

THE CURRENT STATUS AND DISTRIBUTION OF FRESHWATER CRAYFISH IN BRITAIN

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ABSTRACT

The distribution of known sites in Britain to which the American crayfish *Pacifastacus leniusculus* has been introduced is outlined and compared with the distribution of the native crayfish *Austropotamobius pallipes*. The threats posed to the continued survival of the native species by disease, loss of suitable habitat and competition from introduced species are reviewed. The distribution and status of other species which may occur in Britain are described. A key for the identification of all species which may be found in the U.K. is included.

INTRODUCTION

IN 1880, T. H. Huxley published his treatise “The Crayfish—An introduction to the study of zoology” (republished, Huxley, 1973). This detailed and finely illustrated monograph was written as a guide and stimulus to the natural historians of the period and was intended to promote a more scientific approach to the study of animals. The freshwater crayfish was subsequently cast in the role of a “type” animal and its study was included in many school and college zoology syllabuses.

In view of this background it is perhaps surprising that our knowledge of these animals remains sparse. A single species, *Austropotamobius pallipes*, occurs naturally in the British Isles. It is our largest freshwater invertebrate and has a wide distribution in alkaline waters in Britain (Thomas & Ingle, 1971; Holdich, Jay & Goddard, 1978; Jay & Holdich, 1981) and in Ireland (Moriarty, 1973; Reynolds, 1979). There have been few studies of the abundance of this species in those areas where it is known to occur. The existence of crayfish at high population densities has, however, been reported for certain sites where detailed investigations have been made (Holdich *et al.*, 1978; Brown & Bowler, 1976).

Whilst a scavenging role is often attributed to crayfish they, in fact, possess diverse omnivorous feeding habits. These range from cannibalism and active predation on other invertebrates to cropping of soft-leaved vegetation and detritus feeding (Reynolds, 1979). There is also some evidence that they are able to filter-feed on finely suspended particulate matter (Budd, Lewis & Tracey, 1978).

The important role of the crayfish in freshwater ecosystems has been most readily identified in those situations where crayfish populations have declined, through disease or other factors, or where new species have been artificially introduced. Premature ageing of lakes, caused by excessive weed growth, has been observed in Sweden, following the spread of disease in populations of the crayfish *Astacus astacus* (Abrahamsson, 1966). In contrast, introductions of crayfish of the genus *Orconectes* into lakes in New Mexico (Dean, 1969) and Wisconsin (Magnuson *et al.*, 1975) led to dramatic reductions in aquatic vegetation and changes in plant species composition. These changes in turn affected the structure of animal communities. A detrimental effect on a commercial fishery has been

Table 1. *Crayfish species occurring in Britain*

Scientific name	Common name
FAMILY ASTACIDAE	
<i>Austropotamobius pallipes pallipes</i> (Lereboullet, 1858)	White clawed or White footed crayfish
<i>Astacus leptodactylus</i> (Eschscholtz, 1883)	Turkish or Slender clawed crayfish
<i>Astacus astacus</i> (Linnaeus, 1858)	Noble or Red footed crayfish
<i>Pacifastacus leniusculus leniusculus</i> (Dana, 1852)	Signal crayfish
FAMILY CAMBARIDAE	
<i>Procambarus clarkii</i> (Girard, 1802)	Red swamp crayfish

reported from Lake Naivasha in Kenya following the introduction of the red swamp crayfish, *Procambarus clarkii* (Lowery & Mendes, 1977).

Our limited knowledge of these animals is probably, in part, a consequence of their nocturnal and secretive habits and, until recently, the absence in Britain of any commercial interest in the exploitation of crayfish in our inland fisheries. This situation has, however, changed in recent years with the introduction of disease resistant American species for novel crayfish rearing projects (Goddard, 1980) and increasing imports of live crayfish for consumption. Until the 1981 Wildlife and Countryside Act there was no legislation controlling the release of non-native species into the wild. The balance of our crayfish stocks is, therefore, changing and the native crayfish is threatened by the introduction and spread of disease, loss of suitable habitat and competition from introduced species.

The following review includes an identification key for those species which may now be found in Britain and details of their current status and distribution. The distribution maps, Figures 6 and 7, have been compiled from published information, personal observations and personal communication with interested commercial and research workers. The authors acknowledge that the records are both incomplete and require continual updating; information concerning additional distribution records or changes in the status of crayfish populations would be gratefully received.

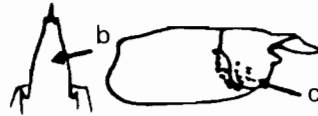
CLASSIFICATION AND IDENTIFICATION

Crayfish are classified in the Order Decapoda of the Class Crustacea. Characteristically they possess five pairs of walking legs, one pair of which carry substantial claws or chelae. They may further be divided taxonomically into two major families, the Astacidae ("Old-World" crayfish) and the Cambaridae ("New-World" crayfish). There are some 500 species distributed throughout the world. The majority of these are native to Australasia and North America whilst some four species, all members of the Astacidae, are native to Europe (Albrecht, 1982). Historically, however, widespread movements have occurred for commercial purposes and several North American species are now widely distributed in Europe. Whilst Britain has a single native crayfish species several others have been introduced for aquaculture purposes or are imported live into wholesale fish markets. Some are also imported within the ornamental fish trade.

Table 1 lists those species which may now be found in Britain. Of these the most commonly occurring are the native *A. pallipes* (Fig. 6) and the introduced *P. leniusculus* (Fig. 7). The following key will enable identification of those species listed in Table 1 to be carried out.

A KEY TO THE SPECIES OF FRESHWATER CRAYFISH IN THE U.K.

N.B. The size ranges given are for mature adults and are approximate; except for ovigerous females maturity is not readily ascertained. Males generally grow larger than females. After leaving the female, at 2–4 weeks old, juveniles are recognisable as crayfish and can readily be identified.



- 1 Large spine on the carpopodite (Fig. 1a), curved and with associated small spines. No median ridge on the rostrum (Fig. 1b). Spines/tubercles anterior to the cervical groove (Fig. 1c). Colour generally maroon/red. Adult length: 10–12 cm

Procambarus clarkii

- No spine on the carpopodite. Median ridge on the rostrum (Fig. 2d) (except *Austropotamobius torrentium*). No spines or tubercles anterior to the cervical groove (Fig. 2e) 2

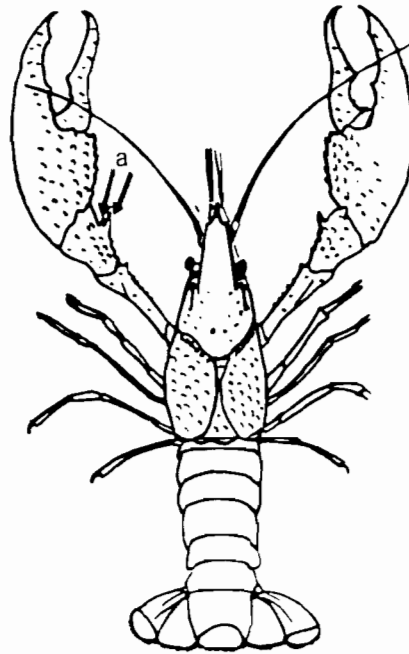
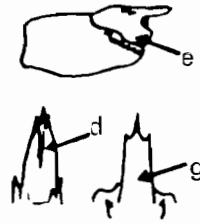


FIG. 1.
P. clarkii



- 2 A single post-orbital ridge (Fig. 2f). Rostrum narrows from the ocular region to the apex (Fig. 2d). Colour olive/brown to red/brown; claws white ventrally. Adult length: 5-8+ cm . *Austropotamobius pallipes*

Note. *Austropotamobius torrentium* is similar to *A. pallipes* but with no ridge on the rostrum (Fig. 2g)

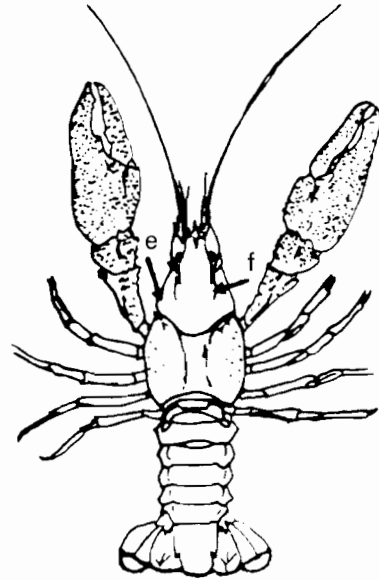
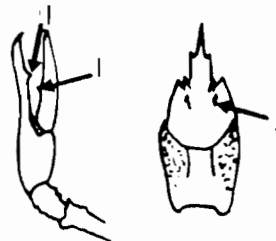


FIG. 2.
A. pallipes

- Two post-orbital ridges (Figs 3h, 4n). Edges of the rostrum almost parallel 3



- 3 Claws very characteristically elongated (Fig. 3i). Rostrum concave. Second post-orbital ridge may be a group of spines (Fig. 3j). Tubercles on the cephalothorax (Fig. 3k); large tubercles on the gripping edges of the claws may or may not be present (Fig. 3l). Colour sandy or buff/olive. Adult length: 8-10+ cm. . . . *Astacus leptodactylus*

- Large, robust claws. 4

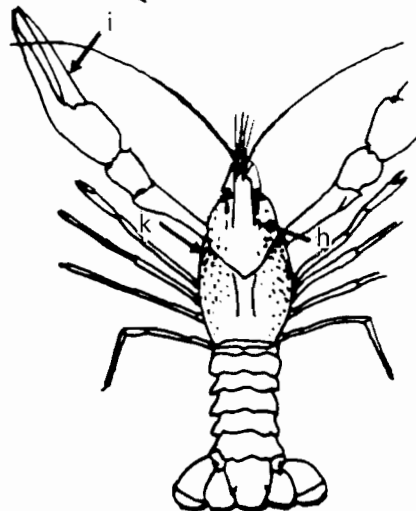


FIG. 3.
A. leptodactylus

- 4 Rostrum with median ridge clearly toothed (Fig. 4m). Two post-orbital ridges (Fig. 4n). Claws and carapace "rough" (Fig. 4o). Colour olive/brown to red/brown, red on the ventral surfaces of the claws. cf. *Austropotamobius pallipes* which is white on the ventral surface of the claws. Adult length: 7-10+ cm. . . . ***Astacus astacus***

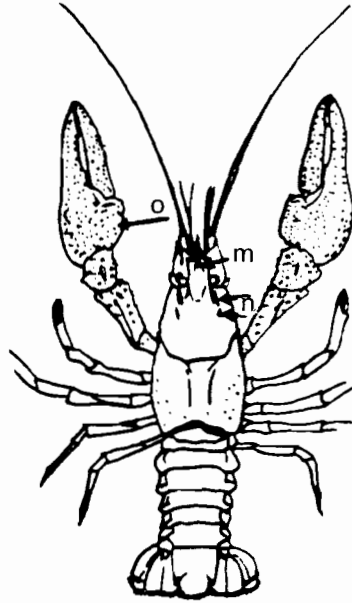


FIG. 4.
A. astacus



- Rostrum always with a smooth median ridge (Fig. 5p). Second post-orbital ridge insignificant (Fig. 5q). Claws very robust. Colour blue/brown to olive/brown; claws with a characteristic dorsal white patch (Fig. 5r) and bright red ventrally. Adult length: 7-14+ cm. . ***Pacifastacus leniusculus***

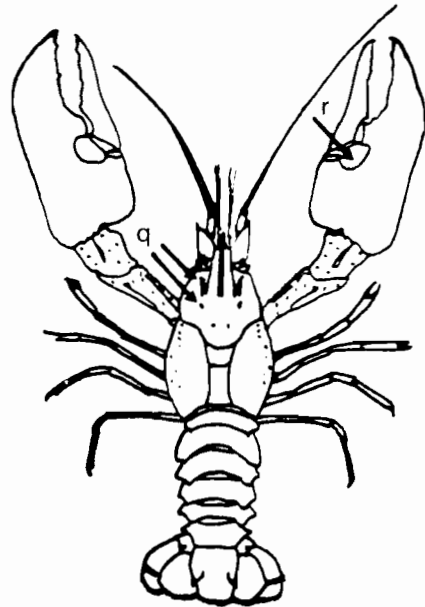


FIG. 5.
P. leniusculus

DISTRIBUTION

Austropotamobius pallipes

Native to the British Isles, France and south-west Europe (Laurent & Forest, 1979) and is found in both still and flowing waters. Its distribution in Britain has been described from pre-1970 records (Thomas & Ingle, 1971) and post-1970 records (Jay & Holdich, 1981). It has a wide distribution in England and the Welsh borders although it rarely occurs in Scotland (Figs. 6 & 8). It is found in areas associated with base-rich, easily weathered substrata, in waters of neutral to alkaline pH and a calcium context exceeding 5 mg l^{-1} (Jay & Holdich, 1981). There is no established commercial fishery for *A. pallipes* in Britain although small quantities are trapped in some areas for local consumption.

Astacus leptodactylus

Native to eastern Europe and Asia Minor (Laurent & Forest, 1979). Crayfish harvested from within this region, particularly from Turkey, form the basis of the crayfish trade in Europe. Some 6000 tonnes of Turkish crayfish are consumed annually in Sweden, France and West Germany (Huner, 1984). About 50 tonnes a year of Turkish crayfish are imported into Britain (Wickins, 1982). Breeding populations of this species have recently been reported from lakes in a London park. Presumably these have arisen from individuals purchased for consumption and subsequently released.

Astacus astacus

Widely distributed throughout northern and eastern Europe (Laurent & Forest, 1979). It was once the most abundant crayfish in Europe and the most highly valued commercially. Stocks have, however, been severely depleted by the "crayfish plague", a fungal disease that has spread through Europe since the 1860s (Unestam, 1973). Although reports suggest that *A. astacus* has been introduced into Britain on several occasions these have not been substantiated (Holdich *et al.*, 1978) and there are no current records of its occurrence. Some specimens have, however, recently been imported from Germany and offered for sale for culture purposes.

Pacifastacus leniusculus

This species is native to the western U.S.A. and Canada (Shimizu & Goldman, 1983). It has been widely introduced into Europe for the restocking of ponds and lakes (Laurent & Forest, 1979). In Britain, it has been imported for novel crayfish "farming" ventures. The majority have been obtained from the Simontorp hatchery in Sweden, as juveniles, and released into enclosed waters. Since 1976, introductions have been made to several hundred sites spread throughout Britain (Figs. 7 & 9).

Procambarus clarkii

This is a warm-water species native to the south-eastern states of the U.S.A. (Huner & Barr, 1980). It has also been introduced into a number of other countries including Japan, Kenya, Sudan and southern Spain (Huner & Avault, 1978). Of all species, it is the most widely farmed and harvested, forming the basis of the American crayfish industry which is centred in Louisiana. It has been introduced into Britain for culture trials in warm-water recirculation systems on several separate occasions and is also imported, mainly from Kenya, into wholesale fish markets. Importation with batches of ornamental fish for the aquarium trade has also taken place. There is no current evidence that this species is established in the wild at any locations in Britain.



FIG. 6.

Austropotamobius pallipes (White-footed crayfish). Mature female.



FIG. 7.

Pacifastacus leniusculus (Signal crayfish). Mature female.

CRAYFISH STOCKS IN BRITAIN

The pattern of crayfish stocks in Britain has changed in recent years. The decline in distribution and abundance of *A. pallipes* is, in part, due to increased human pressure on watercourses as flood-relief channels and a means of effluent disposal. Dredging and bank realignment can drastically affect crayfish populations through the removal of cover, food sources and large numbers of crayfish (Hogger & Lowery, 1982). Conversely, where bank protection is necessary it may provide suitable habitats but is now likely to consist of sheet piling or smooth concrete rather than the more hospitable wood or stone-block banking.

The use of rivers to carry urban run-off and effluents generally reduces water quality in the long term, possibly affecting suitability for crayfish (Hogger, 1984), whilst short-term pollutions may eradicate whole populations. Agricultural pollutions, resulting from increased farming intensity, tend to have the most severe effects as they occur in relatively unpolluted rural areas where *A. pallipes* may be locally abundant.

However, the two most significant changes to affect stocks of native crayfish in recent years have been the widespread introductions of the signal crayfish *Pacifastacus leniusculus*, following initial imports in 1976 (Richards & Fuke, 1977), and the recent evidence, following heavy mortalities of crayfish in several rivers in southern England, of the presence of the crayfish plague (Alderman, *et al.*, 1984; Polglase & Alderman, 1984). These are the first substantiated reports of the occurrence of this fungal disease in the U.K.

CRAYFISH INTRODUCTIONS

Figures 8 and 9 illustrate the geographical overlap in distribution which now exists between the sites to which *P. leniusculus* has been introduced and populations of the native *A. pallipes*. As can be seen, the majority of *P. leniusculus* introductions have been into southern and eastern England where climatic conditions result in excellent growth rates (Hogger, 1984). Natural populations of *A. pallipes* are also most common in this part of the U.K. where water quality, particularly in terms of calcium content, is most suitable.

In marked contrast to the introduction of signal crayfish in other European countries, most notably in Sweden and Finland, there has been no attempt to control its import or distribution in Britain. Prior to the implementation of Section 14 of the Wildlife and Countryside Act, 1981, there was no relevant legislation to support such control. Under the present interpretation (currently under review) of that Section, it is now an offence to release any non-indigenous species to the "wild". However, any species may be imported and distributed for proposed crayfish farming projects if reasonable precautions are taken to maintain them in isolated ponds or lakes. Implementation of such precautions poses considerable problems since crayfish are remarkably mobile animals and are able to traverse damp terrain. If conditions in a pond deteriorate there is evidence that crayfish will leave that body of water and seek a more favourable environment (Huner & Barr, 1980). At least one site is known, on the River Whitewater in north Hampshire, where a breeding population of escaped *P. leniusculus* has become established (Hogger, unpublished observation). In view of the numerous introductions and the known location of ponds adjacent to suitable watercourses it is inevitable that populations of escapees will become established in other river systems.

The effects of signal crayfish, or other introduced species, on existing populations of *A. pallipes* can only be matters for conjecture and have been discussed elsewhere (Holdich *et*

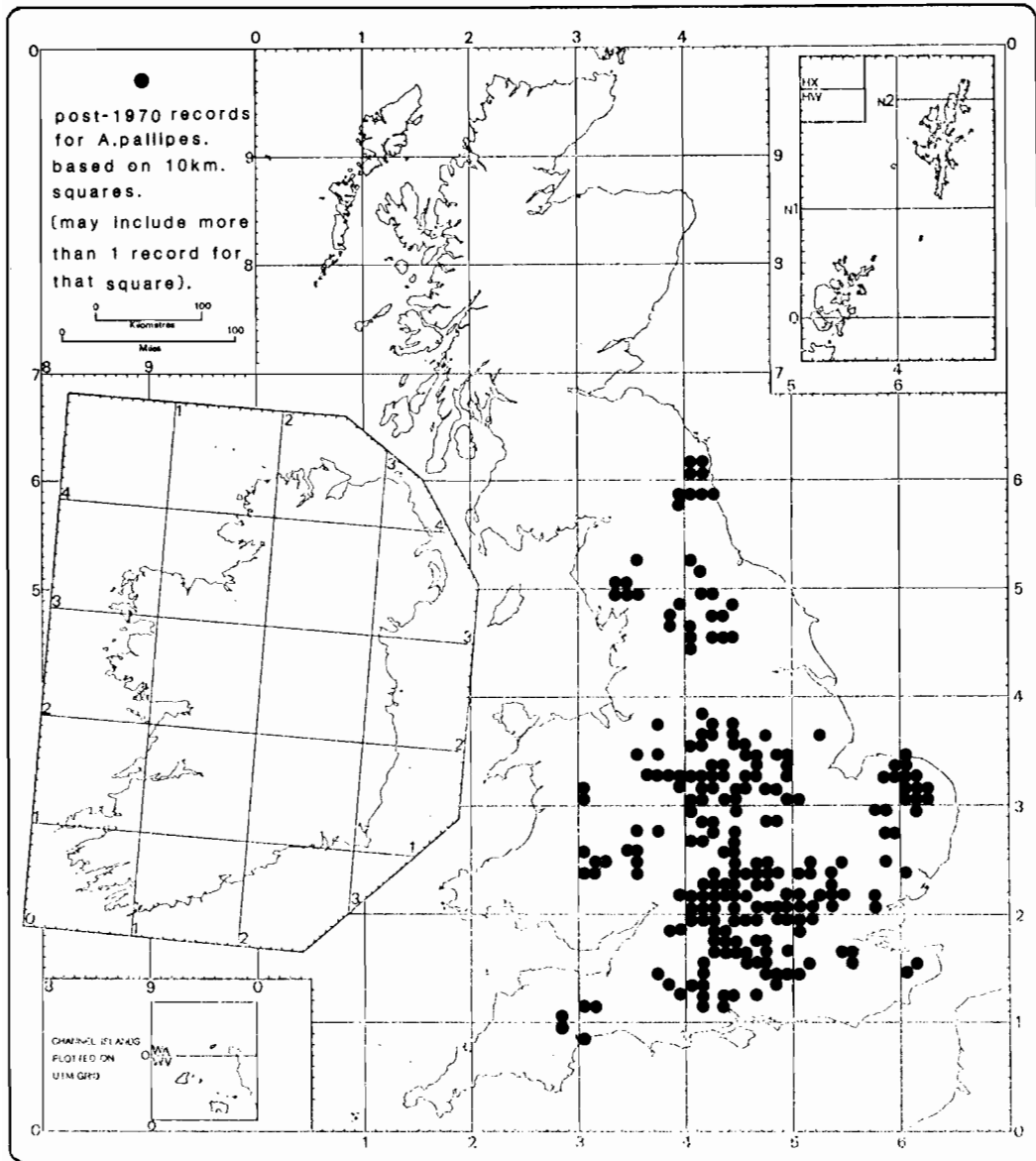


FIG. 8.
Distribution of *Austropotamobius pallipes* in the U.K.

al., 1978). The risks of interspecific competition and spreading disease are major factors for concern. There is also the possibility of species inter-breeding. Successful mating has been observed, under laboratory conditions, between *A. pallipes* and *P. leniusculus*. On these occasions the mated females of both species laid eggs which failed to hatch (Hogger, unpublished observation).

Of the other crayfish species which are imported into Britain only *A. leptodactylus* has so far been found living in the wild. Populations are established in two London lakes

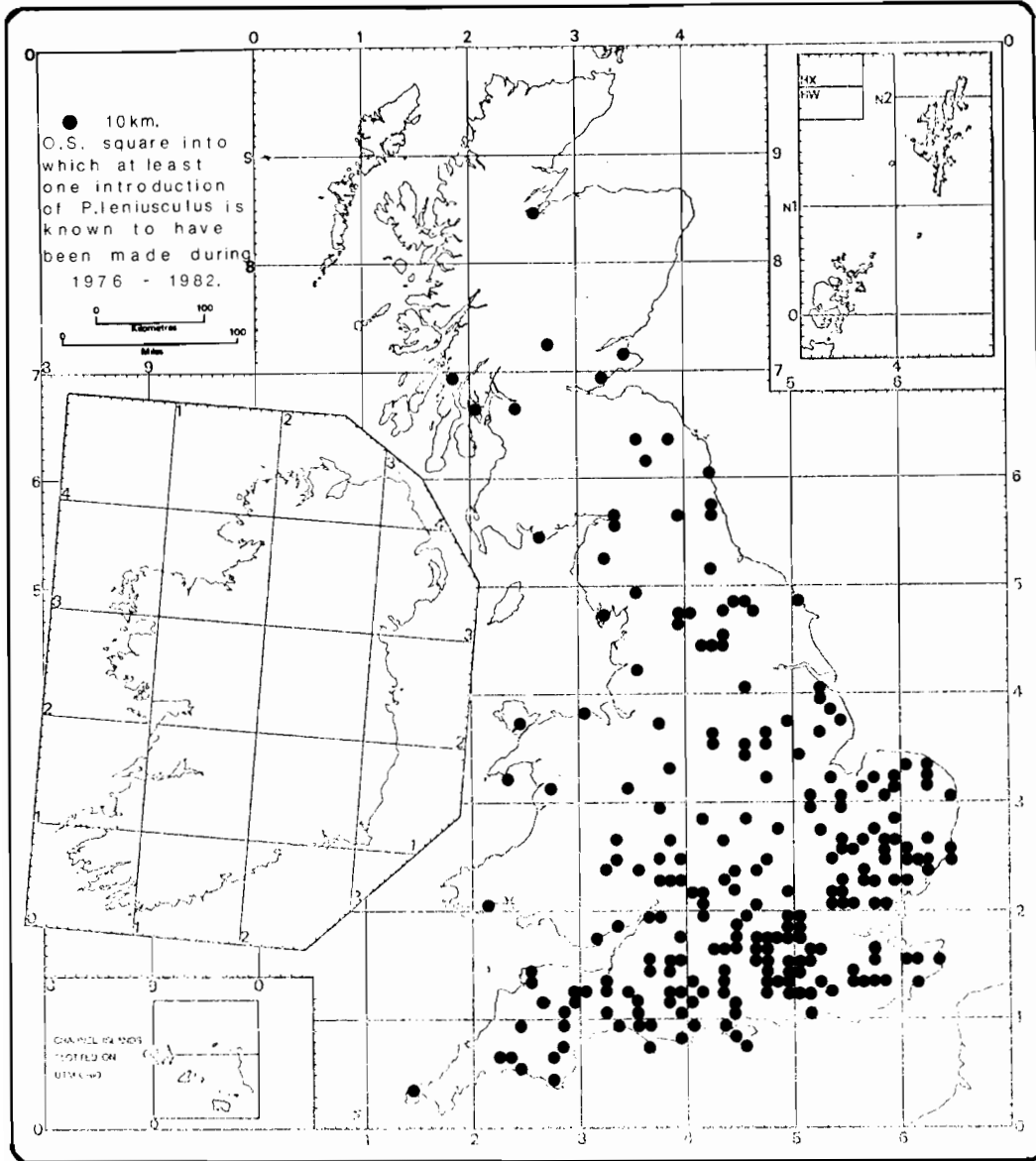


FIG. 9.
Distribution of known introduction of *Pacifastacus leniusculus* in the U.K.

which, when sampled, included ovigerous females (Hogger, unpublished observation). This recent evidence suggests that conditions, at least in southern England, are favourable for this species. Since these crayfish are imported and distributed live from wholesale fish markets the potential clearly exists for further releases. Any such unlicensed releases would be in contravention of Section 14 of the Wildlife and Countryside Act, 1981. It is known that at least one attempt is being made to farm this species, in a lake in Surrey.

CRAYFISH PLAGUE

Prior to 1981 there was no evidence that the crayfish plague, a disease caused by the parasitic fungus *Aphanomyces astaci* (Schikora), was, or has been, present in the U.K. (Jay & Holdich, 1981). In 1981, however, heavy mortalities of native crayfish were reported from the Bristol Avon and the River Lea in Hertfordshire. In 1982, crayfish mortalities were also reported from the River Whitewater in Hampshire and the River Rib in Hertfordshire. Further mortalities were reported from the Bristol Avon in 1983 and there was also an outbreak on the River Wey in Hampshire. From these latter three sites, moribund animals were collected and the crayfish plague fungus isolated and identified (Alderman *et al.*, 1984; Polglase & Alderman, 1984). *A. pallipes* has recently been reported to also have disappeared from some 65 km of the River Avon in Hampshire and Wiltshire (A. Frake, personal communication).

The nature of this crayfish disease and the pattern of its spread in mainland Europe has been well documented (Unestam, 1973; Polglase & Alderman, 1984). The first occurrence of the disease was recorded in northern Italy in 1860 from where it spread, and continues to spread, throughout Europe. It is believed to have been introduced with infected crayfish imported into Europe from North America. North American species display a high level of resistance to infection by the fungus, although they act as reservoirs or carriers of the disease (Unestam, 1973). In contrast, all European and Australasian species display no resistance and death rapidly follows the initial infection (Unestam, 1973, 1975). *Austroptamobius pallipes*, *Astacus astacus* and *A. leptodactylus* are susceptible to the disease whilst both *P. leniusculus* and *P. clarkii* are resistant and potential carriers.

The disease spreads with characteristic rapidity through crayfish populations causing total, or near-total, mortalities. Since the disease is now established in several river systems in southern England further outbreaks must be anticipated. These will be most evident during the summer months when crayfish are normally at their most active. The implications of the presence of the plague in Britain are most serious since, at worst, it may eventually destroy populations of the native *A. pallipes* in all but isolated areas. Movements of infected animals and equipment by fishermen are generally held responsible for the spread of disease between watercourses and attempts to control the spread of the disease in Europe have rarely met with success. Measures introduced in Europe, now under consideration for use in the U.K., have included the banning of crayfish trapping and trade in infected areas, disinfection of fishing equipment with formalin, restocking with native species and the operation of electrical barriers on rivers, designed to prevent the spread of infected animals (Soderhall, Svensson & Unestam, 1976). The possibility also exists, however, that natural agencies such as birds may transport fungal spores or infected crayfish.

GENERAL CONCLUSIONS

The threat posed to *A. pallipes* by disease and potential competition from introduced species are of particular significance. The British Isles have, until the present time, represented a stronghold for this species which is currently listed as "rare" in the I.U.C.N. Invertebrate Red Data Book (Wells, Pyle & Collins, 1983) and is declining throughout its range in western Europe. Ireland has effectively banned the import of exotic crayfish (Davies, 1980); a course of action which, if sustained, may safeguard the species in that country.

In view of the evidence outlined above it seems probable that a decline in the abundance and distribution of *A. pallipes* in Britain will be paralleled by the establishment of populations of *P. leniusculus* in lakes and rivers. This may not, however, result in the total disappearance of *A. pallipes* from the U.K. as both *A. astacus* and *P. leniusculus* successfully cohabit waters in parts of Scandinavia (Westman & Pursiainen, 1979). The current limited knowledge of the ecological role of crayfish in our fresh waters does not permit any realistic appraisal of the possible effects of any such changes.

The future status of the native British crayfish is, then, likely to decline drastically over the next decade, with the possibility that it may disappear from many parts of the U.K. Measures attempting to restrict the spread of the crayfish plague or to establish disease-free areas would have to be introduced as soon as possible to be effective. By contrast, populations of the signal crayfish have rapidly become established and although the total success rate of introductions is unknown it is probable that the majority will result in breeding populations. Coupled with the increasing demand for this species for the table it seems unlikely that stocking and restocking prospective crayfish farms will cease. Consequently, movements of this species around the U.K. will continue together with the potential for increasing threats to the survival of stocks of the native species.

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REFERENCES

- ABRAHAMSSON, S. A. A. (1966). Dynamics of an isolated population of the crayfish *Astacus astacus* (L.). *Oikos* 17: 96–107.
- ALBRECHT, H. (1982). Das system europaischen flusskrebse, verslag und begrundung. *Mitt. Hamb. Zool. Mus. Inst.* 79: 187–210.
- ALDERMAN, D. J., POLGLASE, J., FRAYLING, M. & HOGGER, J. B. (1984). Crayfish plague in Britain. *Journal of Fish Diseases* 7: 401–405.
- BROWN, D. J. & BOWLER, K. (1976). A population study of the British freshwater crayfish *Austropotamobius pallipes* (Lereboullet). *Freshwater Biology* 3, 33–50.
- BUDD, T. W., LEWIS, J. C. & TRACEY, M. L. (1978). The filter feeding apparatus in crayfish. *Canadian Journal of Zoology* 56: 695–707.
- DAVIES, R. (1980). Ireland's export based market is under pressure. *Fish Farmer* 3(6): 8–10.
- DEAN, J. L. (1966). Biology of the crayfish *Orconectes causeyi* and its use for control of aquatic weeds in trout lakes. *Technical Papers, United States Bureau for Fish & Wildlife* No. 24: 15 pp.
- GODDARD, J. S. (1980). Crayfish culture. *Proceedings of the Institute of Fisheries Management 11th Annual Study Course*: 123–130.
- HOGGER, J. B. (1984). *Aspects of the biology and distribution of freshwater crayfish in the Thames catchment*. Unpubl. Ph.D. thesis.
- HOGGER, J. B. & LOWERY, R. S. (1982). The encouragement of freshwater crayfish populations by attention to the construction and maintenance of waterways. *Journal of the Institute of Water Engineers and Scientists* 36(3): 214–220.
- HOLDICH, D. M., JAY, D. & GODDARD, J. S. (1978). Crayfish in the British Isles. *Aquaculture* 15: 91–97.

- HUNER, J. V. (1984). Market potential for Procambriid crayfishes in western Europe: General impressions. *Crayfish Bulletin* 1(4): 5–11. (Publ. by Hampshire College of Agriculture.)
- HUNER, J. V. & AVAULT, J. W. (1978). Introductions of *Procambarus* sp.—A report to the Introductions Committee of the International Association of Astacology. *Freshwater Crayfish* 4: 191–194.
- HUNER, J. V. & BARR, J. E. (1980). *Red Swamp Crayfish: Biology and Exploitation*. Sea-Grant Publication No. L.S.U.-T-80-001, Baton Rouge.
- HUXLEY, T. H. (1880). *The Crayfish: An introduction to the study of zoology*. Kegan-Paul & Co., London. 371 pp. (Republished 1973, M.I.T. Press, Massachusetts.)
- JAY, D. & HOLDICH, D. M. (1981). The distribution of the crayfish *Austropotamobius pallipes* in British waters. *Freshwater Biology* 11: 121–129.
- LAURENT, P. J. & FOREST, J. (1979). Donnees sur les ecrevisses qu'on peut rencontrer en France. *La Pisciculture Francaise* 56: 25–40.
- LOWERY, R. S. & MENDES, A. J. (1977). *Procambarus clarkii* in Lake Naivasha, Kenya, and its effects on established and potential fisheries. *Aquaculture* 11: 111–121.
- MAGNUSON, J. J., CAPELLI, G. M., LORMAN, J. G. & STEIN, R. A. (1975). Consideration of crayfish for macrophyte control. pp. 66–74 in: *The proceedings of a symposium on water quality management through biological control*. Eds P. L. Brezonik & J. L. Fox. Rep. No. ENV 07-75-1, University of Florida, Gainesville.
- MORIARTY, C. (1973). A study of *Austropotamobius pallipes* in Ireland. *Freshwater Crayfish* 1: 57–68.
- POLGLASE, J. & ALDERMAN, D. J. (1984). Crayfish plague threatens U.K. stock. *Fish Farmer* 7(3): 16–17.
- REYNOLDS, J. D. (1979). Crayfish ecology in Ireland. *Freshwater Crayfish* 4: 215–220.
- RICHARDS, K. J. & FUKU, P. (1977). Freshwater crayfish: the first centre in Britain. *Fish Farming International* 4(2): 12–15.
- SHIMIZU, S. J. & GOLDMAN, C. R. (1983). *Pacifastacus leniusculus* production in the Sacramento River. *Freshwater Crayfish* 5: 210–218.
- SODERHALL, K., SVENSSON, E. & UNESTAM, T. (1977). An inexpensive and effective method for elimination of the crayfish plague: barriers and biological controls. *Freshwater Crayfish* 3: 333–342.
- THOMAS, W. & INGLE, R. (1971). The nomenclature, bionomics and distribution of the crayfish *Austropotamobius pallipes* (Lereboullet) (Crustacea: Astacidae) in the British Isles. *Essex Naturalist* 32: 349–360.
- UNESTAM, T. (1973). Significance of diseases on freshwater crayfish. *Freshwater Crayfish* 1: 135–150.
- UNESTAM, T. (1975). Defence reactions in and susceptibility of Australian and New Guinea crayfish to European crayfish plague fungus. *Australian Journal of Experimental Biological and Medical Sciences* 53: 349–359.
- WELLS, S. M., PYLE, R. M. & COLLINS, N. M. (1983). *I.U.C.N. Invertebrate Red Data Book*. Cambridge. pp. 632.
- WESTMAN, K. & PURSIAINEN, M. (1979). Development of the European crayfish *Astacus astacus* (L.) and the American crayfish *Pacifastacus leniusculus* (Dana) populations in a small Finnish lake. *Freshwater Crayfish* 4: 244–250.
- WICKINS, J. F. (1982). Opportunities for farming crustaceans in western temperate regions. In: *Recent advances in aquaculture*. Eds J. F. Muir & R. J. Roberts. Croom Helm, London.