

The invasion of the Chinese mitten crab (*Eriocheir sinensis*) in the United Kingdom and its comparison to continental Europe

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Abstract

Owing to its catadromous lifestyle, the Chinese mitten crab, *Eriocheir sinensis*, allows comparison between a coastal and an inland biological invasion of the same species. Information about the distribution of this species in the United Kingdom has been collected from sightings made by governmental agencies, The Natural History Museum (London) collection, literature, and from the general public. This information indicated that the range of the species has expanded since the species' arrival in 1973. The spread has been most marked along the east coast northwards to the river Tyne, on the south coast westwards to the river Teign. The expansion range was quantified and compared using geographic information software, and then compared to recorded spread in Europe. Mitten crabs dispersed along the coast at an average rate of 78 km per year (1976–1999), with a recent sharp increase to 448 km per year (1997–1999). These values are comparable with the historic outbreak in continental Europe where the average rate of dispersion along the Baltic Sea coast (1928–1935) was 416 km per year. Comparable figures for the North Sea coast (1923–1954) were 75 km per year with a peak of 168 km per year in 1927–1937. The upstream spread along rivers in the United Kingdom was 16 km per year in 1973–1998 with a marked increase since 1995 to 49 km per year (1995–1998). These data, in combination with population data published for the river Thames, indicate that the population has been increasing since the early 1990s, causing further range expansion into previously uninvaded river systems. The comparison of the spreading behaviour of the ongoing invasion in the United Kingdom with the historic invasion in northern Europe suggests that *E. sinensis* in future has the potential to establish itself in all major UK estuaries.

Introduction

The Chinese mitten crab (*Eriocheir sinensis*, H. Milne Edwards, 1854) is native to the Far East where its range extends from Hong Kong ($\approx 22^\circ\text{N}$) to the border with North Korea ($\approx 40^\circ\text{N}$) (Hymanson et al. 1999). This species has two likely pathways of introduction: through

ballast water (Peters 1933; Cohen and Carlton 1997) and through escapes or deliberate releases associated with the transport of this valued aquaculture species. The mitten crab supports a \$1.25 billion per annum aquaculture industry in China supplying local and international markets with live animals (Hymanson et al. 1999). *E. sinensis* is catadromous, spending most of its life in fresh-

water, and only returning to estuaries to reproduce, after which it dies. The downstream migrations of sexually mature crabs occur from August to October in the rivers Elbe and Weser (Germany) (Peters 1933, 1938c) and from September to December in the River Thames (United Kingdom) (Robbins et al. 1999). After mating, the females migrate to higher estuarine salinities and release up to three batches of larvae in early spring (Peters 1933). This migratory behaviour has also been observed in more recent studies on *E. japonica* (Kobayashi and Matsuura 1999; Kobayashi 2001). Field data on the larval duration of *E. sinensis* are limited, but laboratory experiments indicate a period of ≈ 90 days from hatching to the megalopa (Anger 1991). Following the migration of juvenile mitten crabs upstream in the spring, individuals can reach rivers, lakes, and ponds as far as 1200 km from the coast (Peters 1933). *E. sinensis* reaches sexual maturity at 1–3 years in China (Jin et al. 2001) and 3–5 years in Europe (Schubert 1938). A proposed life cycle of the Chinese mitten crab in the northern Europe is shown in Figure 1.

There have been a number of reports that suggest that *E. sinensis* has a high invasive potential in continental Europe. During the first half of the 20th century, widespread outbreaks were observed in all major rivers along the continental European North Sea and Baltic Sea coasts, as

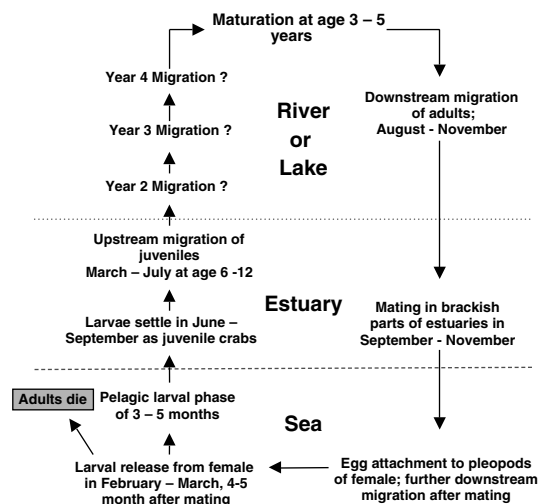


Figure 1. Proposed life cycle for *Eriocheir sinensis* based on historic observations from the Elbe (Panning 1938a) and laboratory experiments (Anger 1991).

well as in the River Gironde on French Atlantic coast (Herborg et al. 2003). Records of this event show very high population densities in core areas such as the river Elbe in Northern Germany, where there was an annual catch of 242 metric tonnes in 1936, equivalent to an estimated 4.4 million crabs (Panning 1938b). These observations lead Elton (1958) in his classic account on the ecology of invasions to conclude that ‘...this crab has not taken hold in Britain, though it may very likely will one day ...’; a prediction that came true 15 years later. The invasion has led to ecological and economical impacts. The crab interferes with recreational and commercial fishing (Ingle 1986; Veldhuizen and Stanish 1999), causes river bank erosion through extensive burrowing (Peters 1938b; Dutton and Conroy 1998), and may compete for resources with native freshwater crustaceans (Clark et al. 1998). Since the description of Clark et al. (1998) highlighted the spread of the Chinese mitten crab in River Thames for the year 1996, the species has undergone a further range expansion to other parts of the UK. This publication describes changes in the distribution of mitten crabs and analyses its spreading behaviour, providing a rare opportunity to compare invasion in marine and freshwater environments by the same species.

Materials and methods

Information about the distribution of the Chinese mitten crab was gathered from the scientific literature, The Natural History Museum collection, Environment Agency reports (Clark and Rainbow 1996), and through contact with staff of the Environmental Agency and the public. The latter was done through a public awareness scheme run from Newcastle University. Commercial crayfish traps were deployed in the river Tyne (northeast England) to assess the northern distribution.

The sightings furthest upstream in each year were used to build a database of geographic coordinates describing the distribution. Where records could not pinpoint the precise location along a river, the most conservative location (i.e., furthest downstream) was assumed. Geographic Information System (GIS) Grass 4.3 software was used to

measure the total length of river occupied per year by the crab species. The measurements were taken annually from the furthest upstream record of the previous year to the furthest upstream record for the next. In the case of several possible routes (e.g., through a canal or a river) to a particular location, the shortest was chosen. The average annual migration rate was based on the period in which observations were available for each particular area or coastline.

The increase in coastal and river spread has been plotted as km per year. The rate of range expansion was calculated as follows: if in year 1 the crabs dispersed 30 km along the coast and in year 2 they spread 20 km further than the previous year, the average rate of spread was 25 km per year. Within rivers, if in year 1 the crabs were found 50 km from the estuary and in year 2 they were 80 km from the estuary, the average annual rate of range expansion was 40 km per year. When mitten crabs were reported from a location in a tributary of an already invaded stretch of river, the rate of spread used was the distance between the reported location and the point where the tributary joined the river. If graphs of spread showed a distinct period of rapid (near exponential) spread, the average rates for these periods were also calculated (see Table 1 for details).

Since *E. sinensis* invaded continental Europe in the last century, the data set of this historic invasion (1913–1960) (Herborg et al. 2003) was analysed further to assess the extent of for coastal spreading along the North Sea and Channel coast

Table 1. GIS based measurements of the mean (\pm SD) annual spread of *Eriocheir sinensis* in river systems for northern continental Europe, southern France (both from (Herborg et al. 2003) and the United Kingdom. The peak period of spread was determined by selecting the asymptotical periods of spread on the curves of Figure 5. Due to the short period of range expansion, no separate period of peak spread could be distinguished for southern France.

River spread	Total observation period		Peak spread period	
	Period	km/year (\pm SD)	Period	km/year (\pm SD)
Northern Europe	1913–1956	196 (\pm 388)	1928–39	562 (\pm 599)
Southern France	1954–1960	104 (\pm 116)	NA	NA
United Kingdom	1973–1998	16 (\pm 28)	1995–1998	49 (\pm 34)

and the Baltic Sea coast. Thus, two data sets were obtained, each giving the rate of spread along one distinct coastline, and providing a clearer picture of the spreading dynamics.

Results

The spread in UK rivers

Despite the extensive outbreak of *E. sinensis* in continental Europe during the first half of the 20th century, there were only two isolated reports of its occurrence in the UK. In 1935, the first mitten crab was caught on the intake screens of Lots Road Power Station, Chelsea (river Thames) (Harold 1935) (for location of rivers in the United Kingdom, see Figure 2). Another crab was collected, in 1949, from the South Field Reservoir, which is connected to the Humber estuary through the New Junction Canal (Wall and Limbert 1983) (Figure 2). The distance between these two estuaries is \approx 400 km along the coast and \approx 390 km through the canal system, and the absence of any reports at intermediate locations suggests separate introductions. The absence of reports for the next 34 years suggests that these populations had not become established and were therefore omitted from the current analysis.

In 1973, a specimen was caught at West Thurrock Power Station (river Thames) (Ingle and Andrews 1976), and with recurring catches, and increasing numbers, reported for the Thames since then (Figure 2) (Clark and Rainbow 1996). In 1976, the first specimen was recorded from the river Humber, close to the river Ancholme outflow, with further reports in 1979, 1984, 1986 and 1991–1994 (Clark 1984; Clark and Rainbow 1996). So until 1996, UK reports of the mitten crab were confined to river Thames and river Humber and their respective tributaries. The available data indicate a total range increase of 109 km upstream from Humber, into the river Ancholme (1979) (Figure 2), the South Field Reservoir (1983) and the New Junction Canal (south Yorkshire) in 1995 (Figure 2) (Clark and Rainbow 1996; Hemsley – Flint, personal communication). In conjunction with more recent observations by local fishermen (Mouncey, personal communication), it is suggested that either a small population

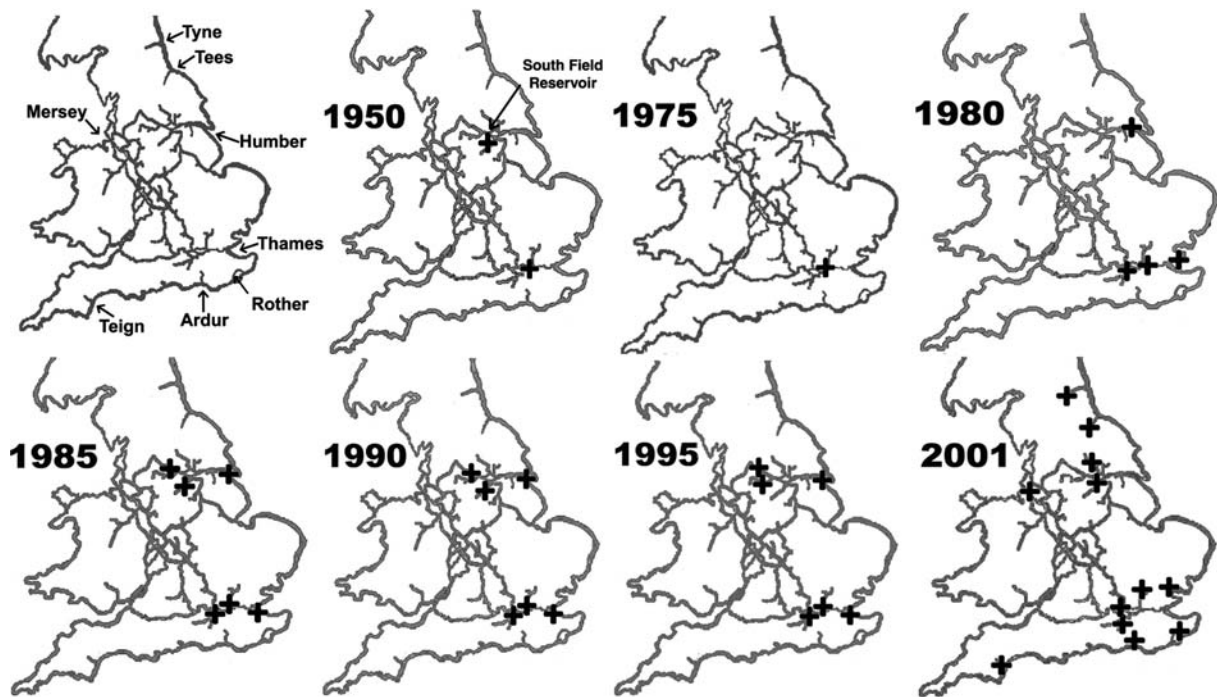


Figure 2. Reports of *Eriocheir sinensis* in the United Kingdom; only new sightings outside the previous distribution limit are displayed.

has established itself in the Humber estuary and/or there is a constant supply of propagules to this estuary. The invasion in the Thames had spread 120 km upstream by 1995 (Clark et al. 1998) (Figure 3). In 1996, a public awareness programme was carried out by The Natural History Museum (London) to determine the distribution

within the Thames and its tributaries (Clark et al. 1998) (Figure 2). *E. sinensis* was found to have spread a further 150 km upstream, into 12 tributaries and canals, from its previously known limit in the Thames (Clark et al. 1998). Since the establishment of the Chinese mitten crab in the UK, the highest rates of spread within these rivers occurred in 1995–1998 (Table 1).

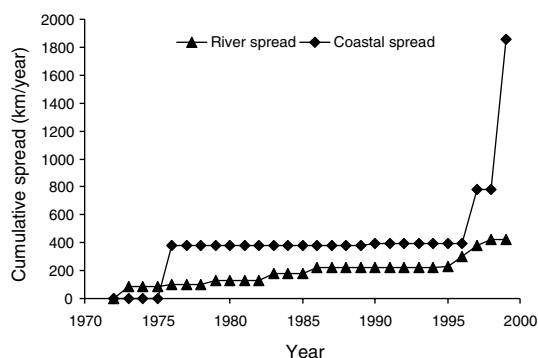


Figure 3. A comparison of the cumulative coastal and river spread by *Eriocheir sinensis* in the United Kingdom. The length of river occupied from the estuary to the furthest upstream record for each year (▲) and along the coast (◆) measured using Geographic Information System (GIS) Grass 4.3 software.

The rate of spread along the UK coast

For the first 19 years (1976–1995) after the initial sightings in the Humber and Thames rivers, no further expansion along the coast was observed. In 1997, additional sightings were reported along the south, west and east coast of the UK. On the east coast, there were records from the river Chelmer (Stansfield, personal communications), river Tees (Dutton, personal communication), and as far north as the river Tyne (230 km north of the Humber estuary) (Herborg et al. 2002).

On the south coast, sightings occurred in the river Rother/Royal Military Canal in 1997 (Dutton, personal communication) (105 km from the Thames) and the river Teign in 1999 (Robbins,

personal communications) (340 km west of the Rother). In 1999, a single Chinese mitten crab was caught in the Manchester Ship Canal, connected to the Mersey estuary on the west coast (Basterii, personal communication) (Figure 2). In 2001, migrating mitten crabs were caught at Shoreham power station, which takes cooling water from the river Ardur (Leach, personal communications).

Rate of coastal spread in Europe

The first report of a mitten crab in continental Europe, was in a tributary to the river Weser in

northwest Germany (Figure 4) in 1912 and in the Elbe in 1914. No further range expansion along the European coast was reported until 1927 (Figure 5). In the following 10 years the species dispersed rapidly in a westerly direction along the North Sea and English Channel coast and into northern France as far as St. Malo (1954) (André 1954). There was an average rate of spread of 441 km per year during the peak period of 1927–1931 (Table 2). In 1954, *E. sinensis* arrived at the west coast of France in the Gironde and Loire estuary, which are 206 km apart. Within 4 years (1958) it spread 256 km in a southerly direction from the Gironde to Hendaye on the French-

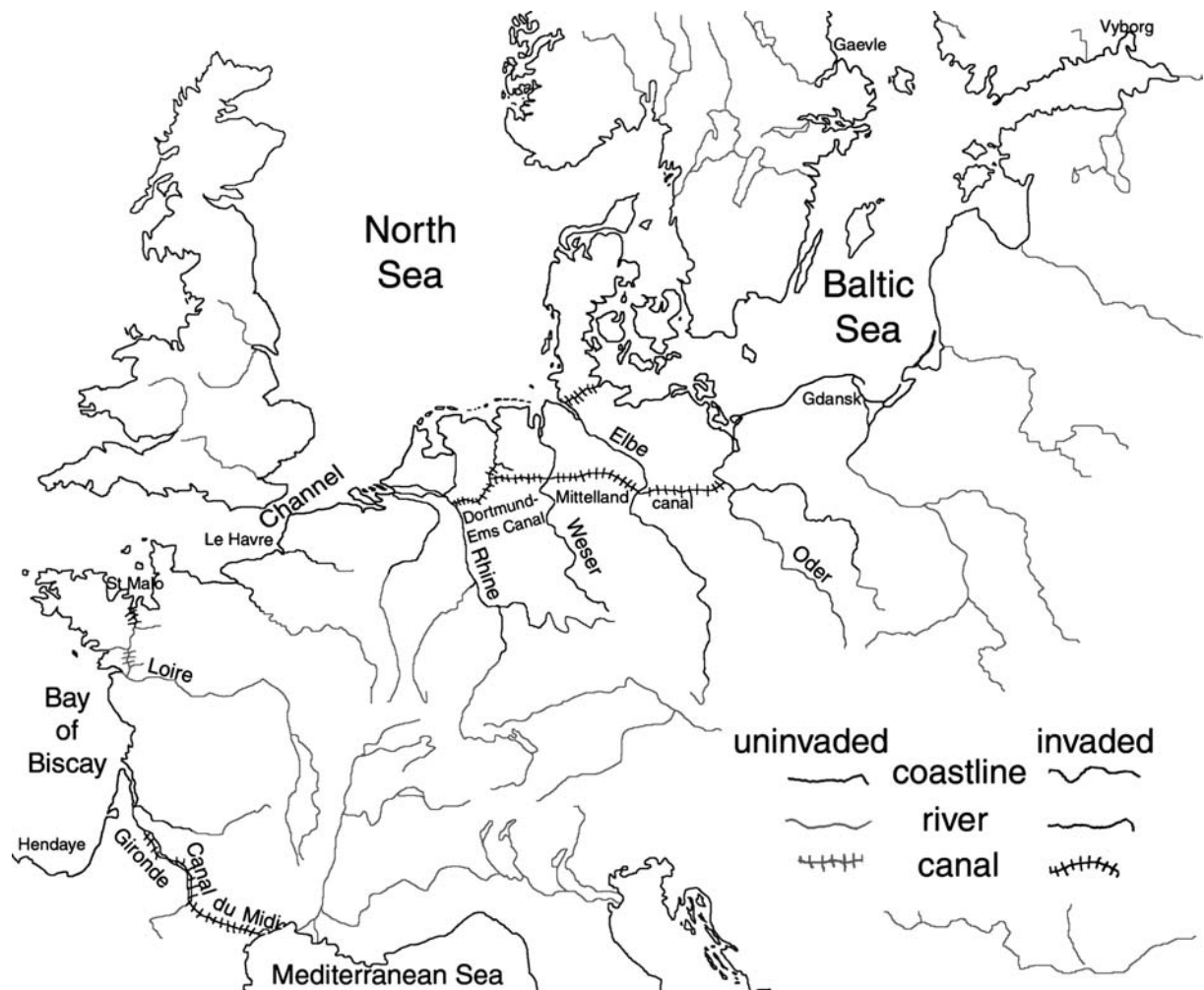


Figure 4. Distribution map of *Eriocheir sinensis* in Europe up to 1970, adapted from (Herborg et al. 2003). Grey line: coastline or major river; crossed grey line: canal; black line: coastline or river invaded by Chinese mitten crab; black crossed line: canal with *E. sinensis* sightings.

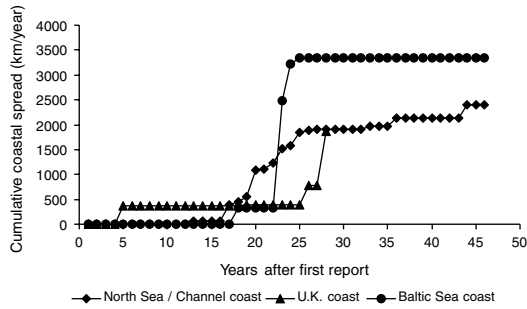


Figure 5. Comparison of cumulative coastal spread of *Eriocheir sinensis* in the United Kingdom (▲), North Sea/English Channel coast (◆) and the Baltic Sea coast (●).

Spanish border (Hoestlandt 1959) (Figure 4). The range expansion along the west coast of France is not included in the current data set, as it was treated as a separate invasion and the coastal data consisted of only three data points.

To the east, the mitten crab entered the Baltic Sea in 1928, spreading as far east as Vyborg in Finland by 1933, and as far north as Gävle in Sweden by 1934 (Peters 1938a) (Table 2). During the period 1928–1935, *E. sinensis* spread at an average rate of 355 km per year in the Baltic Sea.

Discussion

Observations on the spreading behaviour within UK rivers

The delay between the establishment of populations in UK rivers (Thames and Humber) and

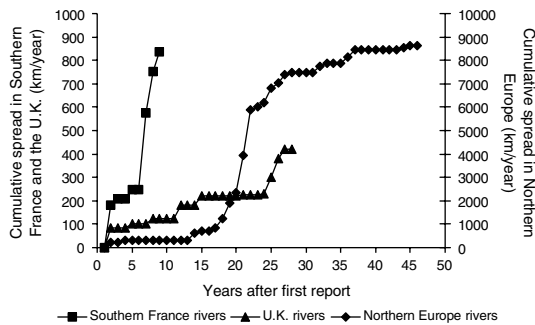


Figure 6. Cumulative river spread of *Eriocheir sinensis* in southern France (■), northern continental Europe (Poland, Germany, Denmark, Belgium, The Netherlands, northern France) (◆) and United Kingdom (▲) rivers in years after establishment. The first two curves are from (Herborg et al. 2003).

Table 2. Annual mean (±SD) coastal spread of *Eriocheir sinensis* along the United Kingdom coast, North Sea/English Channel coast and the Baltic Sea coast. The peak period was determined by the asymptotic section of the curves in Figure 5. The spread in the Baltic Sea does not display a distinct period of peak spread.

Coastal spread	Total observation period		Peak spread period	
	Period	km/year (±SD)	Period	km/year (±SD)
North Sea/Channel	1923–1954	75 (±128)	1927–1937	168 (±163)
Baltic Sea	1928–1935	416 (±746)	NA	NA
United Kingdom	1976–1999	78 (±238)	1997–1999	448 (±545)

their subsequent range expansion has also been observed in northern Europe (Herborg et al. 2003). A period of establishment is characteristic of many invasive species, such as the Japanese beetle (*Popillia japonica*) (Elton 1958; Hengeveld 1989), the red deer (*Cervus elaphus* L.) (Clarke 1971) and the European starling (*Sturnus vulgaris*) (Elton 1958; Hengeveld 1989). In contrast, there was a continuous expansion of the Chinese mitten crab in the Gironde river in southern France (Figure 6), although the possibility that the crab arrived earlier than reported cannot be excluded (Herborg et al. 2003).

There are several possible explanations for the large increase in distribution of the Thames population during the interval 1992–1996 (Figure 3). The climate in the UK was particularly dry in 1989–1990, and consequently low river flows (Attrill and Thomas 1996). This could have resulted in larval retention through reduced wash out to the ocean. Another consequence of low river flow is that the estuarine salt wedge projects further up the estuary. Since salinity is a key factor for larval mitten crab development (Anger 1991) and migrations in other species of catadromous crustaceans (Paula 1998), a preference for high salinity water could account for larval retention through a behavioural mechanism. Therefore, *E. sinensis* larvae may be retained to a greater degree within the estuary during drought years.

Low river flow in the Thames over the period of 1989–1990 resulted in the disappearance of taxa intolerant to increased salinity (Attrill et al.

1996). This disturbance event, which caused the die-off to many sessile species, in combination with better larval retention and more favourable salinities for development, resembles conditions described by Cohen and Carlton (1995). They suggested that similar microhabitats act as incubators for invasive species and may explain the rapid invasion of San Francisco Bay by *Carcinus maenas*. The hypothesis was based on their observations of artificial Lagoons where sessile organisms were killed during winter by reduced water levels and freshwater influx, whilst in summer a favourable constant water level and salinity was maintained, allowing larvae to survive.

Reduced pollution levels in the Thames and the Humber in the 1990s could also have increased the reproductive success of the present populations (Attrill et al. 1996). Moreover, the increased sampling and public awareness in 1995 likely account, at least in part, for the increased number of citations. Nevertheless, an ongoing monitoring programme in the West Thurrock Power Station (river Thames) recorded a several-fold increase in mitten crabs in 1992, indicating an increase in population number (Clark et al. 1998). Sampling in Tilbury Power Station (river Thames) in 1996 also supported a real population increase (Clark and Rainbow 1996).

The average rate of range expansion upstream per river system in the UK during the peak period of range expansion (1995–1998) was 49 km per year. This is lower than values at the time of peak spread in northern Europe (562 km per year) and southern France (104 km per year) (Herborg et al. 2003) (Table 1). These differences in rates may reflect differences in the river systems of continental Europe and the UK. In contrast to the UK, there are several long rivers (Elbe, Weser, Rhine, Oder, etc.) in continental Europe, interconnected by canals that offer extensive invasion corridors, linking the North Sea to the Baltic as well as the Black Sea and the Caspian Sea (Bij de Vaate et al. 2002). Once mitten crabs became established in the Elbe and Weser they were able to disperse via the Mittelland canal and the Oder into the Baltic Sea. The average overall annual rate of spread upstream is also much lower in the UK (16 km per year) in comparison to northern Europe (196 km per year) which could reflect a

longer period of establishment in the UK of 22 years (Table 1; Figure 6).

Coastal spread in Europe and the UK

Spread of *E. sinensis* between estuaries in close vicinity to each other, like the Elbe and Weser (≈ 60 km), could be caused by larval drift. Where estuaries are further apart, the duration of the pelagic larval phase, as well as the prevailing currents, have to be taken into consideration. Although the main current along the English Channel and North Sea coast of continental Europe runs in a north easterly direction, simulations of dispersal dynamics showed that winds can move coastal larval patches against this prevalent current in a south westerly direction (Ellien et al. 2000). This would allow the coastal dispersal of *E. sinensis* by larval drift from Germany to the Netherlands, then Belgium and France. Alvarez et al. (2001) found that the net transport along the Bay of Biscay, on the west coast of France, ran in a northerly direction, the opposite direction of the Chinese mitten crab's main range expansion.

Due to the limited knowledge on the larval biology of this species, it is difficult to determine a maximum distance of 'natural spread' along the coast as opposed to 'unnatural', human-aided transport. Part of the range expansion of the Chinese mitten crab along European coasts was almost certainly facilitated by human transport, particularly some of the very long distance 'jumps' e.g., in the UK from Thames to Humber (390 km) (Figure 2), in the Baltic Sea from Gdansk to Vyborg (964 km), and along the French coast from Le Havre to Gironde (855 km) (Figure 4). The two most likely routes of migration of this species are as larvae in ballast water (Cohen and Carlton 1997), and as crabs associated with mussel and oyster stock transfers which occurred along the north and east coasts of France (Gouletquer et al. 2002). *E. sinensis* could have been introduced to the river Loire, by two routes (1) human transport along the coast or (2) by the canal system that links St Malo to the Loire through Rance, Vilaine and the Brest-Loire canal (240 km) (André 1954). It is therefore difficult to distinguish between 'natural' and 'human-mediated' spread.

Table 3. Rates of coastal spread for aquatic invaders from the literature (adapted from (Grosholz 1996).

Species	Spread (km/year)	Coastline	Source
<i>Carcinus maenas</i>	20, 31	Western North America	(Grosholz and Ruiz 1996)
<i>Carcinus maenas</i>	63	Eastern North America	(Grosholz and Ruiz 1996)
<i>Carcinus maenas</i>	16	South Africa	(Grosholz and Ruiz 1996)
<i>Carcinus maenas</i>	1.7	South Australia	(Thresher et al. 2003)
<i>Hemigrapsus sanguineus</i>	12	Eastern North America	(McDermott 1991)
<i>Elminius modestus</i>	30	Northwest Europe	(Crisp 1958)
<i>Mytilus galloprovincialis</i>	115	South Africa	(Hockey and van Irsome 1992)

Rate of coastal spread in Europe and UK compared with other species

The reported coastal rates of dispersal can be compared to those of other marine invaders from comparable climatic regions (Table 3, adapted from (Grosholz 1996)). Marine decapod crustaceans such as *C. maenas* and *Hemigrapsus sanguineus* show relatively slow rates of spread (except *C. maenas* of the eastern North American coast where it reached 63 km per year) (Grosholz and Ruiz 1996; McDermott 1991). The barnacle, *Elminius modestus*, spread at an average rate of 30 km per year along the northwest coast of Europe (Crisp 1958), and the mussel *Mytilus galloprovincialis* reached 115 km per year along the South African coast (Hockey and van Irsome 1992). The comparable rate of range expansion for *E. sinensis* suggests this species and other marine invaders with a pelagic larval phase are influenced by similar natural and human associated transport vectors.

UK invasion in comparison to northern Europe

The Chinese mitten crab became established in the UK (1973) much later than the rest of Europe (1912). This is remarkable in view of the constant ship traffic between mainland Britain and continental Europe where there were thriving populations of *E. sinensis* and from where one might expect to have been a constant propagule supply. Nevertheless, this did not lead to the species' establishment in the UK for more than 60 years. There is evidence for at least two separate introductions in 1935 and 1949 (Ingle and Andrews 1976; Wall and Limbert 1983), both of which failed to become established. It seems, therefore, that the establishment was either

dependent on some change in environmental conditions, or a chance event (Carlton 1996).

Coastal spread in the UK and Europe in comparison to river data

The Chinese mitten crab is one of few aquatic invaders which allows observations of freshwater spread caused by juveniles, adults actively searching for a suitable habitat, and coastal dispersal based on passive larval drift and human-aided transport, to be made simultaneously. Coastal spread within the UK, as well as in northern Europe, shows similar temporal patterns to upstream dispersal (Figure 5). In both cases, an increase in range expansion within the rivers occurred at the same time as the spread along the coast (Tables 2 and 3). These observations suggest that populations increased, causing them to exceed the carrying capacity in the home range and to extend into other habitats further upstream. The available catch data in the Elbe shows an increase in the annual catch in the 1930s, up to 242 tonnes in 1936, during which period the annual spreading rates were at their highest as well (Panning 1938b; Herborg et al. 2003). Higher numbers were also caught in the Thames in 1992 (Clark et al. 1998) which was followed by a marked increase in range expansion of *E. sinensis* in 1995 (Figure 3). The recent invasion of San Francisco Bay (since 1992) also shows a close link between population number and inland range expansion (Rudnick et al. 2003). These observations point towards a population increase at the same time as range expansion. In the marine environment, an increased population would give rise to increased numbers of pelagic larvae which could arrive in adjacent estuaries, either naturally or

through human-aided transport, in sufficient numbers to establish new populations.

Conclusions and outlook

An overall analysis of the range expansion of *E. sinensis* clearly illustrates the invasive potential of this species. Focusing on the UK, there is little doubt that that *E. sinensis* will spread along the west coast and become established in larger estuaries with shipping traffic, like the Severn and Mersey estuaries, as it has done on the east coast. Also small dormant populations in the larger estuaries will most likely increase and disperse further inland. This emphasises the importance of a monitoring programme for an aquatic invader like the Chinese mitten crab, even if it is 'just' a rare occurrence in an estuary; prior records demonstrate its ability to rapidly expand once the local population reaches a critical density, and/or conditions become favourable.

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