenoxide)

**Species specificity:** Used in the control of Lepidoptera.

**Availability:** Annex 1 listed under 1107/2009 until 31.3.15. The compound is registered in the UK.

Chlorantraniliprole (Rynaxypyr)

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**Toxicity:** WHO classification 111 (unlikely to present an acute hazard)

**Environmental impact:** With a logP of 2.86 and water solubility of 1.02 mg/l the compound will likely move in the aquatic environment. However, it is fast degraded by aqueous photolysis. Fish toxicity is moderate whilst toxicity to aquatic invertebrates is high.

**Target specificity:** active on Lepidoptera, coleopteran, diptera and homoptera. Activity on crayfish unknown. Selectivity could be conferred by application as bait.

**Availability:** inclusion in Annex 1 pending – has been granted extended provisional authorisations until 30.6.2012.
7. **Autocidal control**

7.1. **Male sterilisation**

Male sterilisation in its traditional form is a technique whereby a population of a pest invertebrate is reared in the laboratory, and exposed to a radiation source which induces genetic aberrations in the individual males. The males are then mass released whereupon they mate with wild females, producing non-viable progeny. The method is associated with population control to a level where eradication of the pest is possible. It has primarily been used on terrestrial insect pests, the famous example of its use being the successful elimination of the screw worm (*Cochliomyia hominivorax*) from North America starting in the 1950s (Knipling 1960). The technique has been used successfully against a number of other pest species such as Mediterranean fruit fly (*Ceratitis capitata*) (Wiedemann 1978), melon fly (*Bactrocera cucurbitae*) (Coquillet), pink bollworm (*Pectinophora gossypiella*) (Saunders), codling moth (*Cydia pomonella*) (L.) and tsetse fly (*Glossina austeni*) Newstead (Wyss 2000; Hendrichs *et al.* 2005; Klassen and Curtis 2005). The technique is species specific and inversely density dependent. As the population of fertile males decreases, the rate of control increases as an increasing portion of the female population is mated by released sterile males. This makes it an ideal method for eradication of invasive alien species (Franz and Robinson 2011).

The sterile male technique has been subject to some preliminary studies as a method for the control of invasive alien crayfish (Aquiloni *et al.* 2009). Exposure of male *P. clarkii* to X-rays was found to not compromise the survival or mating ability of the males, but did result in a reduction of the size of the testes and a significant reduction in spermatogenesis. The number of aborted eggs in the clutches sired by treated males was higher than in those sired by untreated males. There are however some distinct drawbacks of the process, such as the catching or mass rearing of male crayfish in sufficient numbers, the transport of the animals to a facility where they can be treated and transport back to the water to be treated, or the setting up of mass rearing units. There is also a requirement for highly trained staff to operate the irradiation equipment. In addition to the technical difficulties there may be other public concerns about the release of irradiated animals into the food chain. Despite these drawbacks, which could lead to a prohibitive cost to such operations, the general principle of male sterilization by irradiation has been demonstrated.

The mass rearing of crayfish to the extent required to release sufficient numbers of sterilised males seems unlikely given current knowledge. As the sex ratio in crayfish is normally 1:1, and the technology to breed only males does not currently exist, then farming sufficient numbers would be very time consuming and costly. However, there are a number of commercial crayfish trappers in GB able to supply substantial quantities of male crayfish. An alternative approach would be to combine
the male sterilisation method with a trapping programme. The trapping would lower the female population density, while providing male animals for sterilisation and return to the remaining population. By operating these programmes over an extended period, the proportion of sterile adult males could be steadily increased, while numbers of breeding females would be suppressed.

Alternative methods of achieving functional sterilisation of crayfish should be investigated. A collaborative study between Cefas and the Universities of Newcastle and Portsmouth has examined the manual removal of the modified 1st and 2nd pleopods used by males to deposit spermatophores onto the females as a form of sterilisation. Preliminary trials have shown that the removal of the pleopods does not impact on the males’ ability to compete within the population or to find a mate. The males have been shown to mate as per normal, but spermatophore deposition is significantly impaired. This technique results in functional male sterilisation, which from initial results would appear to be almost 100% successful. It is cheap to apply (only requiring a pair of scissors), can be applied by anybody without any need for specialist training or equipment, and does not involve the transportation of animals away from their point of capture. When applied to large adult males the technique has been estimated to remain effective for approximately 3 years, although further studies are required to confirm this. Male sterilisation has formed a cornerstone of terrestrial pest insect control for several years. It would therefore likely that the concept could be applied to the aquatic environment with the same degree of success with the development of the correct methodology.

7.2. Semiochemicals and pheromone control

Most, if not all, animals that have been studied use chemical signals to trigger behavioural responses. Examples can be found in groups including ciliated protozoans (Alimenti et al. 2011), insects (Heinbockel et al. 2004), molluscs (Cummins et al. 2006), fish (Li et al. 2002), crustaceans (Hardege et al. 2011; Zhang et al. 2011) and amphibians (Kikuyama et al. 1995) These behaviour altering chemicals are called semiochemicals.

Semiochemicals in the form of pheromones are commonly used in the management of insect (specifically lepidopteran and coleopteran) pest populations. The significance of insects as pests has led to them being extensively studied in order to identify effective control strategies. The importance of semiochemicals has grown as entomologists have moved more to integrated control strategies. They can be used to monitor insect populations using pheromone dispensers linked to traps which allow numbers to be counted. Sampling the population allows the population size to be estimated, particularly for time comparisons e.g. the relative catches from the same trap in the same
location at the same time of year. The use of pheromones to control insect pest populations can be divided into two strategies:

a) Mating disruption (“sexual confusion”) whereby pheromone dispensers release plumes of pheromones which saturate the canopy of a crop, so that the natural release of pheromone by females to attract males is masked. In this situation, males will be unable to locate females and mating will not occur, leading to a decline in population size over time.

b) “Attract and kill” whereby the pheromone dispenser lures males to a trap, removing them from the population and preventing them from mating, thereby controlling the population in the subsequent generation (El-Sayed et al. 2009).

A crayfish sex pheromone was first described in *Procambarus clarkii* (Ameyaw-Akumfi & Hazlett 1975). There are several studies that have demonstrated the presence of sex pheromones in *P. leniusculus* (Stebbing et al. 2003; Berry and Breithaupt 2008). Stebbing et al. (2004) went on to test *P. leniusculus* pheromone traps, and with partial success were able to demonstrate that a putative pheromone was able to attract sexually mature males to a trap during the breeding season, but unable to attract as many individuals as a normal food baited trap (including both males and females). Similar results were obtained by Aquiloni et al. (2009) when using a similar method to control *P. clarkii*. In conclusion, significant further development is required before pheromones could be used in the control of crayfish, but the effectiveness of such a control mechanism should not be discounted.

It has also been demonstrated that crayfish utilise a number of other semiochemicals, such as brood pheromones. Crayfish have an extended period of brood care during which time the female carries an egg mass, and later the juveniles up to stage four of their life cycle (Little 1976). During stage three, the juveniles start to explore and feed away from the female. There is evidence to suggest that the female produces a pheromone which she starts to release after egg deposition and which becomes maximally effective when the eggs hatch (Little 1976). The pheromone allows the young to discriminate between the mother and non-brooding adults and therefore avoid cannibalisation by other adults. The mother’s behaviour changes at this time and she will not eat the larvae, spending time away from other adults and in shelter. Once the larvae have become independent from the female the mother reverts back to her normal behaviour. It may be possible that further knowledge of this pheromone may provide the basis for methods of control, such as how to attract juveniles or how to disrupt parental care.
Other pheromones that may prove to be useful for the prevention of spread of invasive crayfish are disturbance pheromones (Stebbing et al. 2010). Zulandt-Sneider and Moore (2000) classified disturbance chemicals into context specific categories: avoidance chemicals are released directly from a repellent stimulus e.g. a predator; alarm chemicals are released from a damaged conspecific; while stress chemicals are released from a stressed but un-damaged conspecific. Zulandt-Sneider and Moore (2000) showed that *Procambarus clarkii* can detect stressed and damaged conspecifics. An alarm pheromone is then released in the urine due to the presence of predator odours, warning nearby conspecifics of impending danger. Urine from stressed individuals caused conspecifics to walk significantly faster and retreat from the source of the signal. This exhibits the use of avoidance chemical signals against certain predators. Hazlett (1994) demonstrated that *Orconectes virilis* and *O. propinquus* also responded to alarm pheromones released by damaged and stressed, as well as crushed, congenerics. Similar effects have been found in *P. leniusculus* (Stebbing et al. 2010). Such chemicals could be used to deter crayfish away from certain areas and prevent their further spread.
8. Legislative control

8.1. Legislation relevant to the keeping of non-native crayfish in Great Britain (GB)

There are a number of pieces of legislation that have been used in GB to prevent the introduction of new species of non-native crayfish and to prevent the further spread of such species within this region. This section reviews the role of this legislation, as implemented, to assess where it has been effective and where it has failed to deliver the intended outcome. The review makes recommendations on whether the legislation continues to have value and identifies options to improve the effectiveness of this legislation, and options to employ more recent legislation to improve the management of non-native crayfish in Great Britain.

8.2. The principal legislation under review

1. The Wildlife and Countryside Act 1981 (WCA)
   a. Article 14 of the Act made it an offence to release, or to allow to escape, into the wild, any non-native organism in GB except under a licence issued by the relevant Minister.
   b. The Wildlife and countryside Act 1981 (Variation of schedule) Order 1992 listed certain non-native crayfish species, namely the signal crayfish (*Pacifastacus leniusculus*), the Turkish crayfish (*Astacus leptodactylus*) and the Noble crayfish (*Astacus astacus*) under Schedule 9 of the Act, as established species the release or escape of which was still subject to the controls applying in Article 14 of the Act.

2. The Import of Live Fish Act 1980. (ILFA): The Import of Live fish Act (Scotland) 1978

This legislation enables the relevant Minister, by Order, prohibit the import, keeping and release of specified types of fish. A court case taken under the Salmon and Freshwater Fisheries Act 1975, resulted in a judicial ruling that crayfish could be considered fish under UK legislation where the definition of fish was not otherwise specified. Following advice from JNCC on the control of non-native crayfish, the Prohibition of keeping of Live Fish (Crayfish) Order 1996 was made under ILFA. This Order, widely known as the Crayfish Order, made it an offence to keep any non-native crayfish species in England and Wales except under licence. An exception was made for the keeping of signal crayfish in areas where that species was already widely established, as it was believed to be impractical to control the keeping of this species in such
areas. This exemption resulted in the division of England and Wales into what were termed either ‘go areas’, where the signal crayfish was not subject to control, or ‘no-go areas’, where the keeping of this species could only be carried out under licence. Two general licences were issued under the Crayfish order.

a. A licence to keep live crayfish in hotels markets and restaurants for human consumption.

b. A licence to keep tropical crayfish for ornamental purposes in heated indoor aquaria.

This licence applies only in respect of one species, the redclaw (*Cherax quadricarinatus*).

At the same time, in Scotland, an Order with the same title was made under the Import of live Fish Act (Scotland) 1978, but the prohibition on keeping was more comprehensive than in England and Wales, as there was no exemption for signal crayfish, nor any general licences to cover the food or ornamental trades. This Scottish Order was repealed and re-cast under The Prohibition of Keeping and Release of Live Fish (Specified Species) (Scotland) Order 2003 simply to consolidate the Crayfish Order with the equivalent Order covering freshwater fish.

3. EC Regulation 708/2007 concerning alien and locally Absent Species in Aquaculture, and The Alien and Locally absent Species in Aquaculture Regulations 2011 (ASR)

The EC Regulation requires all EU Member States to control the movement of alien or locally absent species for aquaculture, such that they do not have an adverse impact on biodiversity within the EC. The ASR provides the operational structures to enable enforcement of the EC Regulation in Great Britain. The EC Regulation requires Member States to prevent the movement of species for aquaculture without a risk assessment having been carried out, except where previous experience can demonstrate that the movement poses no environmental risks. The introduction of this legislation led to the repeal of the Crayfish Order as regards the keeping of non-native crayfish for aquaculture. Government policy on the farming of non-native crayfish however remains unaffected by the transfer of legislative control from ILFA to the ASR.


In 2005, the Environment Agency, in exercise of its powers under section 210 of, and Schedule 25 to, the Water resources Act 1991, made a series of byelaws relating to crayfish, which are known as the Crayfish trapping byelaws. These byelaws provide the Agency with a coherent base from which to manage the trapping of non-native crayfish in waters within England and Wales. Prior to these byelaws being made the use of crayfish traps, which were defined as fixed engines under the Salmon and Freshwater Fisheries Act 1975, was legal in some EA regions but not
others. This created problems for the Agency both with regard to the management of nuisance crayfish populations in fishery waters, and as regards the commercial exploitation of signal crayfish. The byelaws allow the trapping of non-native crayfish in inland waters in those parts of England and Wales defined as go areas under the Crayfish Order, subject to the written permission of the Agency. The byelaws prohibit the trapping of non-native crayfish in those areas defined as no-go areas in the Crayfish Order, except for scientific, conservation or fishery management purposes, again with the written permission of the Agency.

8.3. Operational benefits and problems arising from this legislation

The legislation above, and the government policy through which it has been enforced, has largely been in place for a period of 15 years. This is an appropriate timescale to allow a rational review of any benefits that have arisen from its implementation, and of its shortcomings.


This Act is important in that it enshrines the UK Government’s policy principle that alien species should not be released into the wild unless such release poses no risk to UK biodiversity. Current policy is against the release of any non-native crayfish to the wild. The only exemption to this policy applies in respect of the release, into the same location, of crayfish caught as part of a scientific study, where that release is an integral part of the study design.

As a practical tool for the enforcement of this policy for aquatic animals, the Act is not adequate. Unlike organisms released into terrestrial habitats it is very difficult to detect when an aquatic animal has been released or allowed to escape to the wild. In addition, in most cases it would be impractical to pursue a case against someone for a breach of the relevant Articles of the Act, because of the lack of evidence as regards the actual commission of the offence. The difficulties of catching someone in the act of releasing animals into a body of water are further compounded by the lack of clarity over whether such a water body constitutes the wild. A further problem, which has exacerbated the above difficulties, is the fact that there are no dedicated enforcement officers for the Act. The lack of specific enforcement responsibilities has enabled legal teams in most of the relevant Agencies to step aside from addressing these issues in practice, with the result that there has been no development of case law, to resolve issues such as defining the wild or to drive changes in the legislation to make it more enforceable. There have, however, been a number of amendments to the WCA in recent years, some of which provide management options that may be valuable in future attempts to manage non-native crayfish. These are discussed below.
8.3.2. The Import of Live Fish Act, Crayfish Orders.

This Act has gone some way in addressing the problems identified within the WCA. Defining the wild is less problematic, as licensing under this Act is required whether the animals are kept in a water body that is clearly not the wild or whether they are released into a water body that is the wild. It is therefore clear that anyone who has placed non-native crayfish in a body of water, without a licence, has committed either a keeping or release offence. Government policy in respect of this legislation has developed the principle that if the animals can be recovered from a site with reasonable ease they can be considered to be kept, and if they cannot then they have been released to the wild. Similarly, as regards crayfish, if the animals are placed into an environment from which they are able to escape under their own efforts then they are in the wild, whereas if they are in isolated, escape-proof waters they would be considered to be kept.

While these provisions do not make it any easier to detect an offence as it is taking place, they provide much greater scope to take action on the retrospective detection of an offence. In England and Wales the restrictions on the keeping of non-native crayfish imposed under ILFA have resulted in a significant reduction in the threat posed by the trade in crayfish as ornamental animals. Most introductions of ornamental animals to GB originate from third country (non EC) sources, and all have to enter GB via Border Inspection Posts (BIPs) at British airports. The Fish Health Inspectorate (FHI), which has enforcement powers for ILFA have worked closely with Defra staff at the BIPs to ensure that any crayfish consigned to GB importers other than red claw crayfish are notified to the FHI. The FHI are then able to advise the importer that, while the import of the animals was not illegal, the animals cannot be legally kept in GB for ornamental purposes. This results in the animals being surrendered to staff at the BIP who arrange for their humane slaughter.

Despite these efforts, which have largely prevented the introduction of crayfish from third countries, there has continued to be a trade in ornamental crayfish from EC sources, which until 2010 was totally unregulated. This has resulted in the FHI having to gather intelligence, and seek public information about incidents of crayfish being sold in the ornamental trade in order to trace keeping by individuals back to traders and importers. The FHI also aim to educate all involved about the prohibitions. This work has revealed that the majority of keepers and traders have been unaware of the legislation in force (most individuals assuming that if a crayfish was on a trade availability list, or in display in a shop, then it must be legally available), and as such they have only been required to surrender the animals they were keeping and have been warned about any future transgressions. As yet the FHI have not had to take further legal action against an individual or company for committing the same keeping offence a second time.
Since 2010 a change in the aquatic animal health legislation has required anyone introducing such animals into England and Wales to be authorised by the FHI. This has resulted in previously deregulated trade in ornamental aquatic animals being subject to scrutiny by the FHI with the result that they have been able to slowly reduce the incidence of British importers trading crayfish, the keeping of which is illegal in GB. There remains however an issue with respect to foreign suppliers of ornamental animals who enter GB solely to deliver animals to customers. These suppliers arguably do not commit a keeping offence, and are therefore able to act without fear of sanction under this legislation. The FHI, with the assistance of the ornamental aquatic trade association (OATA), have made attempts to dissuade EU suppliers of ornamental animals from supplying animals that are subject to controls under ILFA within GB, but with a notable lack of success in some cases.

The Crayfish Order has therefore significantly reduced the supply of crayfish into GB for ornamental purposes, but has not completely stopped the trade, even to those persons not seeking to break the law. The trade therefore still poses some risk of causing the release of another invasive crayfish species into GB waters.

The Order has proved somewhat less effective than was anticipated at preventing the spread of signal crayfish from areas where it was well established, in the South of England, to parts of Northern England and Scotland. While the rate of spread has undoubtedly been reduced as the creation of new crayfish farms in the go areas has all but ceased, it is evident that people in no-go areas continue to buy signal crayfish to introduce to ponds, a practice which will inevitably lead to the spread of the animals into other natural aquatic environments. As with purchasers of ornamental crayfish, the FHI have found that buyers of signal crayfish are often unaware both of ILFA and WCA. Where incidents of keeping or release to ponds has been discovered the FHI have usually found the culprit to be remorseful for their actions, and willing to make efforts to recover and destroy the animals where it was feasible to do so. Several persons found to have illegally stocked crayfish in ponds have informed the FHI that the sellers of the crayfish (always suppliers based in go areas), had specifically advised them that there were no restrictions on keeping crayfish in ponds. All of the suppliers identified to have sold signal crayfish to persons in no-go areas had been informed about the keeping legislation at the time it was introduced, and on any occasion that they have been identified as the supplier of illegally kept animals. The FHI has specifically requested these people to stop supplying animals to no-go areas, but clearly these suppliers care more for making money than they do for conservation and environmental protection, as the requests have been ignored. The FHI sought advice on the option to pursue such suppliers for aiding and abetting or procuring an offence under ILFA, but Defra refused to pursue a case on this basis.
While persons in ‘go areas’ are able to supply signal crayfish with impunity to unwitting or irresponsible buyers in no-go areas the ILFA legislation will not be effective in halting the spread of this species within GB. This is equally true as regards the spread of the four other non-native crayfish species that have established populations in a few waters in England, though the scale of activity is likely to be much lower than with signal crayfish. Any measures recommended below as regards the further control of signal crayfish would apply equally to these other established species.

The lack of controls on the keeping of live crayfish for human consumption has also hindered the operation of controls under ILFA, as this has meant that there has been a steady supply of live signal crayfish into no-go areas, with the inevitable consequence that some are bought and released into ponds, lakes and rivers, where they have the scope to cause significant problems. Both FHI and Environment Agency staff warranted under ILFA have had to provide advice to sellers of crayfish for consumption in no-go areas to improve their biosecurity to ensure that stock cannot escape, and to warn them not to dump unwanted stock into a watercourse. Unlike the ornamental trade, which typically sells low volumes of stock at high prices, the wholesale or retail of live signal crayfish for food poses a significant risk because animals are sold cheaply and in numbers that if released could result in the establishment of a new feral population.

The Crayfish Order has effectively eliminated the option to establish new farms for non-native crayfish in open environments. Farming of species other than signal crayfish would be licensed only where the farm facilities are fully isolated and operate a double level of escape prevention. Typically this requires the site to operate indoor tank based systems, where the tanks have to be lidded and screened to prevent the escape of any crayfish (at all life stages) and where the building in which the tanks are housed is also escape-proofed (e.g. no open drains, doors must close onto raised walls, no holes in the walls). For the majority of species, farming in such conditions is largely untried and likely not to be economically viable. Farming of signal crayfish in no-go areas is subject to exactly the same constraints. New signal crayfish farms in the go areas are permitted in enclosed outdoor ponds, but those ponds must be adequately escape proofed. It is no longer permitted to establish a farm in ponds with a contiguous water contact with a natural watercourse.

Overall the Crayfish Order has contributed significantly to the reduction in risk of release of non-native crayfish. However, it has been least effective against the major problem, namely the continued spread of signal crayfish into areas where the conservation of native crayfish is a key priority. There are options available under this legislation which could help to resolve some of the issues regarding the continued supply of signal crayfish into no-go areas. These options are discussed below.
8.3.3. Alien and Locally Absent Species in Aquaculture

The policy standards applied under ILFA have been adopted for the Alien and Locally Absent Species in Aquaculture Regulations. The regulations enable applicants for a permit to appeal against any decision made. Should someone wish to challenge the Defra policy, they would have to carry out (at their own cost) a full risk assessment in line with the requirements of the EC Regulation. Should that risk assessment suggest that the risks from aquaculture of the species were low at the proposed site then Defra would have to consider a revision of its policy. It is unlikely that anyone would challenge the policy, and noteworthy that generic assessments of most of the commercially exploited crayfish have suggested that they pose a medium to high risk of becoming invasive in Europe, so are unlikely to meet the criteria for farming under EC Regulation 708/2007. Development of crayfish aquaculture in GB is therefore likely to be based on fully enclosed warm water recirculation systems, for which the risk of escape is negligible.

8.3.4. Crayfish trapping byelaws

These byelaws have been effective in giving the Environment Agency a uniform degree of control over the exploitation of non-native crayfish in England and Wales. One potential problem that has arisen is the liberal use of trapping for fishery management purposes in no-go areas. When the byelaws were first proposed, the Agency sought to prohibit commercial trapping in the no-go areas as it believed that legitimising the harvesting of signal crayfish in this region would tempt people to illegally stock new waters in these areas with crayfish for the establishment of a fishery. They retained an option to grant permission to trap for fishery management purposes where signal crayfish were posing a significant nuisance in commercial angling waters. It appears that the use of this option has been rather more liberal than first intended and that some people are operating fishery management services based on the income they receive from selling the crayfish caught. This poses the question whether in taking powers to manage the trapping of non-native crayfish in all areas, the Agency may have inadvertently promoted a problem that they were keen to ensure did not arise.

8.4. Options to make the legislation more effective

It is evident from the text above that the existing legislative provisions are effective at controlling further farming of non-native crayfish, and are reasonably effective at controlling the introduction of such animals via the ornamental fish trade. It is equally evident that they have not been so effective at preventing introductions of signal crayfish into the areas of Great Britain that the legislation aimed to protect from such introductions. This raises a number of questions about the future use of
legislation to control non-native crayfish and provide protection for populations of the endangered native crayfish species, the white clawed crayfish (*Austropotamobius pallipes*):

1. Has the spread of signal crayfish extended to the point at which it is no longer worth maintaining the current no-go areas in England and Wales?
2. Are there any other legislative provisions that could close some of the loopholes which have led to:
   a. the movement of signal crayfish into no-go areas, and
   b. the illegal keeping of certain species as ornamental animals?
3. Are there any non-legislative actions that could help address the problems identified?

Addressing these points in turn:

1. Current no-go areas.

We recommend that the signal crayfish should remain subject to control in the existing no-go areas, despite the evidence that the species has now been detected in a considerable number of waters in these areas (Rogers & Watson 2012), and that it has been suggested that existing no go areas should be scrapped, with efforts to protect native crayfish concentrated on only a handful of key water catchments. Our reasons for this recommendation are:-

a. The apparent rate of spread of signal crayfish to no-go areas is almost certainly a significant overestimate. Prior to 1996 there was almost no systematic surveillance for crayfish in England and Wales. For a variety of reasons there has been much more directed surveillance in recent years. This has led to the detection of populations of signal crayfish, some undoubtedly recent introductions, but a number that almost certainly pre-dated the Crayfish Order.

b. Native crayfish populations continue to survive in a number of the catchments colonised by signal crayfish. While some believe that the presence of signal crayfish will inevitably lead to the demise of the native crayfish, we believe that more effort should be made to establish methods to control or eradicate signal crayfish such that we could target these mixed stock catchments for eradication efforts and protect the native species.

c. Removing the controls on signal crayfish in no go areas would certainly increase the rate of spread of the species, as it becomes more readily available and as the risks of being prosecuted for illegal release diminished. This would inevitably increase the risk that the species will be introduced to catchments that currently contain high value un-impacted native crayfish populations.

d. We have identified the pathways by which we believe the majority of new introductions of signal crayfish to waters in the no-go areas take place, and we believe there are a number of
legislative options that would enable these pathways to be closed. If we can make the Crayfish Order operate in the manner that was originally intended, then there may be scope to prevent further damage to habitats both in the no-go areas and in Scotland, which is affected by the same introduction pathways.

Having established our position that the existing legislation still has a purpose to serve, we must consider the options available to improve the effectiveness of that legislation.

2. Legislative opportunities

The key problems that have been identified with the current regulatory framework are:

a. The continued, unregulated supply of signal crayfish into no-go areas by persons in go areas.

b. The lack of knowledge of go area residents about the legislation preventing the keeping and release of signal crayfish.

c. The lack of import controls for non-native crayfish which places an unnecessary burden on regulators responsible for the enforcement of the keeping legislation, and results in GB traders unaware of the legislation committing offences by accident.

We have identified a number of options within the existing primary legislation in England and Wales, which could, through the implementation of secondary statutes, address the problems identified above and enable more effective enforcement of the existing policy principles (The legislative situation in Scotland is less clear and is discussed separately). The options identified for England and Wales would present only a minor regulatory burden on existing industries, with the burden specifically targeted on aspects of trade that result in breaches of the current legislation. The options are:-

A. Amendment to the Prohibition of Keeping of Live Fish (Crayfish) Order 1996

I. We recommend that consideration is given to amendment of the 1996 Order such that suppliers of live signal crayfish within the current go areas are subject to licensing. The licences would prohibit the supply of live signal crayfish into the no-go areas.

This amendment would help to stop the current trade in signal crayfish into no-go areas as most suppliers will cease to do so once that activity becomes an offence. It will not stop those determined to ignore the legislation, but will make such persons vulnerable to prosecution where they are detected to have committed an offence. If suspected of committing an offence a supplier could be subject to test purchase to determine whether they were compliant with the legislation. The burden
on industry would be minimal as most of these suppliers are also licensed crayfish trappers so a joint licensing system for trapping and supply could be easily set up.

II. We recommend that consideration is given to the amendment of the 1996 Order such that it prohibits the import and keeping of non-native crayfish except under licence.

Both Norway and Sweden have successfully presented cases to the WTO for the imposition of import controls on non-native crayfish, based on the risk of environmental impacts and threats to protected native crayfish species. We see exactly the same justification for such action in England and Wales. The burden on UK businesses and regulators would be lessened by this measure. There would be no loss of legitimate business, except perhaps for the food trade (see below), as the legislation could be used to licence the import of any species that are currently legally kept in GB.

III. We recommend that consideration is given to the revocation of the general licence which enables the keeping of live non-native crayfish for human consumption in markets, restaurants and hotels. We further recommend that there is a presumption against the keeping of any live non-native crayfish for human consumption in England and Wales.

The trade in imported live crayfish has declined substantially since the 1996 Order was introduced, as a result both of the increased import of processed crayfish tails in brine, and the increased availability of alternative farmed marine prawn product, which have greatly reduced the demand for freshwater crayfish. The restaurant trade is now used to ordering fresh dead crustacea with short shelf life and therefore has systems in place which eliminate the requirement to hold live crustacea (other than lobsters). The revocation of the general licence should therefore have little impact on trade. The benefits arising from this change will be that there will be no justification for having live signal crayfish in your possession in a no-go area, unless you have an individual licence to do so under the Crayfish Order. This will greatly decrease the risk of casual or inadvertent introduction of signal crayfish to natural waters by discarding from trade sites. The presumption against any live crayfish keeping for consumption is a logical extension of the revocation of the general licence, but may face some opposition from industry in the go areas, where the signal crayfish is probably readily available live from local suppliers. We would argue that industry could readily alter their practices to deal with fresh dead crayfish supplies.


There have been a number of recent changes to the Act, of which the most relevant for future crayfish management is the introduction of an amendment to Section 14 of the Act, which was given force by Article 50 of The Natural Environment and Rural Communities Act 2006.
Section 14ZA (1) of WCA makes it an offence for a person to sell, offer or expose for sale, or have in their possession or transport for the purposes of sale, any non-native animal or plant subject to an Order made by the relevant Minister. Section 14ZA (2) makes it an offence for a person to publish or cause to be published any advertisement likely to be understood as conveying that he buys or sells, or intends to buy or sell any non-native animal or plant subject to an Order made by the relevant Minister.

I. We recommend that consideration is given to the introduction of an Order under Section 14ZA of the Wildlife and Countryside Act 1981, which prohibits the sale and the advertisement for sale etc of any live non-native crayfish within Great Britain, except for the ornamental species *Cherax quadricarinatus*.

For the reasons established above we believe this provision would have little impact on the food trade other than to force suppliers to kill crayfish prior to sale. We would need to ensure that some suppliers who market their product live in other EU Member States would not be prevented from doing so by this legislation. We assume that such sales would be considered to occur in the destination member state but, if not, an exemption would be required to enable such trade (live crayfish attract a price premium in some EU countries). If this recommendation was pursued then the recommendation at A (i) above to amend the Crayfish Order in respect of suppliers may be unnecessary. The one disadvantage of using Section 14Z of WCA is the lack of a dedicated regulatory body to enforce these provisions. The advantages are that it could control the advertising for sale of live crayfish, which in addition to the significant benefits it would bring regarding the sale of signal crayfish into no go areas, would place useful obligations on the ornamental trade not to advertise illegal species. At present importers and internet sellers of ornamental animals often advertise the availability of crayfish which cannot be kept legally in GB. The FHI has sought voluntary measures from industry and private sellers to ensure they do not make such animals available for sale, but has no mechanism to enforce such measures. An advertising ban would force importers to remove crayfish from their GB trade availability lists and so avoid the situation whereby their customers order crayfish that should not be traded. Action could be taken against companies listing crayfish for sale on their websites, and co-operation could be sought from companies such as eBay to block any advertisements for non-native crayfish. These measures would reduce the current burden on regulators such as the FHI, but in practice would increase slightly the burden on the ornamental industry with regard to their having to ensure that they did not offer for sale any illegal species. In theory the industry should already take action to prevent such trade, but it is evident that some
members of the industry do not. We do not believe that the OATA would object to such constraints as they are fully supportive of controls on undesirable species.

C. Legislative options in Scotland.
There has been a radical recent change in the Crayfish legislation in Scotland. Article 14 (3) of The Wildlife and Natural Environment (Scotland) Act 2011, introduced further amendments to Section 14 of the Wildlife and Countryside Act 1981 in Scotland. These new provisions under Article 14ZC of the WCA made it an offence for a person to keep, have in their possession or have under their control any invasive non-native species of animal or plant specified in an Order made by the Scottish Ministers. This effectively duplicated aspects of the Import of Live Fish Act (Scotland) 1978 and as a result the 1978 Act was repealed.

Unfortunately, and we assume inadvertently, no provisions were made in this repeal to save the Prohibition of Keeping and Release of Live Fish (Specified Species ) Order 2003 or to replace it with an appropriate Order under the new WCA section 14 provisions. As a consequence it appears that Scotland is now without any specific legislation with respect to the keeping of non-native crayfish (and a range of fish species), until the Scottish government introduces a new Order under the WCA. The authors of this report have been unable to ascertain whether any plans exist to introduce such an Order at present, but it appears that the implications of the repeal of the 1978 Act only became apparent when we sought clarification from colleagues in Scotland. We strongly recommend that the Scottish government looks to address this problem at the earliest opportunity, and in doing so looks to address relevant aspects of the advice given above in respect of legislation applying in England and Wales. We believe for example that sales controls would be equally valid in Scotland. We note that the transfer of ILFA powers to the WCA in Scotland took away the option to control importation of non-native crayfish. This is however less of an issue for Scotland than it is for England as the vast majority of relevant trade takes place into England, hence the English legislation, if appropriately amended, would serve to manage trade into Scotland. There are a number of further amendments to Section 14 of the WCA in Scotland that deal with the notification of non-native species, Codes of Practice for non-natives, powers to make controls orders for such species and the enforcement of these powers. We believe that the use of these powers could prove valuable in the future management of non-native crayfish, providing the Scottish Ministers decide to implement an Order for crayfish under Article 14 ZC.

3. Non legislative options.
It is apparent from the regulatory work of the Fish Health Inspectorate that the legislation relevant to the keeping and release of non-native crayfish in Great Britain is generally not well understood,
except by the more commercially active members of the industries on which it has an impact. The
majority of people operating at the retail end of the food industry and the ornamental aquatic
industry are at best aware that legislation exists but generally are unaware of its specific provisions.
They typically assume that their suppliers will only supply animals that can be legally traded. This
same assumption appears to guide the actions of people who think that it would be interesting to
stock their pond with crayfish as a future source of food for their barbeque. It is therefore important
that the regulatory authorities make regular attempts to advertise the existence of the legislation. In
that regard, many public bodies and some industry bodies and wildlife charities have produced
guidance about the crayfish legislation, much of which is available online, but despite this most of
the population of GB remains ignorant of the law. We conclude therefore that because of the great
difficulty of taking the message to the general public, even the best of publicity campaigns is no
substitute for proper legislative control on those areas of industry which, if not compliant, do most
to undermine the intention of the legislation.
9. Combined control mechanisms

It is clear from previous attempts to control pest species that ‘silver bullets’ are rare, and that an integrated approach is more effective and more likely to lead to the control and/or eradication of the target population. For example, in Switzerland extensive trapping in addition to the introduction of predatory fish (eel and pike) significantly reduced the size of a population of *P. clarkii* by a factor of 10 over 3 years (Hefti and Stucki 2006). A nuisance population of crayfish in a lake in Wisconsin was treated using a combination of methods (Hein et al. 2006). The control programme involved intensive trapping combined with a change in legislation relating to the capture of predatory fish from the lake. After five years of intensive trapping and fisheries management practices, a decline in crayfish of up to 95% was seen. Similarly a combination of control mechanisms was applied to a population of *P. leniusculus* in Spain (Dana et al. 2010). Trapping, manual removal and electrofishing resulted in a sharp decline in the target populations size over a 4 year period, with a catch rate (crayfish per worker, per day) of 30 in the first year decreasing to 10 in the fourth year. One of the key features of these combined approaches is that they target multiple life stages, potentially resulting in a greater level of control than if a single mechanism was applied. The ability to target multiple life stages simultaneously is a feature absent in current control mechanisms with the absence of pesticides. Despite the effective control of populations using a combination of mechanisms, there have been few recorded attempts at using a multi-disciplinary approach, so there is a lack of data on the effectiveness of combined control mechanisms. This report makes some suggestions for potential combinations of methods in the final sections.
10. Population model

10.1. Aims

The third objective of this report is to develop a simple mathematical model to describe crayfish population growth. The model could be used to describe all species of crayfish but was parameterised for signal crayfish and hence the results are for that species. A baseline population model was developed. A variety of population control measures were then investigated and their impact compared. These control measures were: trapping, sterilisation, predation, electrocution, biocidal control and biological control mechanisms e.g. pathogens. We carried out sensitivity analysis to determine which parameters have the greatest impact on population dynamics. In this section we draw conclusions about the control methods, and identify which aspects of the crayfish life cycle require greater understanding in order to identify the best methods of control. We then make suggestions about improvements to the model which would take it beyond this preliminary stage and improve its accuracy in describing crayfish population dynamics.

10.2. Methods

10.2.1. Population model development and assumptions

![Figure 2. Schematic of population model without control]
A deterministic compartmental mathematical model was developed to describe the basic dynamics of a closed population of crayfish. It is a mechanistic model and was built following discussions with experts on the current knowledge of the life cycle of the crayfish as presented in this report. The model tracks the development of male and female crayfish from juvenile to adults independently. It is a preliminary model designed to inform future decisions regarding control and research into crayfish populations, and forms a basis for the development of subsequent models. Figure 2 is a schematic of the basic population dynamics captured by the model, and is based on the following assumptions about crayfish development and population structure:

- Eggs are hatched at a constant rate and the number of eggs produced by a female which result in successful hatching is dependent on the total population density, with the number decreasing with increased population density.
- The eggs are hatched with a 50:50 sex ratio.
- Juveniles will mature at a rate which is dependent on the number of adults in the population. At high densities of adults, juveniles will mature at a slower rate.
- Juvenile males mature initially into a subdominant male class, and will become dominant males at a rate dependent on the number of adults in the population. Subdominant males will not mate and produce offspring.
- Juvenile females will mature approximately a year later than males at a rate which is dependent on the density of the adult population, and once mature, females are sexually active.
- Adults are assumed to mate once per year, and are removed from the fertile population once mated. This is due to an assumption that each male will mate successfully on average once per mating season. We do not explicitly model the fact that females may be mated several times. This is justified by the fact that only the final mating will result in offspring, and the number of matings will not change the number of offspring.
- All females remain gravid for the same period of time and, once eggs are released, return to the fertile class and are available for mating in the following breeding season.
- Males, once mated, are removed from the mating class at the same rate as females, so they also wait until after eggs are released to return to the mating class.
- All classes of crayfish are subject to natural, density dependent death. Juveniles have a significantly higher death rate than adults, which increases with total population density. Adult death rate increases with adult population density.
- Females will mate with dominant and sterile males at equal rates.
The population is made up of 70% juveniles: this is only used to calculate the values of the density dependent parameters and is not a forced output of the model.

10.2.2. Model equations

All of the following models are given as a series of coupled non-linear ordinary differential equations describing the change over time of the density per m$^2$ of each subset of the population. These equations can be solved numerically in a number of different software packages including Mathematica, Matlab and R. We have also submitted a programme which will simulate these models over time in R.

**Model 1: Baseline Model**

Juvenile Males:  
\[
\frac{dJ_M}{dt} = \sigma e F_G (\lambda - s_1 A) - J_M (y_1 - s_2 A) - J_M (\mu_j + s_3 N)
\]

Juvenile Females:  
\[
\frac{dJ_F}{dt} = (1 - \sigma) e F_G (\lambda - s_1 A) - J_F (y_2 - s_2 A) - J_F (\mu_j + s_3 N)
\]

Subdominant Males:  
\[
\frac{dS_M}{dt} = J_M (y_1 - s_2 A) - S_M (\alpha - s_3 A) - S_M (\mu + s_4 A)
\]

Dominant Males:  
\[
\frac{dD_M}{dt} = S_M (\alpha - s_2 A) - M_D (\mu + s_4 A) - \beta F M_D + \varepsilon M_G
\]

Mated Males:  
\[
\frac{dM_G}{dt} = \beta F M_D - M_G (\mu + s_4 A) - \varepsilon M_G
\]

Females:  
\[
\frac{dF}{dt} = J_F y_2 - F (\mu + s_4 A) - \beta F (M_D + M_G) + \varepsilon F_G + \varepsilon F_G
\]

Gravid Females:  
\[
\frac{dF_G}{dt} = \beta F M_D - \varepsilon F_G - F_G (\mu + s_4 A)
\]

Where A is total the adult population density and N is the total population density.

10.2.3. Parameter estimations and notation

The majority of the parameters in Table 2 are life history parameters which come directly from the literature cited in this report. The values in the table are based on a low population density, as are maximum birth rates, minimum death rates and the fastest maturation rates. However there are a number of parameters which are more difficult to interpret directly from the biology of the system. The contact rate $\beta$, a measure of how likely males and females are to contact one another and mate, is one such parameter. We have used a value of 5 here but we have also varied this in the sensitivity analysis. The density dependence parameters $s_i$ are also difficult to interpret biologically. However we do have information on the range of densities that crayfish can live at, and the range of values that the relevant parameters can take. We have assumed linear density dependence and used the data as described in the following section.
To estimate $s_1$: We know adult population densities can range from 0.9 to 4.2 and as high as 7.3 per m$^2$. We also know that the number of eggs hatching per female can vary from 500 at low population densities through 300 at medium population densities to 100 at high population densities. From the first equation in model 1, number of eggs hatching per female $= \lambda - s_1 A$, here $A$ is the total adult density, therefore:

- at high densities $100 = 500 - 7.3s_1$ which gives $s_1 = 54.79$
- at medium densities $300 = 500 - 4.2s_1$ which gives $s_1 = 47.62$

If we average these two estimates we get $s_1 = 51.2$. Equivalent calculations were made for the other density dependence parameters.
10.2.4. Baseline population dynamics

Based on these assumptions and parameter estimations, we modelled the predicted dynamics of each of the classes of the crayfish population when introduced at low densities into a new environment (Figure 3).

10.3. Control strategies

In the following sections we outline the main assumptions of the model relating to each control strategy.

10.3.1. Mechanical control through trapping

Crayfish populations may be controlled by constant removal of individuals through trapping. This is modelled by removing individuals at a constant rate, $\zeta$. In order to include this in the equations we add a trapping term to the end of each equation. For example, for dominant males the equation becomes:
We assume that trapping is carried out continuously, with traps removed, emptied and replaced each day. We investigate the effect of selective trapping on the total population density in four ways:

- **Sex biased trapping**: dominant males only are removed.
- **Size biased trapping**: all adults are removed, with the exception of gravid females which are assumed to be much less likely to move around and be caught in traps.
- **Small size trapping**: the juvenile population only is targeted and removed.
- **Unbiased trapping**: each class of the population is removed at an equal rate.

It is likely that size biased trapping is the most realistic of the trapping methods considered, since it is practically difficult to target one specific class such as dominant males or juveniles. We consider two different cases of size biased trapping: firstly where all adults are equally likely to be caught, and secondly where dominant males are approximately twice as likely to be caught as subdominant males and females. In order to give an idea of how the model output relates to the number of crayfish removed from a population, we model a case study of a closed lake of area 1 hectare.

### 10.3.2. Autocidal control through sterilisation

We test the impact of sterilising males upon trapping and returning them to the environment. Both dominant and subdominant males can be sterilised. Firstly we assume that only dominant males are sterilised. To incorporate this, we keep the trapping term as discussed in the previous section and include the following equations in the model:

\[
\frac{dM_D}{dt} = S_M (\alpha - s_2A) - M_D (\mu + s_4A) - \beta F M_D + \varepsilon M_G - \zeta M_D
\]

Sterilisation is included in the model based on the following assumptions:

- All trapped males are sterilised and returned to the environment.
- Sterilised males will mate with females at the same rate as dominant males, thus preventing female eggs being fertilised.
• Whilst females are not actively sterilised, we include the class ‘Mated Sterile Females’ to
discern those females which have been mated with a sterile male, and thus will not produce
viable eggs.
• It is assumed that sterile males will behave as dominant males, and are removed from the
fertile population once mated and will become available for mating again once the female
has spawned.
• Sterility is lost after approximately 3 years, after which time males will return to the
dominant male class and resume successful mating. However they may still be trapped again
and sterilised subsequently.

It may be possible to sterilise both dominant and subdominant males, and the results from both of
these strategies are compared. It is assumed that subdominant males are removed and sterilised
immediately before they become dominant. This assumption, whilst limiting, is reasonable since
larger subdominant males are more likely to be trapped than the smaller individuals.

10.3.3. Physical control through draining or electrocution
In this case we assume that the whole body of water is treated, and in the first instance we assume
that a fixed proportion of the population is killed. In terms of the model, this treatment occurs as a
discrete event. In order to incorporate this into the model we run the model to equilibrium and then
stop it, kill a proportion in each class then restart the model at the new densities. Firstly, we consider
one treatment and look at how quickly the population recovers, we then go on to look at multiple
treatments at different time intervals and vary both the proportion of the population killed and the
frequency of treatment. Finally we consider what happens if the water body is drained but adults
have burrowed and some manage to survive. In this case different proportions of juveniles and
adults are killed.

10.3.4. Biological control
Predators
Whilst the model does not include the dynamics of a predator explicitly, we are able to infer the
effects of increased mortality through a change in environmental conditions by varying the density
dependent mortality rates in the baseline model or by considering predators to impact on the
population in the same way as traps.
Parasites

We investigate the possibility of using a sterilising parasite as a method of control by introducing transmission of the parasite between males and the environment. The modelled parasite is a spiroplasma which has recently been identified in crayfish and is the most promising parasite in terms of potential biological control seen so far in this system (Longshaw, 2011). To do this we introduce the following equation to give the parasite density in the environment:

\[
\frac{dE}{dt} = \nu(M_S + M_{SG} + S_S) - \rho E(M_D + M_G + S) - dE
\]

It is assumed that all sexually mature males (dominant or subdominant) are equally susceptible to the parasite and get infected by coming into contact with the environment at rate \( \rho \), therefore we add \( \rho EM \) terms to each of the sterile male equations. We also assume that all infected males will release parasites into the environment at the same rate, \( \nu \). This method of control is speculative at the moment, and there is little data from which to estimate these parameters, but the model can give us an initial indication of the impact this type of control could have.

10.4. Results

10.4.1. Trapping: comparing methods and trapping rates

The "trapping rate"

This section deals with the effects different trapping methods and trapping rates. The trapping rate, or trapping intensity, can be thought of as a product of the number of traps put out, and the frequency with which they are emptied. Thus an increase of trapping effort from 1 to 10 represents either 10 times the number of traps, emptying of traps being carried out 10 times more frequently, or a combination of increased effort. Therefore the trapping rates, or trapping intensities, given in this report should be thought of a relative measures of trapping effort that can be compared in order to compare of trapping methods. For clarity, we have calculated the number of crayfish removed per m² per year for each trapping intensity and each trapping approach, in the section entitled “Trapping: numbers of crayfish removed”, on page 68.

In this section however, we focus on the impact of the different trapping methods (sex biased, size biased, juvenile trapping and unbiased trapping) at different trapping rates. Figure 4 compares the impact of different types of trapping (represented by the coloured lines), for different trapping rates (graphs a, b, c and d) by showing the percentage change in the total population density caused by the treatment over time. A value of -100 on the y axis indicates that the total population has been
eradicated and anything above the zero line is where the population has increased as a consequence of control.

**Sex biased trapping (Figure 4: red dashed line)**

If trapping efforts are focussed solely on dominant males, then any level of trapping will lead to a reduction in population over long time periods, through both the physical removal of males, and the reduction in birth rate of juveniles but it is not possible to totally eradicate the population within 50 years. At low trapping intensities, this removal will lead to an increase in the growth rate of subdominant males which will mature to replace the males removed by trapping. The removal of a proportion of the dominant males will also lead to an increase in the fecundity of the females due to density dependence, thus an initial increase in the juvenile population is observed, which leads to a subsequent increase in the female population. However, as the dominant male population is removed continuously, this initial increase in juveniles is followed by a reduction in the juvenile population due to the reduction in the number of gravid females. However, if the male population is not entirely removed then the juvenile population reaches equilibrium, and thus subsequent generations are maintained.

As trapping intensity is increased it is possible to reduce the juvenile population density significantly, however the population will remain in the environment, and will quickly regenerate if continuous trapping is ceased. At very high trapping intensities, it is possible to reduce the male population sufficiently that the population begins to die out. However this reduction is not sufficient for complete removal of the population in less than 50 years. The population will survive at low levels since the remaining population will consist of females, which may survive for several years in the absence of males. The reduction in adult population density through removal of males only, will lead to a reduction in competition for resources between the females, and may therefore lead to an increased lifespan of the remaining female population. For this reason, unless trapping efforts can be continually maintained for a long time period, to ensure sufficient reduction in male numbers, and to allow the female population to die naturally, trapping of the dominant male crayfish in isolation is not recommended as a control method for the complete removal of a population.
Figure 4. The percentage change in the total crayfish population from equilibrium over a period of 20 years. The four graphs compare the effects of trapping rates of 1, 10, 100 and 1000. The coloured lines represent the different control methods.
Size biased trapping (Figure 4: dashed green line)

In practice, whilst dominant males are more likely to be caught due to their increased movement, trapping with standard Swedish Trappy Traps will result in a proportion of traps also containing females or subdominant males. We modelled this by assuming that all adults (females and dominant and subdominant males) are equally likely to be removed by trapping. If this is the case, then at low levels of trapping, the juvenile population will increase rapidly to very high levels in response to the reduction in adult population density. This increase in juvenile population is then sufficient to sustain the adult population in later years if the trapping intensity is too low (\(\zeta = 1\) or 10, Figure 4 a and b). However, a significant increase in trapping intensity will lead to an initial increase in the juvenile population density, followed by a crash as juveniles are removed, upon or soon after maturation into adults (Figure 4 c and d). At high trapping intensities this crash results in the population being eradicated. Simulations show that it is possible to eradicate such a population in less than 10 years, however this will depend on the trapping intensity used, and the specific environmental conditions.

If it is assumed that dominant males are more likely to be caught than subdominant and females then a similar increase in the juvenile population is observed and overall the population is less likely to be eradicated.

In general, simulations show that size biased trapping of all adults will result in total eradication of the population if sustained at high levels for long enough periods. Whether these levels are feasible will depend on the resources available for control.

Trapping juveniles only (Figure 4: blue line)

If the juvenile population alone is targeted, then at low trapping intensities, the initial decrease in juvenile population density is followed by an increase to a new lower equilibrium level. As trapping intensity is increased, the reduction in juvenile numbers is followed by a gradual reduction in subsequent adult generations. However, unless the juvenile population is removed at a rate such that all juveniles are removed before maturation, the population will persist. At high trapping intensities, the juvenile population will decline more rapidly than at low trapping intensities. However the time to total population removal is limited, with simulations showing that even for very high intensities it is not possible to remove the entire population within 50 years.

Unbiased trapping (Figure 4: pink line)

If all individuals are targeted for trapping, complete removal of the population can be achieved in less than 10 years at very low trapping intensities. Unbiased trapping, although obviously providing the fastest and least intensive method of population control, would require the use of several
different trap designs to target both juveniles and adults. The results shown assume that all individuals are removed at the same rate.

10.4.2. Trapping: numbers of crayfish removed

Sex biased trapping

At the lowest trapping intensity only around 0.35 dominant males per m² are removed in the first year, while an increase in the trapping intensity by a factor of 10 leads to the removal of approximately 0.65 dominant males per m² in the first year (Figure 5). However, if the trapping intensity is increased by a factor of 100 (ζ = 1000), a similar number of crayfish are removed in the first year (approximately 0.67). This implies that almost all of the dominant males available have been removed in the first year and increasing the trapping rate does not provide any benefit. In subsequent years the number removed per year remains steady with a higher trapping rate resulting in more dominant males being trapped (although this increase is not proportional to the increase in ζ). We do not get eradication for any value of ζ and in order to maintain the reduction in population density we have to maintain the trapping rate.

Figure 5. Number of dominant males removed per m² each year for 20 years of continuous, sex biased control for the simulations shown in Figure 4, at different trapping intensities.
Size biased trapping

The numbers of crayfish removed for each trapping rate, if all adults are targeted by traps, are presented in Figure 6. The assumption made is that traps are twice as likely to catch dominant males as females or subdominants, and these proportions are fixed throughout the control period. To gain a better understanding of the behaviour of the crayfish around traps, this model would need to be extended. This is however beyond the scope of this study. For size biased trapping, with low levels of control, the population can increase dramatically in density (Figure 4). Increasing the trapping intensity with this method not only increases the total number of crayfish removed, it also affects the proportions of crayfish classes removed. For a low intensity $\zeta = 10$ (green line with circles), the catch in the first year will contain more dominant males (approximately 1.3) per m$^2$ than a higher
trapping intensity of $\zeta = 100$ (red lines). This level of intensity will cause approximately 0.8 dominant males per m$^2$ to be caught in the first year.

**Juvenile trapping**

For juvenile trapping, the number removed at a trapping intensity of $\zeta = 100$ is almost equivalent to that for $\zeta = 1000$ for the first three years (Figure 7). It is only after this period, when the number of juveniles in the population has dropped significantly, that a higher trapping intensity is required to force the population into decline. However, a significantly higher trapping intensity than was tested here would be required to eradicate the population, with eradication only achieved after 50 years of constant control.

![Figure 7. Number of juveniles removed per square metre each year if only juveniles are targeted, at different trapping intensities.](image)

**Unbiased trapping**

The simulation results show that unbiased trapping is the most effective of the trapping strategies, even at very low intensities. If the numbers removed in year 1 are very low (trapping intensity $\zeta = 1$), the population is not eradicated, and high trapping numbers have to be maintained in order to continue to depress the population (Figure 8). If sufficient trapping is carried out in the first time period then the population will be eradicated, hence the number of crayfish removed after the first year is shown to be zero in Figure 8 when trapping intensity $\zeta = 10, 100$ or 1000.
Case study

All the results for trapping rate presented above are based on the number of crayfish that need to be removed per year per m$^2$. However in a real system we will simply know the total number of crayfish that have been removed. We will therefore illustrate the results of the model by using a sample lake. We assume we have a lake which has an area of 1 hectare. The baseline model, with the parameters as described above and with no control effort, predicts that in a lake of the size, at equilibrium the population will consist of around 243,000 individuals, of which around 153,000 are juveniles. In this model lake, we tested each trapping strategy, in order to predict the numbers of crayfish that should be removed each year in order to eradicate the population.

Sex biased: no eradication possible, even if we remove 6,500 dominant males in the first year.
Size biased: for eradication within 10 years we need $\zeta = 100$ which requires a first year catch of approximately 8,500 dominant males, 200,000 sub-dominant males and 170,000 females.
Juvenile biased: no eradication possible even if you remove 250,000 juveniles per year at highest trapping rate.

Figure 8. Numbers of juvenile, subdominant males, dominant males and females removed per m$^2$ for 20 years of continuous unbiased trapping. The different coloured lines represent different trapping intensities, as in Figures 5-7.
Unbiased trapping: for eradication we need to remove 150,000 juveniles, 20,000 subdominant males, 5,000 dominant males and 60,000 females in the first year. This is a total of 235,000, which is nearly the entire population. Eradication occurs after this first year of trapping.

10.4.3. Autocidal control through sterilisation

Trapping males only: no removal of females

Upon removal by trapping, it is possible to sterilise the male crayfish and return them to the water. This is done to reduce the number of successful mating attempts and thereby reduce the number of juveniles produced. We are able to compare the results of trapping and removing dominant males with those of sterilising and returning. The sterilisation techniques proposed are assumed to last approximately 3 years, with males losing sterility after this time and re-entering the dominant male class. Once sterility is lost, males are able to be re-trapped and sterilised any number of times throughout the period of control. If dominant males alone are sterilised, then the population density is reduced slightly more when compared to trapping dominant males (Figure 9).

Sterilisation of males and removal of females

Size biased trapping is likely to be the most feasible trapping strategy, and any sterilisation strategy will be largely determined by which crayfish are trapped. Therefore it is useful to compare the impacts of: (i) a combined strategy of size biased trapping and sterilisation of all males; (ii) size biased trapping and the sterilisation of dominant males only; and (iii) size biased trapping only. The combined strategy would involve sterilising both the dominant and subdominant males trapped, and removing the females. It is clear that the combined strategy is beneficial at low trapping intensities. However, at these intensities population eradication is not achieved. At the higher trapping intensities, the combined strategy results in the population being sustained for longer periods (Figure 10). However the population density recorded will be made up entirely of sterile male crayfish and once these individuals have died, the population will be successfully eradicated (Figure 11). There is very little difference in the time taken to eradicate the population with either sterilisation method or with trapping alone. Trapping has the advantage that all individuals are permanently removed from the population and can no longer contribute once trapping has ceased. If the crayfish are sterilised and returned, and the trapping and sterilising scheme is not upheld throughout the lifespan of the remaining population, then if any female crayfish were introduced or migrated into the population, we would observe a boom in crayfish due to the low population density. It is for this reason that trapping alone in the absence of sterilisation is likely to be the better option.
Figure 9. Comparison of percentage change in total population density between trapping only, and trapping and sterilising dominant males.
Figure 10. Comparison of percentage change in total population density when trapping only, trapping and sterilising dominant males, and trapping and sterilising all males.
Figure 11. Comparison of percentage change in population density between trapping only, trapping and sterilising dominant males, and trapping and sterilising all males (as Figure 10), ignoring the sterile males in the population density.
To summarise the results in the previous section we compare all trapping and sterilisation rates, comparing how high the trapping rate would have to be and how quickly the population could be eradicated for the different methods of control (Table 3). The trapping rate is a measure of trapping effort i.e. the product of number of traps and frequency of emptying.

Table 3. Comparison of sterilisation and trapping methods.

<table>
<thead>
<tr>
<th>Trapping Method</th>
<th>Time to Eradication</th>
<th>Trapping Rate Required</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex Biased</td>
<td>50 Years</td>
<td>2000</td>
</tr>
<tr>
<td>Size Biased</td>
<td>10 Years</td>
<td>35</td>
</tr>
<tr>
<td>Juvenile</td>
<td>50 Years</td>
<td>4600</td>
</tr>
<tr>
<td>Unbiased</td>
<td>10 Years</td>
<td>3.2</td>
</tr>
<tr>
<td></td>
<td>5 years</td>
<td>3.6</td>
</tr>
<tr>
<td>Sex Biased Sterilisation</td>
<td>50 Years</td>
<td>3600</td>
</tr>
<tr>
<td>Sterilisation &amp; Size Biased</td>
<td>45 Years</td>
<td>70</td>
</tr>
<tr>
<td>Trapping</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

10.4.4. Physical control

Figure 12. Total population over time (years) where 80% of population were culled at t=50 years (single event).

There are a number of control methods that do not happen continuously, but rather are one off reductions in crayfish numbers. These include electrocution, draining water bodies and some forms of short lived biocidal control. In these cases there is an instantaneous reduction in the population across all age classes. It should be noted that we define eradication to be a reduction in the population to 1% of its equilibrium density. Figure 12 shows the impact of killing 80% of the
population after it has had chance to settle to equilibrium. The reduction is very short lived due to
density dependence in the model, which means that the population recovers very quickly. Unless we
kill 100% of the population we cannot eradicate the crayfish with one treatment.

Multiple treatments
If treatment (culling) occurs every year for 5 years, the population can be controlled. However if the
efficacy of the treatment is not high enough then the population will not be eradicated (Figures 13
and 14); a very high death rate (97%) is required to eradicate the population within 5 years (Figure
15). Table 4 presents the impact of varying the percentage of individuals killed, and the frequency of
treatment, and shows the duration of treatment in years that would be required to achieve
eradication.

Figure 13. Total population over time, where 80% of the population were culled every year for 5 years, starting at t=50 years.

Figure 14. Total population over time, where 96% of the population were culled every year for 5 years, starting at t=50 years.
Table 4. Approximate time in years to eradicate the population for different treatment frequencies and different efficacies of treatment assuming treatment continued until the crayfish were eradicated

<table>
<thead>
<tr>
<th>Percentage killed</th>
<th>Every 10 years</th>
<th>Every 5 years</th>
<th>Every 2 years</th>
<th>Every year</th>
<th>Every 6 months</th>
<th>Every 3 months</th>
</tr>
</thead>
<tbody>
<tr>
<td>50%</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
</tr>
<tr>
<td>60%</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
</tr>
<tr>
<td>70%</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
</tr>
<tr>
<td>80%</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>9</td>
</tr>
<tr>
<td>90%</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>1.5</td>
<td>1</td>
</tr>
<tr>
<td>95%</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>96%</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>4</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>97%</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>99%</td>
<td>Never</td>
<td>Never</td>
<td>Never</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Mixed efficacy

When water bodies are drained, it is possible that some adult crayfish will burrow into the banks and survive. We therefore ran the model where 98% of juveniles and 80% of adults are culled. Frequent applications of this treatment are required for it to be successful (Figures 16 and 17).
Figure 16. Total population over time (years) showing the effect of annual treatment when 98% of juveniles and 80% of adults are culled.

Figure 17. Total population over time (years) showing the effect of treatment every six months when 98% of juveniles and 80% of adults are culled.

Figure 18. Graphs showing percentage change in population over time. From left to right, the graphs show how increasing natural decay of parasite causes different dynamic behaviour of the population.
10.4.5. Biological control

Sterilising pathogen

Here we investigate the effectiveness of controlling the population through the release of a male sterilising pathogen, such as a spiroplasma. As this is a speculative control strategy which has not been tested or researched in depth, there is little data with which to parameterise the model. The model therefore aims to indicate general trends in the behaviour of such a parasite.

- If the parasite decays very slowly in the environment relative to uptake by crayfish, then the crayfish population will decrease over time with approximately 90% of the total population being removed within 20 years.
- If the rate of decay increases then it is possible that the population will oscillate greatly, although the oscillations may obtain a maximum at a lower density than in the absence of control.
- If the parasite has a very high rate of decay, then the population may be reduced significantly over a short time scale, however the parasite will die out and the population return to its initial equilibrium in the long term.

The results (Figure 18) demonstrate a range of possible dynamics upon the addition of a parasite. It seems that in most cases the parasite will mediate the population density, however its presence may lead to cycles of high population densities followed by crashes. Further investigation into the epidemiological properties of the pathogen proposed, and the infection of the crayfish population is needed to give a more accurate picture of the possible risks or benefits of biological control in this way.

10.5. Sensitivity analysis

As discussed earlier the values of many of the parameters are variable in the literature, and density dependent constraints in particular are not well understood. Sensitivity analyses were therefore carried out to identify which parameter estimates the model is most sensitive to. The percentage change in each parameter was compared with the percentage change in each of the classes of the crayfish population, and the total population. It can be seen that the model is most sensitive to the development rates, the egg laying rate and the density dependent parameters associated with them (Table 5).
10.6. Conclusions from the modelling exercise

Modelling has shown that sex biased trapping, which is how the initial stages of current trapping regimes might operate if dominant males discourage other adults from entering traps, will never result in eradication. Trapping adults could result in eradication within ten years if trapping is intensive enough. However if trapping rates are low, this could cause an increase in the population due to the density dependent factors which are believed to exist in this system. Trapping juveniles will not result in eradication. Not surprisingly, trapping all life stages equally would be the most successful strategy, but this would require new trap designs, or a combination of different designs used simultaneously. Sterilisation has a bigger impact at lower trapping rates, but at high trapping rates it is less successful. Indeed the population is eradicated more slowly as sterile males continue to survive in the short term, although they would die off eventually. The results from the model describing trapping could also describe predation or long lasting biocidal control.

Electrocution and water draining has the potential to be a successful control mechanism as long as treatment occurs frequently enough and is continued for a sufficient duration. If treatment is stopped too soon, the population will quickly recover to its original size. In addition there are issues with this method in terms of the damage done to other species. Biological control, illustrated here with the example of the spiroplasma, could succeed in eradicating populations, but we would need to know much more about the system to have confidence in this method.
As discussed earlier, there are number of biological assumptions within the model, some of which are reasonable and some of which require further investigation. We are confident that the results presented here are qualitatively (if not quantitatively) robust, and are realistic in terms of the relative impacts of the different treatment regimes. However there are a number of areas of the biology of the system which require further work and there are some areas of the modelling which need to be expanded further if we wish to develop a realistic control policy.

10.7. Recommended further developments

There are two major ways in which the modelling of this system could be developed. The first is to model the trapping more explicitly, both in terms of quantifying the number of traps used, and how animals respond to them e.g. including that dominant males are more likely to be caught initially but later there is a switch to other adults. This is approximated in the models presented here, but an individual based modelling approach may provide greater accuracy. This may require additional experimental work to be carried out. The second significant way in which the models could be improved is to add spatial factors. At the moment the models describe a closed population which is spread evenly across a lake. In a river situation, there may be immigration of crayfish into treated areas and so it will be much more important to think about the spatial position of sites and their connectedness. The incorporation of this into the model could be based on real river systems and the sites of known crayfish populations.

In the current model, reproduction and death happen continuously throughout the year. Clearly this is not accurate, and for discrete events like electrocution, the time of treatment might be critical to effectiveness. This could be tested using a seasonal model. Finally, it would be interesting to study other treatment regimes or combinations of regimes, for example, biocidal control which has a sterilising effect or electrocution followed by trapping.

10.8. Data deficiencies

There are a number of questions which arise from this work, stemming from gaps in our knowledge of the biology and life history of crayfish. This makes the development of population models difficult as many of the parameters have to be based on ‘best guesses’. This in turn leads to difficulties in interpreting output from the models and how they should be applied. More information on population dynamics and biology is required. This will allow more robust models to be developed, and a greater understanding of how the application of control mechanisms will affect the overall population. This will also inform which age class should be targeted by a control mechanism for maximum effect. This in turn will assist in the development of long term control programmes with
the potential to lead to the eradication of the species. Additional information is required specifically on:

- Mating behaviour and mate selection in the wild
- Rate of mating and levels of reproduction within a population
- Fecundity and its determinants
- If density dependence affects population dynamics
- Spiroplasma transmission and development

The sensitivity analysis tells us that the model output is sensitive to the development rates of the juveniles and subdominant males and, in particular, the density dependent parameters. We have included density dependence in egg laying rates, three development rates and adult and juvenile death rates. There is some evidence that density dependence does act in all of these places, but it has not been quantified. More detailed information would be very helpful in the next stage of the modelling process.
11. Discussion

This review highlights a number of methods that could be developed to control and potentially eradicate populations of invasive species of crayfish in GB. However, there are some key areas that require further investigation and development before a robust control programme can be developed. Although the review is intended to relate to all invasive crayfish species currently in GB, signal crayfish is the most problematic of the non-native crayfish species in GB, therefore has been used as the model species and is discussed in the following sections.

11.1. Mechanical removal

Despite commercial exploitation of crayfish populations and more recent attempts to control invasive crayfish populations by mechanical control, there is limited information on the effects of trapping on the population. Determining the maximum sustainable yield (MSY) of crayfish populations may aid significantly in determining the level of mechanical removal required to control and/or eradicate a population. However, the removal of crayfish from a water system using mechanical means will always be labour intensive and a long term investment, despite various methods of improving the success of trapping (see below for discussion). Given the demand for crayfish as a product for human consumption, there will always be those that wish to remove crayfish for commercial gain, which will involve trapping populations below their MSY. Trapping crayfish populations below their MSY may cause an increase in the population, as seen in the model presented in this report. This may be as a result of density dependence. The effect may not be as extreme as that presented in the model, but does appear to be a factor present in crayfish populations. Despite possible concerns of the effects of commercial trapping on crayfish populations and the potential for new populations to be seeded, such commercial enterprises bring in revenue, and if provided with more effective guidance could result in a self sustaining long term control of crayfish.

The majority of trap designs used for crayfish capture are those used for commercial exploitation. It has been observed that these traps predominantly remove large adult males, however it is not understood if this is a function of the trap (i.e. if a large adult male enters the traps then other, smaller animals will avoid it), or a function of the population (i.e. these are the most abundant proportion of the populations), or a combination of both. Although the true effect that these traps have on a population is not fully understood, it is likely that they are not effective as other trap designs at controlling crayfish, and do not impact on the population as a whole. Traps that can remove large numbers of multiple life stages are likely to be more effective at eradication or long term suppression of a population, as seen in the model outputs presented in this report. The
development of a trapping programme where different trap types are used to target different life stages throughout the trapping programme may also be required. Bait has also been shown to have a significant impact on capture rates; the effectiveness of different bait types may vary with life stage and this need further investigation. While the model used an enclosed population (therefore avoiding complication with issues such as immigration) many crayfish populations are found in riverine habitats where immigration intro control areas can take place. Possible issues of movement of animals into the area of control will have to be considered. This may be overcome using buffer zones, if the trapping of the whole catchment is not feasible. Due to the long term nature of trapping as a control mechanism and the considerable related costs it would seem unlikely that any one organisation could fund such work. Involvement and support of stakeholders and the voluntary sector would be required, e.g. undertaking the work under guidance and support from experts. It is therefore recommended that:

- A method of calculating MSY for crayfish populations is developed.
- The crayfish trapping industry is engaged with, to discuss control mechanisms, trapping regimes and trap design.
- An economic analysis of the value of the crayfish industry in GB is carried out.
- The effects of exploitation (at varying degrees) on crayfish population dynamics is determined.
- The most effective trap design for the removal of different life stages of crayfish is established.
- The most effective bait to attract crayfish is determined.
- Effectiveness of trapping regimes is investigated and a trapping regime is designed that that will lead to the overall reduction of crayfish populations.
- A programme of trapping is developed that is easily followed and applied by stake holders and the voluntary sector under guidance and advice from experts.

11.2. Physical control

Other potential control mechanisms such as draining, habitat modification and barriers have not been extensively examined. However, the studies that have examined the techniques suggest that they are effective at dramatically reducing numbers and limiting spread, but not at control and/or eradication. There are also potential long term environmental issues with the application of any of these mechanisms. However, such techniques could still be applied on an ad hoc or case by case basis in combination with other mechanisms, and should therefore not be ruled out.
Electrocution has been used in the removal of crayfish in the form of electrofishing for a number of years. Robin McKimm has taken this a step further with the development of a system that would electrocute whole stretches of a river system at once. The drawback is that this is a non-selective process with limited application due to environmental requirements. It is therefore difficult to see much difference in the application of this mechanism to that of a biocide, with the only real differences being potentially in the costs, and in the perception of the methods by the public. McKimm has suggested ways in which this mechanism can be improved upon. An attempt was made to model the effects of draining and electrocution on a crayfish population. Both have the potential to control the modelled population, but would need repeated application of the technique, which may not be possible, especially in the case of draining. It is therefore recommended that:

- Draining, habitat modification and barriers are examined as potential mechanisms of control on an ad hoc basis e.g. obtain information from British Water Ways on the habitat modifications that they had undertaken as well as the barrier installed in Scotland.
- Electroflection is considered in terms of how cost effective the process is in comparison to biocide application and how many populations electroflection would be effective against.

11.3. Biological control

Predators such as fish have been shown to assist in the control of crayfish populations, but have to work in conjunction with other methods if eradication is to be achieved. There is evidence to suggest that eels may play a role in the control of signal crayfish. It is hoped that the work that is currently being undertaken to help dwindling eel populations will also aid in the control of crayfish.

This review has covered the major groups of pathogens associated with non-native crayfish. It has deliberately not included those groups of parasites that are unlikely to have any utility as biological agents either due to their lack of demonstrable pathogenicity, or in the case of e.g. digeneans and acanthocephalans, require numerous hosts in the completion of their lifecycle. Bacterial infections of crayfish tend to be opportunistic and non-specific, and several potential agents (e.g. *Vibrio* spp.) cause illness in humans. Fungi tend to also be non-specific and there is generally a lack of proven mortality. The following pathogens show promise as control agents:

- The signal crayfish virus, *PIBV*. The virus may be associated with mortalities, appears geographically isolated and may well be host specific. Furthermore, at least in the short term, signal crayfish established in Great Britain may show no resistance to the virus given their limited exposure over time.
• A bacterial group known as the spiroplasmas. These are sex distorters or male killing agents, and similar bacteria show promise as biological control agents in terrestrial systems (Floate et al., 2006). Most importantly, methods exist for the molecular and ultrastructural identification of the bacteria and for their culture. Further investigation is recommended.

• A fungus *Thelohania contejeani* may have potential, but little is known about it so much work would need to be done.

The impacts of using a spiroplasma as biological control were modelled. Despite a lack of data, which makes it is difficult to draw firm conclusions, initial results suggest it may be effective. It is therefore recommended that:

• The lifecycle and requirements of these pathogens are investigated and host specificity confirmed.

• The geographical spread of the selected agents is studied, and it is ensured that methods are available to neutralise these agents once the target host has been eradicated.

• In addition, the development of methods to mass produce the selected control agents may be necessary.

### 11.4. Biocidal control

A number of biocides have been used effectively in the control of invasive crayfish, but all have the drawback of not being specific in their action. This results in unwanted damage to wildlife in the treated area and considerable care is required in their application. A number of chemicals have been suggested in this report which could affect crayfish and only a limited number of other species: Pyriproxifen, Fenoxycarb, Lufenuron, Cyromazine, Methoxyfenozide, and Chlorantraniliprole. Their delivery could be made even more targeted through appropriate trap and bait design. Given the 6 compounds suggested as potential candidates, it is recommended that:

• The intrinsic activity of these 6 compounds is evaluated upon signal crayfish in the laboratory. Levels of efficacy can then be determined for each molecule. It is recommended that the compounds are administered as bait, capitalising on their ingested activity.

• Once selection has been made (efficacy vs. impact), the HSE needs to be approached for emergency licensing of the compound as a biocide. See below from HSE web site on emergency registration. “Under certain circumstances it is possible for Member States to authorise the use of a plant protection product for a period not exceeding 120 days, for a limited and controlled use where such a measure is necessary because of a danger which cannot be contained by any other means as set out in Article 53 of Regulation (EC)
1107/2009. When issuing such emergency authorisations the MS concerned must inform the other MSs and the Commission of the authorisation given, detailed information about the situation and any measures taken to ensure consumer safety. If necessary the Commission will take a decision as to whether the MS can extend or repeat the emergency authorisation or not or whether the authorisation must be amended or withdrawn. Applications for emergency authorisation cannot be made for plant protection products containing or composed of genetically modified organisms unless such release has been accepted in accordance with Directive 2001/18/EC. Agreement from the Advisory Committee on Pesticides (ACP) would be required before authorisation could be agreed within the UK. Authorisation would be given for a maximum period of 120 days and as such it is a temporary solution to a pest problem for which a more permanent solution must be found.

- The application proposed is not, however, for plant protection and so an authorisation would need to be made under the Biocidal Products Directive under Product Type 18 (insecticides, acaricides and to control other arthropods) where its use would need to be reviewed. It is not clear if there is an equivalent emergency licensing under the Biocides Directive. However, use of a biocidal material in any experiment or test in UK which may involve or result in the release of that product/active substance into the environment can be authorised by application for a Biocidal Products Research Application.

- With approval from the HSE, the company who market the product should be approached. Without explicit approval by the company for this off label use, practical use in the field will be difficult. The company will be concerned with risk to the perception of the product and the perception of the company from a use which is not economic (from the company’s perspective). This could be mitigated by emphasising partnership between Defra and the company for the benefit of the UK (doing the right thing, not just pursuing profit). They may wish to audit the stewardship principles in the proposed use.

Despite the promising nature of these chemicals, there are still some environmental issues to consider:

- If administered as bait, the compound may leak out of the bait before it is ingested. This risk can be mitigated by clear identification of the physical properties of the chosen compound and the appropriate desorption control (oil coating, gelatine binding etc).

- The compound may be excreted by the target organism. However, it is likely that only small quantities of the compound will be excreted by any individual at any one time.

- There may be impacts on the food chain if individual target organisms are eaten by scavengers or predators. The severity of the impact will be limited by:
The bioavailability of the compound within the body (the more lipophilic molecules may be bound to tissues, rendering them not bioavailable to a predator when eaten).

- The stability of the molecule in aquatic environment i.e. whether it is prone to aqueous hydrolysis.

- It is possible that target organisms may eat individuals killed by chemical treatment, so prolonging the effective chemical control (the palatability of the chemical would need to be tested).

11.5. Autocidal control

Although male sterilisation is a method that has been used in integrated pest management for some time with great success, there are some questions over to how the method can be best applied to crayfish populations and how it will ultimately affect population dynamics. The model shows that it may be an effective way of enhancing trapping programmes, with the only potential drawback of the technique being that there is some persistence of the population in the form of sterile males. The removal of 1st and 2nd pleopods may be a method that could be effectively amalgamated into existing trapping programmes enhancing their overall success.

Pheromones have been used in integrated pest management for some time, but not yet for the control of aquatic pests. This is partly due to the availability of commercial funding in this area, and therefore the lack of advancement in the identification of pheromones used by aquatic pests, and methods of releasing them. Despite the potential success in using pheromones as a control agent, the long and expensive development process makes this option less feasible than other methods. It is therefore recommended that:

- The effect of 1st and 2nd pleopod removal on male behaviour is examined in the laboratory.
- The effect of this method on fecundity is determined.
- Small scale field trials should be conducted to determine the impact of treatments at the population level.

11.6. Legislative control

It is concluded that the current legislation controlling non-native crayfish is only partially achieving its intended outcome, and in particular is failing to prevent the spread of signal crayfish within GB. It is believed that a re-cast of existing legislation and the use of recently created legal instruments could together help address the problems which current legislation fails to regulate. It is recommended that:
• New controls are introduced under Article 14 of the Wildlife and Countryside Act 1981, to regulate the sale and advertisement of non-native crayfish.
• The Prohibition of keeping of Live Fish (Crayfish) Order 1996 is amended to regulate crayfish imports and suppliers of signal crayfish.
Appendix A

Total Model

\[
\frac{dJ}{dt} = \sigma eF_G(\lambda - s_1A) - J_M(\gamma_1 - s_2A) - J_M(\mu_j + s_3N) - \delta J_M
\]

\[
\frac{dJ_F}{dt} = (1 - \sigma) eF_G(\lambda - s_1A) - J_F(\gamma_2 - s_2A) - J_F(\mu_j + s_3N) - \delta J_F
\]

\[
\frac{dS_M}{dt} = J_M(\gamma_1 - s_2A) - S_M(\alpha - s_3A) - S_M(\mu + s_4A) - \theta_2 \zeta_S
\]

\[
\frac{dM_D}{dt} = S_M(\alpha - s_3A) - M_D(\mu + s_4A) - \beta F M_D + \varepsilon M_G - \theta_4 \zeta M_D + \kappa M_S
\]

\[
\frac{dM_S}{dt} = \theta_1 \zeta(M_D + M_G) - M_S(\mu + s_4A) - \beta F M_S + \varepsilon M_{SG} - \kappa M_S - \omega M_S
\]

\[
\frac{dM_G}{dt} = \beta F M_D - M_G(\mu + s_4A) - \varepsilon M_G - \theta_4 \zeta M_G
\]

\[
\frac{dM_{SG}}{dt} = \beta F M_S - M_{SG}(\mu + s_4A) - \varepsilon M_{SG} - \omega M_{SG}
\]

\[
\frac{dF}{dt} = J_F(\gamma_2 - F(\mu + s_4A) - \beta F(M_D + M_S) + \varepsilon F_G + \varepsilon F_S - \theta_3 \zeta F
\]

\[
\frac{dF_G}{dt} = \beta F M_D - \varepsilon F_G - F_G(\mu + s_4A) - \omega F_G
\]

\[
\frac{dF_S}{dt} = \beta F M_S - \varepsilon F_S - F_S(\mu + s_4A) - \omega F_S
\]

The 10 equation model given above is the complete model used throughout this report. Those sections highlighted are additions to the baseline model and are included depending on which control strategy used. The parameters used in each of the control strategies used is summarised in the table below. For all constant control methods except juvenile trapping, the trapping intensity is given by \(\zeta = 1, 10, 100, 1000\).

<table>
<thead>
<tr>
<th>Control Strategy</th>
<th>Parameters Used</th>
<th>Values given</th>
</tr>
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<tbody>
<tr>
<td>Sex Biased Trapping</td>
<td>(\theta_1)</td>
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</tr>
<tr>
<td>Size Biased Trapping</td>
<td>(\theta_1)</td>
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</tr>
<tr>
<td></td>
<td>(\theta_2)</td>
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</tr>
<tr>
<td></td>
<td>(\theta_3)</td>
<td>0.5</td>
</tr>
<tr>
<td>Juvenile Trapping</td>
<td>(\delta)</td>
<td>1, 10, 100, 1000</td>
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<tr>
<td>Unbiased trapping</td>
<td>(\delta)</td>
<td>1, 10, 100, 1000</td>
</tr>
<tr>
<td></td>
<td>(\omega)</td>
<td>1, 10, 100, 1000</td>
</tr>
<tr>
<td></td>
<td>(\theta_1, \theta_2, \theta_3)</td>
<td>1</td>
</tr>
</tbody>
</table>
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