Literature review of the ecology of the signal crayfish *Pacifastacus leniusculus* and its impacts upon the white clawed crayfish *Austropotamobius pallipes*

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1. INTRODUCTION

1.1 General

This literature review concerns the ecology of the signal crayfish *Pacifastacus leniusculus* and its impact on the habitat it has been introduced to and on the white clawed crayfish *Austropotamobius pallipes*. Information is given on the ecology of both species to enable comparisons of the two. Where relevant, the ecology of and interactions between other species has been quoted, when it is missing for these two species.

1.2 Sources of references

The majority of references were obtained from a computerised literature search on crayfish and, in particular, on the signal and white clawed crayfish. References were obtained from the Aquatic Sciences and Fisheries Abstracts 1979-1990 and from the Freshwater Biological Association's current awareness files 1970-1991. A database containing 190 records was compiled. Inter-library loans were obtained for the references not held by the Freshwater Biological Association's library at the Ferry House. Examination of the references showed that some items were irrelevant, but identified further references of relevance. These latter references were also obtained, and included in the Bibliography, which contains a total of 162 items.

2. THE NATIVE OR WHITE CLAWED CRAYFISH

The white clawed crayfish is also a member of the Astacidae family, along with the other native european species. It occurs in western Europe, including the British Isles (Laurent, 1988; Lowery & Holdich, 1988). Native european crayfish populations are of post-glacial origin and recolonised Europe from southerly latitudes. There is some doubt whether the white clawed crayfish reached Ireland naturally and it may have been introduced by man (Albrecht, 1983; Holdich, 1988), although Laurent (1988) disagrees. Its current distribution extends from 56°N in Britain to 38°S in Spain, and from 8°W in Ireland to 16°E in eastern Europe (Laurent, 1988), and until recently was the only species of crayfish to be found in the United Kingdom and Ireland.

The number of habitats inhabited by this species is currently in decline, because of the ravages of the crayfish plague, and there is growing concern for its preservation (Holdich & Rogers, 1992). Most crayfish management measures are aimed at preserving this and other native european species (Westman & Westman, 1992).

The white clawed crayfish is protected under the Wildlife and Countryside Act

1981, and this species was listed and protected under Schedule 5 of that act in 1986. It is one of only four British, non-insect invertebrates listed and protected under Appendix III of the Bern Convention on the Conservation of European Wildlife and Natural Habitats.

3. THE AMERICAN OR SIGNAL CRAYFISH

The signal crayfish is a member of Astacidae family, which is the same family that all native european species belong to. It has a native range restricted to the north west of America, west of the Rocky Mountains (Hobbs, 1988). It is believed to have originally consisted of three isolated subspecies (Hobbs, 1988), these being *leniusculus*, *klamathenis* and *trowbridgii* (Lowery & Holdich, 1988). However, transplants by man mixed the allopatric populations of these three subspecies, resulting in their widespread hybridisation, and although individual characteristics of each one occasionally turn up in single populations it is regarded as being one species (Hobbs, 1988).

From its native range it was transplanted to California at the end of the 19th century (Riegel, 1959; Abrahamsson & Goldman, 1970), probably from Nevada (Holdich, 1988). It was thought to have been originally transplanted to provide additional food for fish introduced to the lakes of that region. However, it has been so successful, in its own right, that commercial fisheries have existed in North America, for some time and one is described in Oregon, which commenced in 1893 (Miller & Van Hyning, 1970), and another in the Sacramento River (McGriff, 1983).

When the economically important crayfish populations of Europe were decimated by the crayfish plague in the early 20th century a number of North American species were introduced in an attempt to replace stocks. The signal crayfish was one of these species and was introduced to Europe in the 1960's (Lowery & Holdich, 1988), where it now inhabits a wide variety of habitats.

4. HISTORY OF SIGNAL CRAYFISH INTRODUCTIONS

Once the crayfish plague had spread through Europe destroying many of the economically important native populations there was a demand for a replacement species, particularly for the noble crayfish *Astacus astacus* for which there was a significant fishery in Sweden. Replacement species were required to be resistant to the plague. Although North American species are carriers of the disease, and are known to be infected by it in their natural environment (Smith & Soderhall, 1986) they are resistant, and a number of species have been introduced. The first introductions of signal crayfish to Europe occurred in 1960 (Holdich, 1988) and came from California. Initially imports were to Sweden, but these were ceased when it was decided that the risk of transferring disease and parasites was too great. Signal crayfish were then produced internally (Brinck, 1983) for use in Swedish waters, although exports of juveniles were made to other european countries.

During the late 1970's and early 1980's signal crayfish were introduced to many water bodies for farming in Britain (Holdich, 1988). This was in spite of warnings of the potential consequences, from competition and the introduction of the crayfish plague, of allowing alien crayfish into this country (Holdich & Goddard, 1978; Bowler, 1979).

Escape from the farms is common and these escapees have been very successful at establishing populations in the wild and the two species distribution overlaps considerably (Lowery & Holdich, 1988). In 1991 there were at least 23 wild populations of signal crayfish in England and Wales (Holdich & Reeve, 1991). It is now illegal to introduce this species into the wild under the Wildlife and Countryside Act 1981.

5. ECOLOGY OF THE WHITE CLAWED CRAYFISH

5.1 Habitat and habits

The white clawed crayfish is an epigean species confined to streams and lakes. It occurs in many water bodies including fast moving rivers, canals, lakes and reservoirs. Populations exist in habitats ranging from small shallow streams (< 3m deep) (Arrignon & Roche, 1983) to slow flowing deep rivers (Jay & Holdich, 1981; Duffield, 1933), and small shallow lakes (Moriaty, 1973). Commonly, all habitats must have a sufficient calcium content, reach sufficient temperatures, not be polluted and have sufficient refuges in terms of stones and tree roots.

Crayfish cannot survive in waters without sufficient dissolved calcium, needed for construction of their hard protective exoskeletons. In the British Isles the white clawed crayfish is only found in waters with a pH of between 7 and 9 and with a calcium content above 5 mg l^{-1}. Crayfish are absent from rivers draining catchments with hard insoluble rock geology (Huxley, 1880; Jay & Holdich, 1981).

Growth is temperature dependent in crayfish. Below 10^{o}C first year white clawed crayfish do not moult or grow (Pratten, 1980). Thus it has been recorded as avoiding cold areas near springs or high altitudes (Laurent, 1988). With the exception of its lower temperature restriction it is capable of acclimatising to a wide variety of temperatures (Bowler, Gladwell & Duncan, 1973), and its range thus extends from southern Spain and Italy to northern Britain (Hogger, 1988).

Crayfish have a requirement for refuges and therefore, in disease free natural populations, carrying capacity and population size is controlled by the availability of suitable habitat. For a species whose burrowing activity is limited to excavations in the stream beds and banks (Hobbs, 1988), such as the white clawed crayfish, this is largely the amount of refuges provided by the substratum. Where the amount of refuges is very great, food may become a limiting factor, but usually this will only occur in artificial habitats (Hogger, 1988). Requirements for cover are confirmed by the animals greater abundance in reaches flowing on a north-south line (Duffield, 1933). Refuges need to be in minimum depths of between 10 and 20 cm depending on the size of the crayfish (Daguerre de Hureaux & Roqueplo, 1981). Crayfish size is also important in determining the use of different sized refuges and there is curvilinear relationship between stone surface area used for refuges and crayfish size (Foster, 1993).

Within habitats crayfish populations can exhibit extreme changes in population size and density (Momot, Gowing & Jones, 1978). Declines can be caused by disease, altered habitat, pollution and predation. The capacity of a river to support crayfish can be greatly reduced by dredging practices (Hogger & Lowery, 1982), which tends to denude river habitat of refuges.

5.2 Age and growth

There is a great deal of variation between published works on the parameter used for expressing size in crayfish. The two most commonly used are total body length and carapace length. In this review carapace length (CL) is used almost exclusively, to maintain consistency.

All crayfish have a massive protective exoskeleton and can only increase in size by shedding this during the process of moulting or ecdysis. During this process the exoskeleton becomes soft and the crayfish are extremely vulnerable to predation and cannibalism. Thus the moulting process of crayfish tends to dominate their life (Lowery, 1988).

During adult stages crayfish moulting is often synchronous. It is thought that this may be a mechanism to reduce the incidence of cannibalism (Pratten, 1980). During this period it is difficult to catch animals in baited traps as they are not feeding. There is less evidence of synchrony in the juveniles (Lowery, 1988). The moult increment, which is the increase in carapace length at moulting, tends to decrease as a percentage of pre-moult carapace length with succeeding moults (Brewis & Bowler, 1982; Chaisemartin, 1983).

Calcium is critically important to the crayfish during the moulting process. Despite the resorption of the calcareous components from the exoskeleton during ecdysis, this only supplies about 10% of the calcium required for hardening the new exoskeleton (Greenaway, 1985). After moulting this deficit must be made up rapidly, and calcium has to be adsorbed from the surrounding water. This explains the requirement for waters with a calcium content above 5 mg l^{-1} (Jay & Holdich, 1981).

Newly hatched white clawed crayfish undergo three moults while still in the care of the female. The young animals leave the female when they are about 3.5 mm (CL), typically in May or June, and undergo seven or eight moults in their first year depending on temperature (Pratten, 1980). They cease feeding during the winter and become quiescent. Once the temperature is high enough in the spring they become active and in their second year may go through four or five moults. This process is repeated each summer, except that the number of moults declines in subsequent years, until it reaches only one moult per year (Pratten, 1980).

In females the number of moults declines to one per year as soon as they reach maturity, because they cannot moult during the spring period, when they are carrying eggs. The restriction on growth means that the females grow more slowly than the males once maturity is reached (Lowery, 1988). Sexual maturity can be reached in the second or third year, or as late as the fifth and sixth years in colder latitudes (Brewis & Bowler, 1982)

Differential growth of crayfish morphology often takes place at sexual maturity. The abdomen of juveniles and males grow almost isometrically, but in females the abdomen increases markedly in relative width at the puberty moult (Rhodes & Holdich, 1979; Hogger, 1984, quoted by Lowery 1988). By comparison, chelar growth in juveniles and females is almost isometric, but at the puberty moult in males there is a disproportionate increase in the size of the chelar (Rhodes & Holdich, 1979; Lowery, 1988).

Some published data are available on the size of the white clawed crayfish at various ages from different waters. At three years, for example, they had reached 29 mm (CL) in France (Demars, 1979) and 28 mm (CL) (Pratten, 1980) in southern England. In England males have reached maximum lengths of 60 mm (CL) and females 56 mm (CL) (Laurent, 1988). Similar maximum lengths have been recorded in France (Laurent, 1962) and Spain (Coll Aguado, 1986, quoted by Laurent 1988).

The moulting process, and therefore growth, is influenced by the nutritional status of the crayfish, as well as temperature and light (Lowery, 1988). Temperature has an important impact on growth. First year white clawed crayfish did not moult or grow at temperatures below 10^{o}C (Pratten, 1980), although feeding has been observed in this species at lower temperatures (Hogger, 1984, quoted by Hogger 1988) but there was no significant difference in growth rate at 15^{o}C and 20^{o}C (Pratten, 1980). Optimum growth rates were found to be at 21.4^{o}C for white clawed crayfish (Firkins & Holdich, 1993).

The numbers of and periods between,, moults will vary between habitats and latitudes (Lowery & Holdich, 1988). The growth rate and number of moults per year is reported to be slower in cooler waters, such as in Northumbria

(Brewis & Bowler, 1982), and more frequent in southerly latitudes (Brown & Bowler, 1979; Pratten, 1980).

Density may be a factor in determining growth rates in crayfish either by influencing the availability of food, or increasing behavioural interaction such as territory defence. Studies of other species such as *Orconectes virilis* have shown that in unexploited populations the presence of large males restricted the growth of the females and juveniles, but when they were removed, recruitment and the growth of females increased again (Momot & Gowing, 1977 a, b & c).

Brewis (1978) and Brewis & Bowler (1983) found that there were two types of mortality occurring in crayfish. One was a short duration mortality associated with moulting and the other was a steady mortality over the winter torpid period, which could reduce population sizes by 40-60%. Juvenile mortality was 15% per week during moulting and was probably caused by cannibalism. Typically the white clawed crayfish are recorded as living a maximum of ten to thirteen years (Brown & Bowler, 1978; Pratten, 1980).

5.3 Food and feeding

Crayfish are an important part of the food webs of the habitats in which they live. They tend to feed at night resting in their hiding places during the day (Laurent, 1988). They utilise a wide variety of foods and can aid the transfer of energy from lower trophic levels to higher economically important animals such as fish, which prey on them (Momot, Gowing & Jones, 1978; Momot, 1984), although in at least one case crayfish have been shown to compete with fish for invertebrate food and reduce the growth rate of the fish (Hepworth & Duffield, 1987).

They have been shown to be polytrophic, being herbivores, omnivores, predators and detritivores (Lorman & Magnusson, 1978; Hogger, 1988; Huner & Barr, 1980). They eat detritus, gaining nutritional value both from digesting the epiphytic fungus and bacteria which decompose the detritus, as well as directly from the plant material (Wiernicki, 1984). Their importance in the food chain is emphasised by their being called the rubbish collectors, converting waste to protein (Karlsson, 1977). Additional food items include macrophytes and small prey items such as invertebrates, fish and crayfish. Animal food is important for supplying some amino acids (Huner & Barr, 1984).

The relative composition of food types and feeding behaviour varies with age and probably between species (Goddard, 1988). Both laboratory trials and field studies have shown that there is a shift in predominant food material with age, from invertebrate prey in the young stages to vegetation and detritus in the adult stages of the white clawed crayfish (Reynolds, 1979a). This may partly be due to the ability of the more agile and active juvenile crayfish to capture mobile animal prey (Abrahamsson, 1966). There is also evidence that juveniles can filter feed, by use of the first maxilliped and maxillae, capturing algae and other suspended organic matter. It has been proposed that this method reduces the risk of predation during ecdysis, since it does not require foraging activity (Budd, Lewis & Tracey, 1978; 1979).

Studies of adult stomach contents have revealed that generally submerged vegetation is consumed more readily than emergent vegetation, possible because of the thick stemmed nature of the latter (Abrahamsson, 1966, Goddard, 1988). The white clawed crayfish has been shown to prefer soaked tree leaves over the aquatic plants *Elodea* and *Callitiche* or terrestrial plants *Stellaria* and Gramineae. Detritus has been shown to account for between 13.2 and 21.6%, by weight, of food consumed (Momot, Gowing & Jones, 1978).

Cited carnivorous prey items include molluscs, insect larvae, worms and crustaceans (Abrahamsson, 1966; Moriarty, 1971; 1973; Mason, 1975; Reynolds, 1979a), although cannibalism on juveniles and moulting and weakened individuals is a significant aspect of crayfish feeding, particularly when there are large numbers of adults present (Abrahamsson, 1966; Mason, 1979).

Crayfish populations often form a very great proportion of the biomass in an ecosystem. Estimates have been as high as 30% (Momot, Gowing & Jones, 1978). Density estimates for white clawed crayfish range from 0.4 to 14 m^{-2} in France (Daguerre de Hureaux & Roqueplo, 1981), and were found to be 2.6 m^{-2} at one site in England (Hogger & Lowery, 1982). The impacts of the foraging of noble crayfish on their habitat was felt when the crayfish populations of Sweden were destroyed by plague resulting in a rapid ecological change in lakes and ponds. This manifested itself in increasing eutrophication and growth of aquatic macrophytes (Abrahamsson, 1966; 1973a).

5.4 Reproduction

Reproduction of the white clawed crayfish takes place either in October or November, when the animals have attained at least a carapace length of 33 mm for males and 21 mm for females (Pratten, 1980; Brewis & Bowler, 1982, Carral *et al.*, 1994). Young mature crayfish do not carry many eggs in the first year but the number carried increases with the size of the animal (Carral *et al.*, 1994). The fertilised eggs are carried under the abdomen of the female throughout the winter and these hatch either in May or June, depending on temperature. The juveniles undergo three moults whilst still attached to the female. During this period they use their yolk sacs and do not feed (Lowery, 1988).

Generally fecundity of crayfish females in any single population increases as they get larger (Abrahamsson, 1971; Rhodes & Holdich, 1982; Brewis & Bowler, 1985; Carral *et al.*, 1994), but the relationship between female size and egg number varies between habitat (Rhodes & Holdich, 1982). Most populations of crayfish studied during the egg bearing season, have a proportion of mature females that do not carry eggs (Brewis & Bowler, 1985). There is often a great deal of variation in the number of eggs carried by each female (Lowery, 1988). This may, in part, be due to females losing some of their eggs during the egg bearing period. Reproductive success can be affected by crowding and refuge availability. For example, it is probable that eggs are lost during disputes for the best refuge sites (Mason, 1978). Brewis and Bowler (1985) suggested that the young crayfish females may sacrifice breeding at a young stage to increase growth and thus future fecundity.

The number of pleopodal eggs carried by white clawed crayfish ranged between 18 and 220 with a mean of 64. Egg diameter ranged between 2.3 and 3.25 mm (Carral *et al.*, 1994).

5.5 Disease

The most notable disease for its severity and devastation of populations is the crayfish plague caused by the fungus *Aphanomyces astaci*. However, there are a large number of other diseases that crayfish are susceptible to. These include bacterial, fungal and protozoan infections in addition to a number of metazoan parasites (Alderman & Polglase, 1988). The significance of many of these diseases on crayfish at the population level is often unknown.

The bacterial diseases of crayfish are generally thought to be of a secondary infectious or opportunistic nature (Alderman & Polglase, 1988). They have been placed into three categories by the same authors; bacteraemias of the blood and internal organs; chitinoclastic bacterial infections of the exoskeleton; and gill infections by filamentous bacteria. There are other rare diseases caused by bacteria such as *Nocardia* sp. which infects the tail musculature (Alderman, Feist & Polglase, 1986).

The protozoan disease Thelohaniasis is thought to be the most serious disease of crayfish after the plague. *Thelohania contejeani*, which parasitises the white clawed crayfish, has been reported to infect between 0.7 and 18% of the population, although mortalities seldom have a major impact at the population level (Pixell Goodrich, 1956; O'Keefe & Reynolds, 1983).

There are a number of metazoan organisms that parasitise crayfish, including flukes, tapeworms, round worms, acanthocephalans, temnocephalid flatworms and branchiobdellids. The impacts of many of these are likely to be greater in intensive aquaculture conditions than in natural populations (Alderman & Polglase, 1988).

Fungal diseases of crayfish are divided into two important groups; the Oomycetes, to which the crayfish plague belongs and the Hyphomycetes. Many of the species of both groups are secondary or opportunistic infectors (Alderman & Polglase, 1988), although there are examples of species that can infect intact crayfish, most notably the crayfish plague.

It is widely believed that the first incidence of crayfish plague in Europe occurred in the Po valley of Italy in about 1860 (Ninni, 1865). It has since spread throughout most of Europe, affecting all native European species, although it only reached England as recently as 1981 (Alderman *et al.*, 1984). Confusion over the cause of the disease was not settled until the causative agent was isolated in the 1930's (Nybelin, 1934). The plague is essentially a European problem, since this is where it has done the most damage to crayfish populations. Unestam (1969; 1972) found that the North American species of crayfish had a high level of resistance to the crayfish plague, and that the fungus could be isolated from a population of signal crayfish in their native range. This suggests that the fungus originates from North America and that the disease was introduced to Europe on crayfish, although not the signal crayfish as this was only imported to Europe in the middle of the 20th century (Alderman & Polglase, 1988).

Gross signs of infection of the crayfish plague are variable depending on the number of zoospores that infect an individual (Alderman & Polglase, 1988). When infected with large numbers of zoospores the crayfish is rapidly overwhelmed and dies with few gross signs. However, when infected by a few zoospores brown melanisations become apparent on the exoskeletons of the animals as their defences attempt to encapsulate the fungus (Alderman & Polglase, 1988). These areas often become the site of secondary infections. It is thought that the infection occurs in the connective tissue, and that when the crayfish is close to death the hyphae invade all other tissues (Alderman & Polglase, 1988). The infective agent is an actively free swimming zoospore and has been shown to be attracted to the crayfish exoskeleton (Cerenius & Soderhall, 1984).

Control of the infective zoospores between different water bodies is extremely difficult and probably impractical. It has been shown that they can live and be transported in wet mud (Rennerfelt, 1936), on fish and damp fish nets (Alderman, Polglase & Frayling, 1987). With so much movement between catchments and within catchments, of fish, fishing equipment, dredging equipment and other items it is not surprising that it has spread quickly throughout Europe and the UK. Malachite green was shown to be an effective fungicide against the crayfish plague (Hall & Unestam, 1980).

5.6 Predators

Higher order predators of crayfish are manyfold and include invertebrate predators, such as dragonfly nymphs, water bugs and beetle larvae of young crayfish (Witzig, Avault & Huner, 1983; Huner & Barr, 1984; Hirvonen, 1992). Pike *Esox lucius*, perch *Perca fluviatilis*, barbel *Barbus barbus*, carp *Cyprinus car*pio, chub *Leuciscus cephalus*, dace *Leuciscus leuciscus*, tench *Tinca tinca*, salmonids and eels *Anguilla anguilla* are all known predators of crayfish (Tavener, 1957; Frost & Brown, 1967; Frantz & Cordone, 1970; Svardson, 1972; Kossakowski, 1973; Mann, 1976; Brown & Bowler, 1977; Erencin & Koksal, 1977). Wading birds, such as herons *Ardea cinerea* are also known to feed on crayfish (Macan & Worthington, 1972), as do kingfishers *Alcedo atthis* and tawny owls *Strix aluco* (Eastman, 1969; Fryer, 1976). Crayfish eating mammals include otter *Lutra lutra* and mink *Mustela vison* (Erlinge, 1972; Delibes & Adrian, 1987, Slater & Rayner, 1993).

6. ECOLOGY OF THE SIGNAL CRAYFISH

6.1 Introduction

Generally, the ecological requirements and habits of signal crayfish are similar to the native crayfish, but there are some notable differences, including resistance to the crayfish plague, a faster growth rate, fecundity and greater maximum size.

6.2 Habitat and habits

The habitat of the signal crayfish in its native and introduced range is very similar to that found in white clawed crayfish. In its native habitat in North America this species prefers low gradient streams flowing through agricultural land (Avault, 1973). However, the diversity of habitat that it occupies is much greater than this and it is found in a large number of streams (Hogger, 1988) and lakes (Goldman & Rundquist, 1977) as well as turbid waters of major rivers (Shimizu & Goldman, 1983). In its introduced range it has exploited a wide range of habitats and this has resulted in it establishing populations in oligotrophic lakes (Abrahamsson, 1973a), eutrophic ponds, chalk streams (Lowery & Holdich, 1988) and gravel pits (Arrignon, 1993).

As with other crayfish species it appears to require refuges in the form of tree roots and rocks. Where the river bed provides little cover the availability of cover in the banks determines the density of the population with far greater densities found where the banks are protected with rocks, than places with clay banks (Shimizu & Goldman, 1983).

It will utilise both fast flowing stretches of the river as well as slow flowing reaches, with the juveniles found more commonly in the former, probably as a result of increased predation in deep water (Blake & Hart, 1993a) and the adults in the latter (Lowery & Holdich, 1988). It's requirements for levels of dissolved calcium in excess of 5mg l^{-1} is similar to other crayfish species. In lakes it tends to occupy littoral zones and is more abundant in areas with large substrata sizes (Klosterman and Goldman, 1983). It's ability to colonise greater depths may be limited by temperature which is required to exceed 10°C for growth (Flint, 1975; Flint & Goldman, 1975; Goldman & Rundquist, 1977).

The signal crayfish has been quoted as being a non-burrowing species (Shimizu & Goldman, 1983; Hogger, 1988). However, Guan (1994) has found that signal crayfish in the River Ouse can and do excavate their own burrows, sometimes at high densities in the banks of the river (5.6 burrows per metre length of river bank). Preferentially, clay soils are selected over sand and gravel soils. Burrowing activity seems greater in crayfish with a carapace length smaller than 50 mm, and was least in large males. This burrowing activity has caused the collapse of the banks in some parts of the Ouse.

Density estimates for the signal crayfish range from 0.9 to 1.07 m^{-2} in Lake Tahoe (Abrahamsson & Goldman, 1970; Flint, 1975), which compares with a density of 0.16 m^{-2} in a riverine environment (Abrahamsson & Goldman, 1970; Flint, 1975; Flint & Goldman, 1975). In a gravel pit lake in France estimates ranged from 4.2 to 7.3 m^{-2} for a population that had been introduced (Laurent & Vey, 1986). Density is very dependent on the habitat characteristics and varies depending on substratum type and contour (Flint, 1975).

One significant difference between the white clawed crayfish and the signal crayfish is the ability of the signal crayfish to tolerate salt water of up to 75% seawater for a few days (Wheatly & McMahon, 1983; Holdich & Reeve, 1988), enabling it to inhabit the saline waters of major rivers (Shimizu & Goldman, 1983). Indeed a seasonal downstream migration into brackish water has been reported for signal crayfish during spring in some habitats. This is followed by a return migration to fresh water in the autumn (Henry, 1951). They have been noted copulating, moulting and laying eggs in brackish water (Miller, 1965).

Signal crayfish are quoted as having a temperature tolerance between 1.4 and 3.0°C greater than white clawed crayfish (Firkins & Holdich, 1993). They have been reported to be capable of tolerating temperatures of 25°C (Goldman, 1973), presumably allowing it to colonisation of warmer habitats than the white clawed species.

6.3 Age and growth

In comparison with white clawed crayfish, signal crayfish grow much faster, indeed it may be the fastest growing of the temperate species (Lowery, 1988). Hogger (1984), quoted by Lowery (1988), found signal crayfish had reached 62 mm (CL) after three years in southern England compared to 29 mm (CL) for the white clawed crayfish. There is, however, a wide variation in the growth rate of this species with quoted carapace lengths, at three years, being 28 mm from L.Tahoe, USA (Goldman & Rundquist, 1977), 33 mm from the same place (Flint, 1975), 34 mm in Canada (Mason, 1974), 39 mm in the Sacramento River, USA (Shimizu & Goldman, 1983), 52 mm in USSR (Cukerzis, 1979) and 60 mm in Sweden (Abrahamsson, 1973b). In general, the growth rate of these crayfish is greatest in populations which have recently invaded an unexploited habitat. Once the population has been established for some time the growth rate starts to decrease, probably as a result of increased density (Hogger, 1986a; b).

As with other species, moult frequency declines with age and has been recorded as occurring 11 times in the first year, 6 in the second, 3 in the third, 2 in the fourth and thereafter once every year (Mason, 1975). In their third and subsequent years, populations show a degree of synchrony in moulting. The principal moults occurring in spring, as the temperatures exceed 14°C and in late summer. Egg bearing females do not moult until they have shed their young in May or June (Shimizu & Goldman, 1983).

The faster growth of the signal crayfish probably allows maturation to occur at an earlier age than in the white clawed crayfish. It has been shown to occur at age 2 in the Sacramento river or age 3 in Lake Tahoe (Shimizu & Goldman, 1983). In exceptional circumstance maturation can occur in the first year when growth rates are sufficient (McGriff, 1983).

Studies of signal crayfish populations have shown that growth can be mediated by temperature and density of animals (Abrahamsson, 1972). Those animals growing in a cool lake grew more slowly than those from a warm river and reached maturity at three years instead of two years (Shimizu & Goldman, 1983). Fastest growth in signal crayfish was observed at 21°C (Mason, 1979) and optimum growth rates were found to be 22.8°C, 1.4°C higher than for white clawed crayfish, although growth was higher in signal crayfish at all temperatures studied (Firkins & Holdich, 1993).

The signal crayfish can survive up to nine years in its native habitat (Flint, 1975; Mason, 1975; Goldman & Rundquist, 1977). It would seem that the signal crayfish grows faster and to a larger final size than the white clawed crayfish (Lowery & Holdich, 1988).

6.4 Food and feeding

As with the white clawed crayfish a similar shift in feeding behaviour from invertebrate prey in the young stages to vegetation and detritus in the adult stages has been reported for signal crayfish (Mason, 1975).

Mason (1975) detailed the food budget of a riverine signal crayfish population and found that plant material, chiefly leaf litter formed 67.5% of the food consumed by the population. Laboratory trials carried out by the same author found that alder and maple leaves were preferred to oak or ash leaves. The intake dry weight of food was estimated to be 0.6-0.7% of dry body weight. Similar values were found by Tamkeviciene (1985).

Activity in signal crayfish appears to be greatest and sometimes exclusively limited to dark hours (Abrahamsson, 1983). Rundquist and Goldman (1983) found that in feeding trials at 20°C with juvenile signal crayfish they ate throughout a 24 hour period with only a slight preference for dark hours.

6.5 Reproduction

The timing and pattern of reproduction in signal crayfish is very similar to the white clawed crayfish. Mating occurred when the water temperature dropped below 14°C in periods of declining daylength in British Columbia (Mason, 1975). In the Sacramento River eggs are laid in September or October and hatch in March or April (Shimizu & Goldman, 1983). A similar pattern has been recorded for a population in southern England (Hogger, 1986a; b).

Most of the American crayfish introduced into Europe including the signal crayfish are r-strategists, maturing earlier and producing more but comparatively smaller offspring. Conversely, the native species of Europe, including the white clawed crayfish, are K-strategists, maturing later and producing less but comparatively larger offspring (MacArthur & Wilson, 1967).

Pleopod egg counts of signal crayfish have ranged from an average of 110 (Abrahamsson & Goldman, 1970) per female to 309 (Hogger, 1986a; b). This increased fecundity is at the sacrifice of egg size and signal crayfish eggs are smaller than those produced by white clawed crayfish. Egg sizes were measured at a diameter of between 2.58-2.72 mm (Mason, 1978) and there was a significant increase in egg size with increasing size of female.

Survival of signal crayfish from egg to maturity has been estimated as being 25% in the Sacramento River (Abrahamsson & Goldman, 1970) and 21-33% in Sweden (Abrahamsson, 1973a) and southern England (Hogger, 1986a; b).

6.6 Predators

Some fish species are noted as important predators of signal crayfish. For example, the rainbow trout, *Oncorhynchus mykiss,* (Frantz & Cordone, 1970) is thought to be partly responsible for reducing abundance in some places (Goldman & Rundquist, 1977). Both perch and eels were found to be significant predators of juvenile signal crayfish (Blake & Hart, 1995). The presence of perch reduced the activity (Blake & Hart, 1993a, b) and growth in juvenile signal crayfish (Appelberg & Odelstrom, 1987).

6.7 Disease

Unlike the white clawed crayfish and other native european species, the signal crayfish has a high level of resistance to the crayfish plague (Unestam, 1969; 1972). However, it may not be totally immune and mortalities may occur at times of stress and during moulting (Holdich, 1988).

Differences in the susceptibility of the signal crayfish to other diseases are not known although they are infected by the same diseases as other crayfish species. For example, *Thelohania contejeani* has been found to infect signal crayfish in North America (McGriff & Modin, 1983).

7. IMPACTS OF THE SIGNAL CRAYFISH

7.1 General

Nilsson (1984) states that the introduction of an exotic species can lead to any one of four outcomes. These are:-

1. It is rejected because there are no vacant niches, or predators consume them at an early stage, or they are affected by native disease or abiotic factors.

2. It hybridises with closely related stocks, formerly adapted to the ecosystem.

3. It eradicates a stock that is either an "ecological homologue", or a prey item, or is sensitive to diseases or parasites carried by the exotic.

4. It finds a vacant niche.

In general, where two species of crayfish coexist there will be interspecific, agonistic interaction, although interbreeding and hybridisation (e.g. Smith, 1981) have also been reported. All the American species, including the signal crayfish, have a number of outstanding negative features (EIFAC, 1983). These include vagrancy, aggressiveness, a wide trophic spectrum, a high reproductive potential, faster growth rate and larger size (Holdich, 1988).

Successful transfers for aquaculture will almost certainly lead to the establishment of breeding populations in the natural environment. Signal crayfish kept in overcrowded conditions in farm ponds can migrate out of these and travel several miles across land (Groves, 1985), colonising adjacent water bodies and coming into contact with the white clawed crayfish.

7.2 Disease

Perhaps the greatest impact has been the crayfish plague *Aphanomyces astaci* which is spread with introduced crayfish. Holdich (1988), believed the disease entered Europe from North America during the 1860's and then spread through Europe, causing high mortalities of native populations over a wide area, although its first occurrence in England was in 1981 (Polglase & Alderman, 1984). Although, the signal crayfish is thought to be partly to blame for the spread of the plague, it was not introduced until the mid 20th century.

Alderman (1993) describes the spread of the disease through England and Wales. The first reported outbreaks were in the summer of 1980 in both the Bristol Avon and River Lee. Since then outbreaks have occurred in other rivers such that most populations of the white clawed crayfish south of the Pennines have been eliminated (Alderman *et al.*, 1984; Polglase & Alderman, 1984; Lowery *et al.*, 1986). Outbreaks have also recently occurred in a number of rivers north of the Pennines (Sutton, 1993).

There may be several mechanisms for spreading the disease including the movement, by man, of contaminated equipment or crayfish stock (Holdich, 1988), although stocking of fish such as rainbow trout (Alderman *et al.*, 1987) may have some role to play as well.

As a result of its resistance to the crayfish plague (Svardson, Furst & Fjalling, 1991), the signal crayfish is believed to act as a carrier and its introduction to new catchments is thought to contribute to infection in those catchments (Cerenius *et al.*, 1988). Holdich (1988) and Alderman, Holdich & Reeve (1990) state that signal crayfish produced in Britain could carry the fungus, and naturally producing populations in Finland have been shown to be infected by it (Nylund & Westman, 1983). However, in Ireland there have been outbreaks of crayfish plague and no signal crayfish have been introduced to that country (Reynolds, 1988), suggesting that whilst they can carry the disease, there are other potential mechanisms by which it is spread, including the use of damp fishing gear previously used in infected areas (Reynolds, 1979b; 1988; Davies, 1980; Matthews & Reynolds, 1990).

Once entering a river, the infection rapidly moves downstream. Upstream movement tends to be slower, sometimes 2 km per year, until it reaches some physical barrier such as a weir, although such barriers are often also breached (Alderman & Polglase, 1988). In Sweden a number of techniques such as liming (Svensson *et al.*, 1976) and electrical barriers have been utilised in an attempt to halt upstream spread of the disease (Unestam, Nestell & Abrahamsson, 1972). None of these techniques has proved totally effective (Svensson *et al.*, 1976; Alderman & Polglase, 1988).

In the case of the noble crayfish there is some evidence that european crayfish populations can recover from the plague (Smith & Soderhall, 1986) and, because of the short life of the fungal spores away from their host, it might be possible to reintroduce native species to waters which have laid fallow for several months. This has been attempted in England and Ireland (Holdich & Rogers, 1992), and in Norway (Taugbol, Skurdal & Hastein, 1993), with short term success but there is a worry that the plague will return to these populations once they reach a critical density (Brinck, 1983; Furst, 1989). Thus Lowery (1991) has argued that vacant niches should be filled with signal crayfish, to avoid the need for repeated stocking.

7.3 Competition

Holdich (1988) says that the white clawed and signal crayfish are ecological homologues and are therefore likely to be competitors for the same resources. He goes on to state that there is a consensus of opinion that the introduction of signal crayfish into Europe has done little harm to either white clawed crayfish or the environment, with the exception of being partly to blame for the spreading of the crayfish plague (EIFAC, 1983; Westman & Pursiainen, 1984).

However, where two species of crayfish coexist, one species may dominate over the other. Dominance between individuals of the same species and between individuals of different species is often related to chelae length and body size, although this has a smaller role to play (Caine, 1978). Signal crayfish are larger than the white clawed crayfish, as well as having a greater chelae length, and it might be expected that this species will dominate when the two are found in the same habitat (Lowery & Holdich, 1988).

A number of rivers have coexisting populations of white clawed and signal crayfish. There is a view that provided the carrying capacity of the river for crayfish is not reached then the two species may coexist (Holdich & Rogers, 1992). However, it is likely that the signals exclude the white clawed species from refuges, and eat them at times of moult (Holdich & Rogers, 1992). In one site catches were 10:1 in favour of signals in August 1991, but this figure increased to 72:1 the following February (Holdich & Rogers, 1992). When an attempt was made to cull the signals by exploitation of the larger size classes, to determine the effect on the white clawed species there was greater recruitment and faster growth of the smaller age classes of the signal crayfish.

The interactions of the signal crayfish with some other european crayfish species has been studied. Where it coexists with the noble crayfish in Sweden the signal crayfish colonises suitable habitats at a faster rate than the noble crayfish. The two species habitat requirements are very similar and thus they compete wherever they coexist and the signal crayfish tends to outcompete this european species (Furst, 1977).

In some cases where two species of crayfish coexist competitive exclusion may be aided or driven by fish predation. Replacement of smaller *Orconectes* species by larger species of the same genus was believed to be driven by size selective predation by fish. Smaller crayfish being eaten preferentially (DiDonato & Lodge, 1993; Mather & Stein, 1993a, b).

A similar pattern emerged in Sweden where signal crayfish have been gradually replacing noble crayfish. The signal crayfish dominates over similar sized noble crayfish and excludes them from predation shelters and hides. The noble crayfish is then more susceptible to predation by fish, and the species is rapidly replaced by signal crayfish (Soderback, 1993; 1994a). In addition, noble crayfish are slower growers and therefore smaller and susceptible to predation for longer than signal crayfish (Soderback, 1992).

Larger size has been found to result in the exclusion of smaller crayfish in other examples of interspecific competition between crayfish (Mather and Stein, 1993a).

7.4 Reproduction

Where exotic species are introduced there is an increased potential for mating and hybridisation with native species due to the possibility of convergent evolution of the previously isolated species. The incidence of interspecific matings is also likely to increase where adults of one species find it difficult to locate conspecific mates because population levels are low e.g. after disease or habitat alteration or pollution.

Interspecific matings are known to occur between signal and white clawed crayfish (Holdich, 1988; Hogger, 1988), although the mated females of both species have been observed to have eggs, these have not been observed to hatch (Goddard & Hogger, 1986). Such matings will reduce the incidence of conspecific matings and threaten the breeding success of the white clawed crayfish already under threat from disease, habitat degradation and pollution.

Reproductive interference has been partly blamed for the replacement of noble crayfish by signal crayfish in Sweden. The impacts of this activity are greater for the species which is least numerous (Soderback, 1994b).

7.5 Habitat

In habitats where crayfish have been eradicated there has been a resultant increase in eutrophication, as well as excessive growths of aquatic vegetation (Abrahamsson, 1966; 1973a; Matthews & Reynolds, 1992) and increases in mollusc abundance (Matthews & Reynolds, 1993). Reintroduction of crayfish has been reported to result in a reversal of the process with reductions in weed biomass and some invertebrates, particularly *Gammarus* and chironomids (Matthews, Reynolds & Keatinge, 1993).

Signal crayfish introduced to previously crayfish-free waters have resulted in a great reduction of weed biomass (Blake & Laurent, 1982; Hogger, 1984, quoted by Hogger 1988; Laurent & Vey, 1986; Elser, Junge & Goldman, 1994). This depletion of weed cover has been blamed for the loss of spawning sites for fish, inhibiting fishery production (Lowery & Holdich, 1988).

8. IMPACTS OF COMMERCIAL FISHERIES ON WILD POPULATIONS OF CRAYFISH

There has been little serious exploitation of the white clawed crayfish in this country, and no studies on the impacts of the small scale exploitation that has taken place.

Studies on the commercial fishery for *Astacus leptodactylus* in Turkey showed that exploitation of crayfish populations tends to preferentially remove the larger individuals, particularly males, resulting in a population of smaller individuals, and increases in survivorship of juveniles and females (Arrignon, 1981). A similar effect has been found in *Orconectes virilis* populations (Momot, 1993), where the presence of large males inhibited recruitment of juveniles. This is presumably a result of predation and competitive exclusion by larger males (Blake, Nystrom & Hart, 1994).

Total control and elimination of crayfish populations with trapping has not been shown to be possible in species of *Orconectes* (Bills & Marking, 1988; Rach & Bills, 1989).

9. CONCLUSION

The introduction of signal crayfish to England and Wales has been comparatively recent (within 20 years). The greatest impact of this species on the white clawed crayfish has been it's implication in the spread of the crayfish plague. Other potential impacts, and their study, have been masked by that diseases devastating effects.

Thus there is very little literature on the impacts, from competitive exclusion or reproductive interference, of introduced signal crayfish on the white clawed crayfish where the plague is absent. This makes prediction of the outcome of coexistence of these two species very difficult, and there is an urgent need for more work on this topic, to facilitate management of these two species.

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In many countries of Europe, the invasive signal crayfish (Pacifastacus leniusculus) has become a huge problem for endemic crayfish species [1â€“4] transmitting the crayfish plague (Aphanomyces astaci), a water mold that eradicates whole populations of European species when introduced into a water bodyâ€”with no effect on the invaders [5, 6]. Since signal crayfish reach impressive densities in short time, the question arises whether they affect not only endemic crayfish but the ecosystem as a whole. Preliminary to a study focusing on that question, we did a literature review on the topic to find o