Hydrobiologia **503:** 21–28, 2003.
M.B. Jones, A. Ingólfsson, E. Ólafsson, G.V. Helgason, K. Gunnarsson & J. Svavarsson (eds), Migrations and Dispersal of Marine Organisms.
© 2003 Kluwer Academic Publishers. Printed in the Netherlands.

Spread of the Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards) in Continental Europe: analysis of a historical data set

L.-M. Herborg[1], S. P. Rushton[2], A. S. Clare[1] & M. G. Bentley[1]
[1]*School of Marine Science & Technology, Ridley Building, University of Newcastle-upon-Tyne, Newcastle upon Tyne, NE1 7RU, U.K.*
[2]*Centre for Life Science Modelling, School of Biology, Porter Building, University of Newcastle-upon-Tyne, Newcastle upon Tyne, NE1 7RU, U.K.*
E-mail: leif-matthias.herborg@ncl.ac.uk

56420

Key words: invasive species, *Eriocheir sinensis*, crustacean, migration, catadromous, Europe

Abstract

The Chinese mitten crab, *Eriocheir sinensis* (H. Milne Edwards), is an invasive species that lives as an adult predominantly in freshwater but migrates seawards to breed. It has spread via ballast water and/or intentional introduction to Continental Europe, Southern France, U.S.A. (San Francisco Bay) and the United Kingdom. Analysis of detailed historic data from the outbreak in Europe was digitised and analysed using Geographical Information Software. This revealed that there were two separate invasions in Northern Europe and Southern France, with an average range expansion during the peak period of 562 km/year from 1928–1938 (Northern Europe) and 380 km/year from 1954–1960 in Southern France. Size class distribution data from the lower estuary of the River Elbe (Germany) (1932–1936) illustrate migration patterns to and from the estuary over the year. Marking experiments determined that the mean rate of downstream migration for adults was 11.5 km/day (SD 3.54; n=7), up to a maximum of 18.1 km/day. The carapace width of upstream-migrating animals increased by 3 mm/100 km. The peak period for upstream migration was March to July, followed by the downstream season from July to September. This data set, extracted from historic references, represents one of the most complete pictures of the life cycle and spreading behaviour of this alien invader.

Introduction

The Chinese mitten crab, *Eriocheir sinensis* (H. Milne Edwards), originates in the Far East, its native range extending from Hong Kong (≈22° N) to the border with North Korea (≈40° N) (Hymanson et al., 1999). It is catadromous returning to the sea to reproduce once or rarely twice and then die. During the upstream migration of juveniles from estuaries, mitten crabs can reach rivers, lakes, and ponds as far as 1200 km from the coast (Peters, 1933). There they grow and mature. The age at which *E. sinensis* reaches sexual maturity varies from 1–3 years in China (Jin et al., 2001) to 3–5 years in Europe (Schubert, 1938). The Chinese mitten crab returns, when sexually mature at the end of its life cycle, to estuaries for reproduction in late summer. After mating, females move into the more marine parts of the estuary and release their larvae in early spring. Similar to *E. japonica* (de Haan), *E. sinensis* releases up to three batches of eggs (Peters, 1933; Kobayashi & Matsuura, 1999; Kobayashi, 2001). After one reproductive season, the life cycle of most *E. sinensis* draws to an end and they die (Peters, 1938c). Larval development consists of 6 pelagic stages (1 prezoea, 5 zoea) lasting ca. 90 days at 12 °C (Anger, 1991; Montu et al., 1996). After settlement, juvenile crabs migrate upstream. The pelagic larval stages are the most likely vector of spread for *E. sinensis* in ship's ballast water (Peters, 1933; Cohen & Carlton, 1997).

This invasive species has several impacts on humans and biodiversity. Firstly, it interferes with recreational and commercial fishing; in the San Francisco Bay area, the presence of mitten crabs has lead to commercial shrimp trawlers abandoning certain fish-

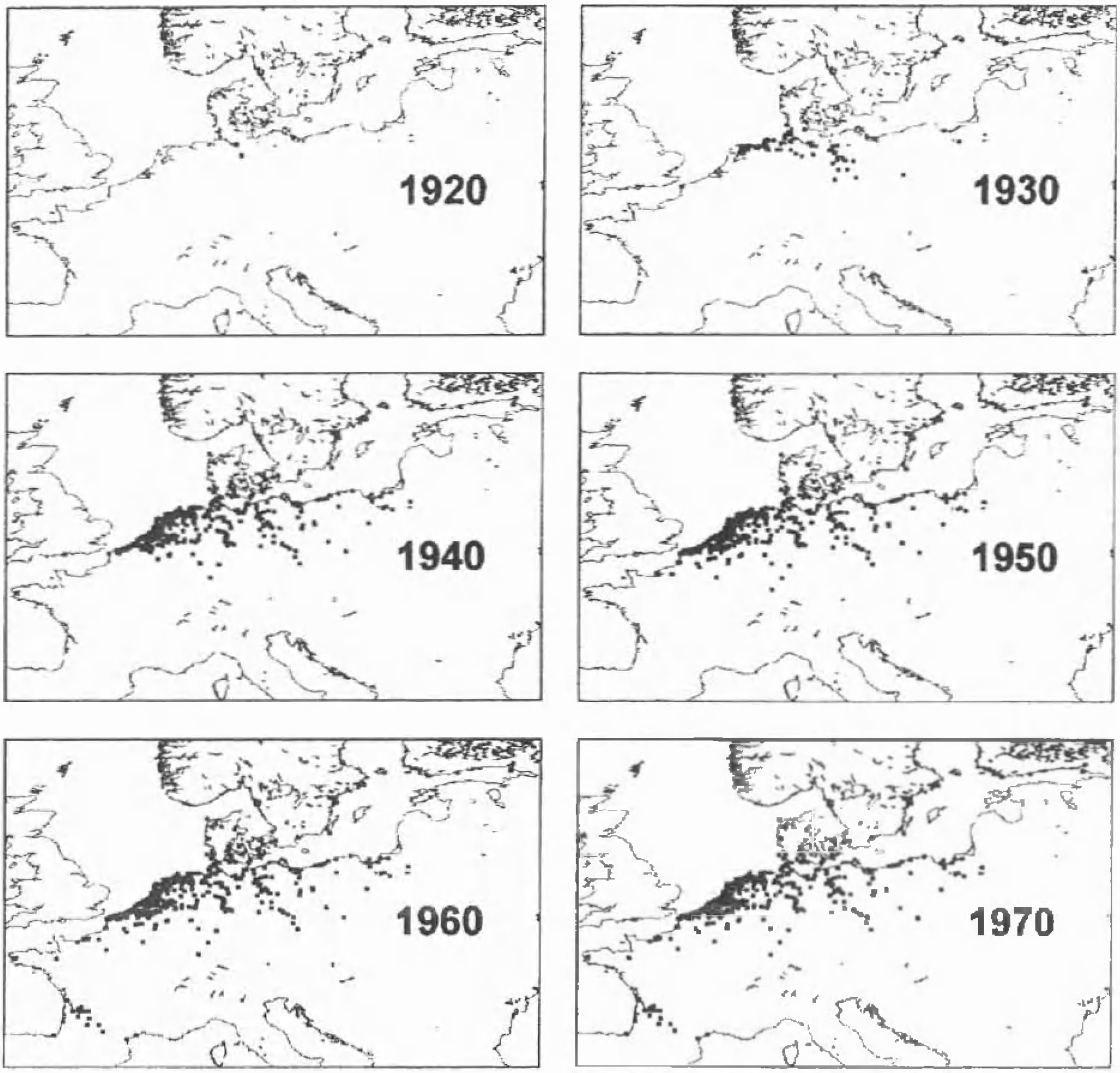

Figure 1. Cumulative sightings of *Eriocheir sinensis* from the literature across Continental Europe between 1912 and 1970.

ing areas. In the same area, there have been numerous complaints from recreational fishermen who blame the crabs for causing an increased loss of bait (Veldhuizen & Stanish, 1999). Similar problems have been recorded in Europe where Ingle (1986) reported that, in 1981, Dutch fishermen suffered serious net damage from mass occurrence of the mitten crab. Secondly, the burrow-digging habit of *E. sinensis* can cause serious river bank erosion. This is observed mainly in tidally-influenced areas, or other stretches of rivers with fluctuations in water level. Burrows are made in river banks with a step gradient, and the necessary structural strength to allow burrowing. They can be located anywhere between the high-water mark, under reed banks to below the low-water mark with the highest occurrence around mid- water level (up to $30/m^2$) (Peters, 1933, 1938b; Dutton & Conroy, 1998). Thirdly, *E. sinensis* may compete for resources with local freshwater fish and invertebrates. Overlap of dietary and habitat preferences with the economical important introduced signal crayfish (*Pacifastacus leniusculus*, Dana) occurs in San Francisco Bay (Veldhuizen & Stanish, 1999). In Britain, the already threatened native crayfish (*Austropotamobius pallipes*, Lereboullet) could face similar pressure (Clark et al., 1998). Large numbers of mitten crabs occurring in some areas, their large size and aggressive behaviour, in combination with overlap in feeding and habitat selection, gives rise to concerns about the possible impacts of current and future invasions (Clark & Rainbow, 1996).

The sight of thousands of crabs migrating overland around weirs in Europe in the 1930s was a major factor in raising public awareness. The scale of the occurrence of this crustacean in rivers and lakes, especially during migrations has caused sufficient public interest to engender many publications documenting its spread. Some of these provide much data on population distribution, migration patterns and spread particularly in Germany (Peters, 1933, 1938a; Panning, 1933, 1938a, b). The aim of this study was to analyse the invasion of *E. sinensis* in continental Europe, using literature contemporary with the major outbreak in.

Materials and methods

The spread characteristics of the Chinese mitten crab during two invasive events in Northern Europe (ca. 1910–1950) and in Southern France (ca. 1950–1960) were quantified. This was achieved by digitising all sightings (*n*=646) from the literature (Fig. 1) and using Geographic Information System (GIS) GRASS 4.0 software to measure the total length of river occupied from the estuary to the furthest upstream record for each year. Therefore, if in year 1 crabs were found 40 km upstream from the estuary in a particular river and in year 2 were 60 km upstream from the estuary in the same river, the average annual distance of upstream migration is 30 km/year. This unit of measurement was chosen since each population found further upstream than any previously observed ones must originate from the estuary due to its migration behaviour.

Size distribution data of the mitten crab populations over several years were collected and a wide area of Germany assessed during the 1930s' invasion (for population distributions see Peters, 1933; Panning, 1938a; for migration, see Peters, 1933; Panning, 1938b). This information from the major invasions in northern Europe has been analysed to describe the life-history characteristics of this species. Data from the Lower Elbe from 1932–6 were pooled for each month of the year to obtain average monthly size-class distributions of *E. sinensis*. The data (*n*=8736) were derived from various sampling methods: small specimens (as small as 2 mm) were collected in large numbers from the banks of the river Elbe throughout the year; larger crabs were collected on an occasional basis from the catches of fishermen using bottom trawls, gill nets and eel buckets. Size classes within the population in the Elbe were determined using modal class progression analysis (Bhattacharya's method) in the FiSAT stock assessment package. Using this method, different cohorts within the monthly size-frequency distribution data could be identified, and a mean and standard deviation derived. It should be noted that all size measurements used in the historic literature are in mm carapace length (cl), rather than the carapace width used in more recent literature. Therefore, carapace length is used during the analysis; this can be transformed into carapace width using the formula derrived by Peters (1933):

$$\text{carapace width (mm)} = 1.13 \times \text{carapace length (mm)}.$$

Migratory behaviour was assessed using catch (in kg) from crabs collected in various types of traps placed at weirs to catch mitten crabs during migration. These were installed in the 1930s to reduce the mitten crab population which was a major pest by this time. Based on the structure of these traps, the only crabs caught were those migrating across or around the weir (Panning, 1938b). Panning (1938b) used carapace marking experiments to determine the downstream migratory speed of *E.sinensis* over various distances. The recatch occurred either in the crab traps around a weir or by fishermen.

Results

Spread across Continental Europe and Southern France

The first record of *E. sinensis* was in 1912 in a tributary of the River Weser in North Germany (Peters, 1933); it was also found in the River Elbe from 1914 onwards (both rivers run into the North Sea only 60 km apart). From there, it reached the Baltic Sea via the Kiel Canal in 1927 (Peters, 1938a). Despite the fact that the number of mitten crabs in the Baltic remained much lower than in the river systems along the North Sea, the species spread as far as Vyborg (Russia) and Finland by 1933. In the Netherlands, the first crab was recorded in 1931 and the population had spread into most rivers by 1936 (Kamps, 1937). It reached Belgium in 1933

(Peters, 1938a and citations within; Leloup, 1937). France was invaded by 1930 (Hoestlandt, 1945) and Denmark by 1927 (Rasmussen, 1987).

An important finding was also the extent of spread upstream in some rivers. *E. sinensis* had migrated along the tributaries of the Elbe as far as Prague in the Czech Republic (700 km inland) by 1932 (Peters, 1938a). In the same year, it had reached 512 km along the Rhine and, by 1934, it had spread 464 km upstream in the Oder to Breslau. Analysis revealed that a separate invasion occurred along the river Gironde (1954–1960) in Southern France. Previously, *E. sinensis* had spread only as far as Le Havre (1943) along the French Channel coast (Hoestlandt, 1959; Vincent, 1996). In 1954, specimens were caught in Nantes in the River Loire estuary and the same year near Bordeaux in the estuary of the Gironde. Migrating upstream in the Gironde, the mitten crab reached the artificial lagoons along the Mediterranean coast via canals by 1959, a distance of 504 km (Petit & Mizoule, 1974). These measurements gave an average total distance of upstream migration of 48 km/year between 1912–1927, 562 km/year for 1928–1939 and 69 km/year in 1940–1955 for Northern Europe, and 104 km/year for Southern France (1954–1960) (Fig. 2). The distance recorded upstream for the northern European and southern French river systems in each year of the invasion is shown in Figure 2. In Northern Europe the Chinese mitten crab spread slowly over a 15-year period (1912–1927) but then spread rapidly from 1928 to 1939, slowing afterwards. Part of the apparent slowing in the spread of mitten crabs in Northern Europe after 1939 might be related to the reduced monitoring effort during the war. In Southern France, records show no establishment phase but a rather sharp increase in spread between 1954 and 1960.

Observations on population distribution and migratory pattern

The size-class distribution (Fig. 3) of mitten crabs (both male and female) in the lower Elbe shows the presence of at least two different cohorts during spring: a larger/adult class (54.6 mm ± 5.3 mm cl for January) disappearing in May, and a smaller/juvenile class (29.8 mm ± 7.6 mm cl for January) decreasing in size considerably by May (12.4 mm ± 3.4 mm cl). The smaller cohort remained over the whole year, fluctuating in mean size between 8.6 mm ± 3.5 mm cl (September) and 20.7 mm ± 4.4 mm cl (December). In June, the larger cohort was found again in the estuary with a smaller carapace length (31.5 mm ± 6.7 mm), increasing gradually until December to 51.7 mm ± 4.9 mm cl.

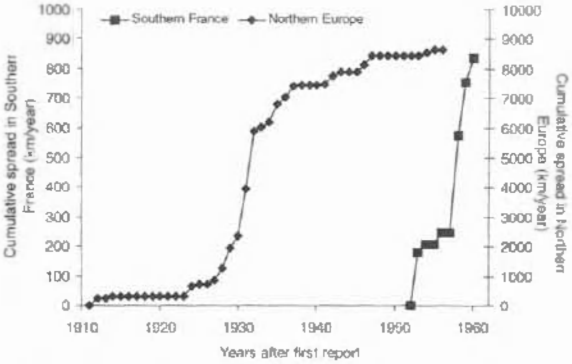

Figure 2. The cumulative total length of river (in km) occupied by *Eriocheir sinensis* from the estuary to the furthest upstream record for each year, measured using Geographic Information System (GIS) GRASS 4.0 software. The spread in Northern Europe (■) is plotted separately from the spread in Southern France (♦). Note the different scales of distance of river invaded used for the two invasions.

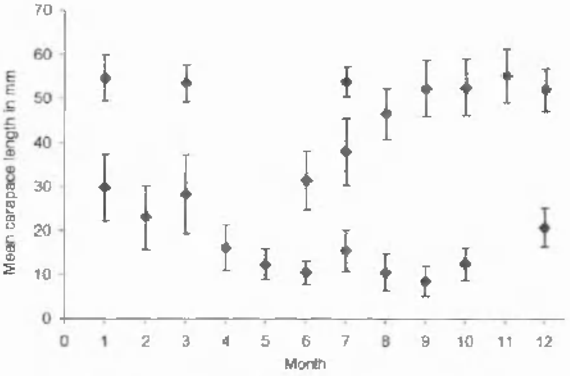

Figure 3. The size-class distribution (± 1 SD) of *Eriocheir sinensis* in the lower Elbe per month as determined using modal progression analysis (Bhattacharya's method) in the FiSAT stock assessment package.

The mean carapace length of upstream-migrating *E. sinensis*, measured using animals caught in traps at weirs along the Weser and Elbe, showed an average carapace length increase of 3 mm per 100 km upstream from the estuary (Fig. 4) (Panning, 1938b). This can be used to estimate the annual growth rate as 6.6 mm over the annual migration distance of 225 km (according to Panning, 1938b). The annual growth rate estimated by (Panning, 1938a) suggests an increase of about 12 mm per year up to year 4. Despite the discrepancy of these growth rates, they are the only available estimates for *E. sinensis* in Europe. The peak downstream migration period at three locations (estuarine, 310 km upstream,

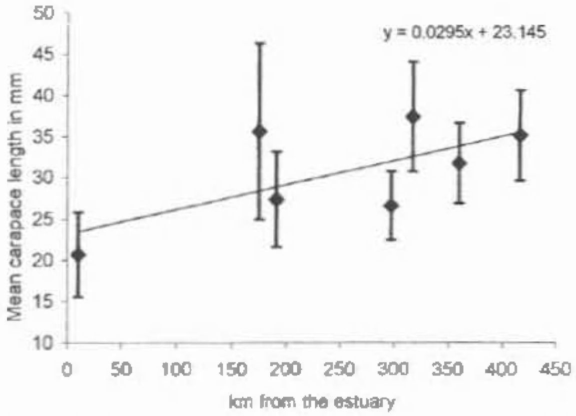

Figure 4. The mean carapace length (in mm) of *Eriocheir sinensis* migrating upstream along the Rivers Elbe and Weser (Germany).

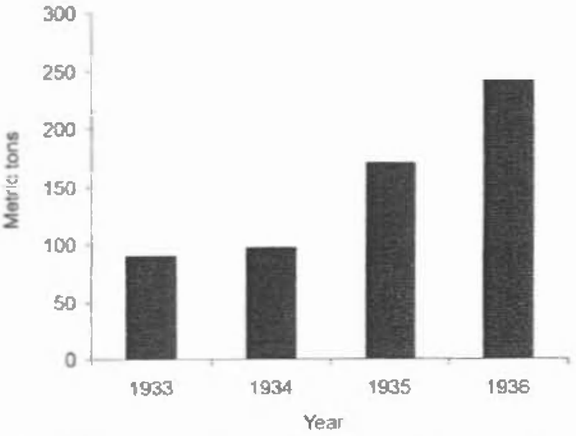

Figure 5. The annual catch of *Eriocheir sinensis* (in metric tons) from the River Weser and Elbe (Germany) during the invasion of Northern Europe (1933–1936).

410 km upstream) was August–October. Absence of a difference in migration period between these sites can be explained using downstream marking experiments. These showed that mature animals can cover large distances (400 km or more) within this 3-month migration period, since analysis revealed an average downstream migration speed of 11.5 km/day (SD± 3.54) (Panning, 1938b).

Using the catch data from the rivers Elbe and Weser, population numbers can be estimated for the mid 1930s; the peak catch occurred in 1936 with an annual catch of mitten crabs totalling 242 tonnes in Germany alone (Panning, 1938b) (Fig. 5). Based on an average weight of 55 g per individual from collections in the river Thames by Herborg (unpubl. data), total catch can be estimated to be the equivalent of 4.4 million crabs. Considering this is only an estimation for two rivers out of many in Europe this species has invaded, the total population must have been very large.

Discussion

The most obvious feature of these results is the similar pattern in expansion in length of river colonised in both Southern France and Northern Europe. In both river systems there is evidence of a sigmoidal relationship between length of river invaded and time. Whilst the pattern may have been similar, comparison of the rates of spread between Northern Europe and Southern France indicates a much faster rate of spread during the exponential phase of the spread in Northern Europe. These differences probably reflect differences in the structure of the two river systems. In Northern Europe, river systems are extensive, especially along the North Sea coast where the Rhine, Weser and Elbe give access to an extended network of tributaries as well as to canals linking to other rivers. The outbreak in Southern France was limited by the nature of the Gironde system, which is less extensive. Towards the south, the Pyrenees form a natural barrier and, to the north of the Gironde, relatively few large rivers run into the Bay of Biscay.

The presence of a 15-year period of slow spread in Germany at the early stage of invasion can be interpreted as an 'establishment' phase which is observed commonly during invasions (Drake & Williamson, 1986). Absence of a establishment phase in Southern France may be due to a lack of data, or perhaps that the Chinese mitten crab population, at this time already present for over 40 years in Europe, was well acclimatised to European environmental conditions. Another factor associated with a sharp population increase of *E. sinensis* is periods of low river flow as observed for the U.K. in 1989–1992 (Attrill & Thomas, 1996).

The pattern of spread of the Chinese mitten crab in Europe compares well with the spread of the European shore crab (*Carcinus maenas*, L.) along the Californian coast. Both species have a similar pelagic larval period in their life cycles (ca. 60 days in 20 °C) (Anger, 1991; Cohen et al., 1995). Observations of the invasion rates of *C. maenas* also showed fluctuations (between 16 and 63 km/year) in the rate of spread along the coast in different invasive events (Grosholz & Ruiz, 1996 and citations within). Grosholz (1996), analysing the rate of spread for 10 invasions of the marine environment, reported an average rate of spread for marine invaders of 50.7 km/year with individual values between 12 and 115 km/year. Estimates of the rate of spread for three invertebrate species (*Balanus improvisus*, Darwin,*Potamopyrgus antipodarium*, J.E Gray, *Marenzelleria viridis*, Verrill) in the Baltic Sea range between 30 and 480 km/year (Leppaekoski & Olenin, 2000). The sigmoidal rate of spread has also been described in other invasions: the spread of red deer (*Cervus elaphus*, L.) on the South Island of New Zealand described a 40-year establishment phase before the area of invasion increased rapidly, flattening off again after ca. 20 years (Clarke, 1971).

Whilst the spread of *E. sinensis* in Northern Europe seems to originate from the Weser area, the question arises as to the origin of the Chinese mitten crab at this site. An introduction via ballast water from China is the most likely vector, since there has been frequent ship traffic from Hamburg (River Elbe) and Bremen (River Weser) to China since the end of the 19th century. The typical steamer on this route had 15 ballast water tanks, each holding 90 tonnes, with an intake grid of 15 × 460 mm, large enough not only for larvae but also juvenile mitten crabs. Peters (1933) mentions the case of two adult mitten crabs (40–50 mm) which were found in the sea chest of one of these vessels during its salvage. Introduction of the Chinese mitten crab is considered as one of the very first known cases of a species being transported via ballast water (Carlton, 1985).

It is likely that invasion of Southern France arose in a similar way. The arrival of mitten crabs in Southern France demonstrated a significant jump in spread along the coast. Before 1954, the year the Chinese mitten crab appeared in the Gironde and the Loire, it had only been reported from the Seine, a distance of 855 and 205 km along the coast, respectively. Considering this distance, as well as the prevailing surface transport going northwards (Ellien et al., 2000; Alvarez et al., 2001), larval transport along the coast is highly unlikely. The most likely vector is human-aided transport, most likely via ship ballast water or in association with the intensive oyster aquaculture along this coast. Furthermore, the long time gap between the invasion of the northern Atlantic coast of France, and that of the Bay of Biscay, also suggests that a chance ship transport across an expansion barrier was the mechanism of introduction rather than natural spread.

The size-frequency distribution of crabs in the Elbe estuary over the year shows the recruitment, departure and arrival of different cohorts of animals according to their life cycle. At the beginning of the year, a large and small cohort was observed. The larger cohort comprised animals in excess of 43 mm, the minimum size for sexual maturity of both sexes, and are most likely animals from the previous autumn's mating season which are either ovigerous females or part of the small fraction which survives the mating season (Peters, 1933). The size reduction of the juvenile cohort from March to April coincided with the peak upstream migration period as determined by migration rates (data not shown). The carapace length of juveniles leaving the estuary may indicate that the smaller cohort observed in the Elbe (January–March) consisted of year-class 1 and 2, whereas from May onwards, only smaller crabs of the year 1 cohort remained in the estuary and the year 2 cohort started their migration further upstream.

Fluctuation of the mean size of the juvenile cohort during the summer and autumn months could be caused by two separate factors. Firstly, the settlement of megalopa larvae from the water column in July–September (Schubert, 1938) at a length of 5mm (Schnakenbeck, 1933) and, secondly, continuous growth of the previous year class. The larger size class appearing in the Elbe as early as July may be explained as being either animals which remained in the lower part of the estuary, or juveniles migrating downstream to the estuary to become sexually mature. Further increase in this cohort is caused by adult crabs arriving downstream during the peak migratory period (August–October). Analysis of catch numbers along the Elbe and Weser showed that August to October is the peak downstream migration period in the River Elbe (data not shown).

Recent invasions of Chinese mitten crabs in Great Britain (Attrill & Thomas, 1996; Clark et al., 1998; Herborg et al., 2002) and San Francisco Bay (Rudnick et al., 2003) show similar patterns of spread to those analysed here. There is also evidence that the invasion process is ongoing, as recent findings of *E. sinensis* in the Black Sea (Gomui et al., 2002) and the Sea of Azov (Murina & Antonovsky, 2001) underline. The study presented highlights the potential of major invasions of *E.sinensis*. There has been little description in the historic work of the ecological impact of invasions such as those discussed here. Nevertheless, considering the size of the population at its peak, ecological impacts may well have been considerable. What is required now is some quantification of these impacts, in order that threats to biodiversity can be assessed and requirements for management of the invasion problem identified.

Acknowledgements

LMH would like to thank the Faculty of Science, Agriculture and Engineering, University of Newcastle (Swales Studentship) and the Esmeé Fairbairn Foundation (RG 01-1816) for their financial support.

References

Alvarez, P., L. Motos, A. Uriarte, J. & Egana, 2001. Spatial and temporal distribution of European hake, *Merluccius merluccius* (L.), eggs and larvae in relation to hydrographical conditions in the Bay of Biscay. Fish. Res. 50: 111–128.

Anger, K., 1991. Effects of Temperature and salinity on the larval development of the Chinese mitten crab *Eriocheir sinensis* (Decapoda, Grapsidae). Mar. Ecol. Prog. Ser. 72: 103–110.

Attrill, J. M. & R. M. Thomas, 1996. Long-term distribution patterns of mobile estuarine invertebrates (Ctenophora,Cnideria, Crustacea: Decapoda) in relation to hydrological parameters. Mar. Ecol.- Progr. Ser. 143: 25-36.

Carlton, J. T., 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanogr. mar. Biol. 23: 313–371.

Clark, P. & P. Rainbow, 1996. The Chinese mitten crab in the Thames catchment. 000208370, Environment Agency Report.

Clark, P. F., P. S. Rainbow, R. S. Robbins, B. Smith, W. E. Yeomans, M. Thomas & G. Dobson, 1998. The alien Chinese mitten crab *Eriocheir sinensis* (Crustacea: Decapoda: Brachyura), in the Thames catchment. J. mar. biol. Ass. U.K. 78: 1215–1221.

Clarke, C. M. H., 1971. Liberations and dispersal of red deer in northern South Island districts. New Zeal. J. For. Sci. 1: 194–207.

Cohen, A. N. & J. T. Carlton, 1997. Transoceanic transport mechanisms: introduction of the Chinese mitten crab, *Eriocheir sinensis*, to California. Pacif. Sci. 51: 1–11.

Cohen, A. N., J. T. Carlton & M. C. Fountain, 1995. Introduction, dispersal and potential impacts of the Green Crab *Carcinus maenas* in San Francisco Bay, California. Mar. Biol. 122: 225–237.

Drake, J. A. & M. Williamson, 1986. Invasions of natural communities. Nature 319: 718–719.

Dutton, C. D. & C. Conroy, 1998. Effects of burrowing Chinese mitten Crabs (*Eriocheir sinensis*) on the Thames Tideway. Environment Agency Report.

Ellien, C., E. Thiebaut, A. S. Barnay, J. C. Dauvin, F. Gentil & J. C. Salomon, 2000. The influence of variability in larval dispersal on the dynamics of a marine metapopulation in the eastern Channel. Oceanol. Acta. 23: 423–442.

Gomui, M. T., B. Alexandrov, N. Shadrin & T.Y. Zaitsev, 2002. The Black Sea – a recipient, donor and transit area for alien species. In Leppaekoski, E. S. Gollasch & S. Olenin (eds), Invasive Aquatic Species of Europe. Distribution, Impacts and Management. Kluwer Academic Publishers: 341–350.

Grosholz, E. D., 1996. Contrasting rates of spread for introduced species in terrestrial and marine systems. Ecology 77: 1680–1686.

Grosholz, E. D. & G. M. Ruiz, 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. Biol. Conserv. 78: 59–66.

Herborg, L.-M., M. G. Bentley & A. S. Clare, 2002. First confirmed record of the Chinese mitten crab (*Eriocheir sinensis*) from the River Tyne, United Kingdom. J. mar. biol. Ass. U.K. 82: 921–922.

Hoestlandt, H., 1945. Le crabe chinois (*Eriocheir sinensis* Mil. Ed.) en Europe et principalement en France. Ann Epiphy. XI: 223–233 (in French).

Hoestlandt, H., 1959. Répartition actuelle du crabe chinois (*Eriocheir sinensis* H. Milne Edwards) en France. Bul. Franc. Pisicul. 194: 5–13 (in French).

Hymanson, Z., J. Wang & T. Sasaki, 1999. Lessons from the home of the Chinese mitten crab. IEP Newsletter 12: 25–32.

Ingle, R. W., 1986. The Chinese mitten crab *Eriocheir sinensis* a continuous immigrant. Lond. Nat. 65: 101–105.

Jin, G., Z. Li, & P. Xie, 2001. The growth patterns of juvenile and precocious Chinese mitten crabs, *Eriocheir sinensis* (decapoda, grapsida), stocked in freshwater lakes of China. Crustaceana 74: 261–273.

Kamps, L. F., 1937. De Chineesche wolhand krab in Nederland. Akad. Proef. Groningen: 1–112 (in Dutch).

Kobayashi, S., 2001. Fecundity of the Japanese mitten crab *Eriocheir japonica* (de Haan). Benth. Res. 56: 1–7.

Kobayashi, S. & S. Matsuura, 1999. Reproductive ecology of the Japanese mitten crab *Eriocheir japonica* (de Haan): a review. Jap. J. Benth. 54: 24–35.

Leloup, E., 1937. Contributions à l'étude de la faune belge. VII. - La propagation du crabe chinois en Belgique pendant l'année 1936. Bull. Mus. Hist. Natur. Belg. 13: 1–7 (in French).

Leppaekoski, E. & S. Olenin, 2000. Non-native species and rates of spread: lessons from the brackish Baltic Sea. Biol. Invas. 2: 151–163.

Montu, M., K. Anger & C. deBakker, 1996. Larval development of the Chinese mitten crab *Eriocheir sinensis* H Milne-Edwards (Decapoda: Grapsidae) reared in the laboratory. Helgolaender Meeresunters. 50: 223–252.

Murina, V. V. & A. G. Antonovsky, 2001. Chinese crab, *Eriocheir sinensis* is an invader into the basin of the Sea of Azov. Ekol. morya 55: 37–39 (in Russian).

Panning, A., 1933. Gestaltkundlicher Teil. In Peters, N., A. Panning & W. Schnackenbeck (eds), Die chinesische Wollhandkrabbe (*Eriocheir sinensis*) in Deutschland. Zool. Anz. (Leipzig): 1–58 (in German).

Panning, A., 1938a. Die Verteilung der Wollhandkrabbe über das Flußgebiet der Elbe nach Jahrgängen. Mitt. Hamb. Zool. Mus. Inst. 47: 65–82 (in German).

Panning, A., 1938b. Über die Wanderung der Wollhandkrabbe. Markierungsversuche. Mitt. Hamb. Zool. Mus. Inst. 47: 32–49 (in German).

Peters, N., 1933. Lebenskundlicher Teil. In Peters, N., A. Panning & W. Schnakenbeck, (eds), Die chinesische Wollhandkrabbe (*Eriocheir sinensis* H.Milne-Edwards) in Deutschland. Zool. Anz. (Leipzig): 59–155 (in German).

Peters, N., 1938a. Ausbreitung und Verbreitung der chinesischen Wollhandkrabbe (*Eriocheir sinensis* H.M.-Edw) in Europa im Jahre 1933 bis 1935. Mitt. Hamb. Zool. Mus. Inst. 47: 1–31 (in German).

Peters, N., 1938b. Neue Untersuchungen über die Erdbauten der Wollhandkrabbe. Mitt. Hamb. Zool. Mus. Inst. 47: 129–139 (in German).

Peters, N., 1938c. Zur Fortpflanzungsbiologie der Wollhandkrabbe (*Eriocheir sinensis* H.M.-Edw). Mitt. Hamb. Zool. Mus. Inst. 47: 112–128 (in German).

Petit, G. & R. Mizoule, 1974. En douze ans le 'crabe Chinois' n'a pu réussir son implantation dans les lagunes du Languedoc. Vie Milieu Ser. C Biol. Terr. 23: 181–186 (in French).

Rasmussen, E., 1987. Status over uldhåndskrabbens (*Eriocheir sinensis*) udbredelse og forekomst i Danmark. Flora og Fauna 93: 51–58 (in Danish).

Rudnick, D. A., K. Hieb, K. F. Grimmer & V. H. Resh, 2003. Patterns and processes of biological invasion: the Chinese mitten crab in San Francisco Bay. Basic appl. Ecol. 4 (in press).

Schubert, K., 1938. Häutung, Wachstum und Alter der Wollhandkrabbe. Mitt. Hamb. Zool. Mus. Inst. 47: 83–104 (in German).

Veldhuizen, T. C. & S. Stanish, 1999. Overview of the life history, distribution, abundance, and impact of the Chinese mitten crab, *Eriocheir sinensis*. California Department of Water Resources, Environmental Services Office.

Vincent, T., 1996. Le crabe Chinois *Eriocheir sinensis* H. Milne-Edwards, 1854 (Crustacea, Brachyura) en Seine-Maritime, France. Ann. Inst. océanogr. 72: 155–171 (in French).