Chapter two

Invasive crustaceans in European inland waters

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INTRODUCTION

At least 52,000 species of crustaceans have been described, although many more probably exist (Martin and Davis 2001). They are amongst the most prolific macroinvertebrates in the aquatic environment, both in terms of numbers and species diversity, but they do not usually cause public concern unless they are large and become invasive, e.g. the red king crab, *Paralithodes camtschaticus* Samouelle, in Norway, the Chinese mitten crab, *Eriocheir sinensis*, in Germany and the UK, and the red swamp crayfish, *Procambarus clarkii*, in African lakes (Chapter 4).

The Global Invasive Species Database (http://www.issg.org/database) lists three crustaceans in its world's worst 100 invasive non-indigenous species (NIS), i.e. the green crab, *Carcinus maenas* Linnaeus; the fishhook waterflea, *Cercopagis pengoi*; and the Chinese mitten crab, *E. sinensis*. However, in the 'Global Strategy on Invasive Alien Species' (McNeely *et al*. 2001) crustaceans are not dealt with, save for a brief mention of non-indigenous crayfish escaping from a London fish market.

Many aquatic crustaceans produce planktonic larvae or resistant propagules (Panov *et al*. 2004) and consequently can be moved great distances, either naturally or by human-mediated means, e.g. they are the commonest faunal component in ballast water of ships (Panov *et al*. 2004). Some attach themselves to solid surfaces or construct tubes on such surfaces, which may then become mobile, e.g. ships' hulls and oil platforms, whilst others burrow into softer materials such as wood – these habits can result in the crustacean being transported outside its home range, and even transcontinentally. Others have

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been translocated for economic reasons such as aquaculture and to enhance fish production, and for the pet and restaurant trades, and have subsequently become established in the wild. The majority of crustacean introductions have been recorded for the marine and estuarine environments, and these have been well documented (e.g. Carlton 1996, Ruiz *et al.* 1997, Rodríguez and Suárez 2001); in general less attention has been paid to introductions into inland waters (Welcomme 1988, Gherardi and Holdich 1999, Leppäkoski *et al.* 2002b), with the exception of fish (Welcomme 1991, Lehtonen 2002).

Despite the large number of crustacean species present in the aquatic environment, relatively few have become established outside their natural range due to accidental or deliberate introductions into European waters. Most of those that have become established occur in the marine and estuarine environments, but a growing number of species are becoming established in inland waters, mainly amphipods from the Ponto–Caspian basin and North America, and crayfish from North America. In this review, details are given of invasive crustaceans that have become established in European inland waters in recent times. Although all groups are dealt with, particular attention is given to the amphipods and decapods as they are currently having the most impact. In total, three species of Branchiopoda, four species of Copepoda, one species of Branchiura, and 46 species of Malacostraca (5 Mysida, 21 Amphipoda, 4 Isopoda, and 15 Decapoda [two Caridea (prawns), six Brachyura (crabs), and nine Astacida (crayfish)]) are listed in Tables 1–3. In the majority of cases it is difficult to assess whether or not an invasive species is having a high impact, but when this is known then it is highlighted in the tables.

In this review, inland waters will be taken as meaning rivers, lakes, and reservoirs. Coastal lagoons, saline lakes, estuaries, and low salinity seas, such as the Baltic, will be mentioned as appropriate. Although the Baltic is, to quote Leppäkoski *et al.* (2002a), "a sea of invaders", particularly for invasive crustaceans, it has been well covered elsewhere, e.g. Jaźdźewski and Konopacka (2002), Leppäkoski *et al.* (2002a, b, c) and Telesh and Ojavear (2002). However, the following facts are of interest. The Ponto–Caspian branchiopod, *Evadne anonyx* Sars, is widespread in the Baltic but cannot tolerate freshwater (V. E. Panov 2006, personal communication) so is unlikely to invade inland waters. The North American copepod, *Acartia tonsa* Dana, is widespread in Europe, particularly in the Baltic, but does not appear to have entered inland waters. The New Zealand barnacle, *Elminius modestus* Darwin, is also widespread in coastal waters, but does not occur in inland waters.

The classification of Crustacea used in this review is mainly based on that of Martin and Davis (2001). However, the higher taxonomic categories other than family have not been given a name, e.g. class, infraorder, order, etc., as in many cases there still seems to be disagreement over the correct terminology. For example, some workers refer to the Cladocera as a suborder (Martin and Davis 2001), whilst others call them a superorder (V. E. Panov 2006, personal communication). Many workers still use the term Mysidacea, whilst Martin and

Table 1 Non-indigenous Amphipoda in European inland waters (those with a + are considered to be highly invasive).

Scientific name, authority, family	Natural range	Introduced range
Malacostraca, Amphipoda		
+*Chelicorophium curvispinum* (G. O. Sars) (Corophiidae)	Ponto–Caspian basin	Widespread in western Europe, including British Isles
Chelicorophium robustum (Bousfield and Hoover) (Corophiidae)	Ponto–Caspian basin	Poland, Germany
Corophium sowinskyi Martynov (Corophiidae)	Ponto–Caspian basin	Poland, Czech Republic
+*Crangonyx pseudogracilis* Bousfield (Crangonyctidae)	USA	British Isles, The Netherlands
Dikerogammarus bispinosus Martynov (Gammaridae)	Ponto–Caspian basin	Hungary, Austria, (poorly known?)
Dikerogammarus haemobaphes (Eichwald) (Gammaridae)	Ponto–Caspian basin	Hungary, Austria, Germany, Poland
+*Dikerogammarus villosus* (Sowinsky) (Gammaridae)	Ponto–Caspian basin	Hungary, Austria, Germany, The Netherlands, France, Italy
Echinogammarus berilloni (Catta) (Gammaridae)	Iberian Peninsula	France, Belgium, Luxembourg, Germany, The Netherlands
+*Echinogammarus ischnus* (Stebbing) (Gammaridae)	Ponto–Caspian basin	Poland, Germany, The Netherlands, Austria, Hungary
Echinogammarus trichiatus (Martynov) (Gammaridae)	Ponto–Caspian basin	Bavarian Danube, Rhine, Austr. Danube
Echinogammarus warpachowskyi (G. O. Sars) (Gammaridae)	Ponto–Caspian basin	Ukraine, Lithuania, Poland
+*Gammarus pulex* (Linnaeus) (Gammaridae)	Most European countries	New water bodies within Europe, including Ireland
Gammarus roeseli Gervais (Gammaridae)	Balkan Penins, Asia Minor	Central Europe, France, Germany
+*Gammarus tigrinus* Sexton (Gammaridae)	USA	British Isles, Germany, The Netherlands, southern Baltic
+*Gmelinoides fasciatus* (Stebbing) (Gammaridae)	Russia (Lake Baikal)	Lakes Ladoga, Onega, Peipsi, R. Neva and Neva estuary
Hyalella azteca (Saussure) (Hyalellidae)	USA	Not yet self-established, high risk
Obesogammarus crassus (G. O. Sars) (Gammaridae)	Ponto–Caspian basin	Lithuania, Poland
+*Obesogammarus obesus* (G. O. Sars) (Gammaridae)	Ponto–Caspian basin	Austrian and Bavarian Danube
Orchestia cavimana Heller (Orchestidae)	Ponto–Caspian basin	Widespread, including England
+*Pontogammarus robustoides* (G. O. Sars) (Gammaridae)	Ponto–Caspian basin	Poland, Germany

Table 2 Non-indigenous Decapoda (Pleocyemata) in European inland waters (those with a + are considered to be highly invasive).

Scientific name, authority, family	Natural range	Introduced range
Malacostraca, Caridea		
Atyaephyra desmaresti (Millet) (Atyidae)	Southern Europe	France (1843), Belgium (1888), The Netherlands (1916), Germany (1932), R. Main (1983), Main-Danube Canal (1990), Bavarian Danube (1997), Austrian Danube (1999)
Palaemon macrodactylus Rathbun (Palaemonidae)	North-east Asia	England (2004)
Malacostraca, Brachyura		
Callinectes sapidus M.J. Rathbun (Portunidae)	USA	Widespread (France, 1901)
+*Eriocheir sinensis* H. Milne Edwards (Varunidae)	SE Asia	Widespread (Germany, 1912)
Potamon sp. (Potomidae)	Unknown	France (1985)
Potamon fluviatile (Herbst) (Potomidae)	Italy, Balkans, Greece	France (early 19th century)
Potamon ibericum tauricum (Czerniavsky) (Potomidae)	Turkey	France (1960s)
Rhithropanopeus harrisii Maitland (Xanthidae)	USA	Widespread (The Netherlands, 1874)
Malacostraca, Astacida		
+*Astacus leptodactylus* Eschscholtz (Astacidae)	Ponto–Caspian basin	Widespread
Cherax destructor Clark (Parastacidae)	Australia	Spain (Spain, 1983), possibly Switzerland
Orconectes immunis (Hagen) (Cambaridae)	USA	Germany (Germany, 1997)
+*Orconectes limosus* (Rafinesque) (Cambaridae)	USA	Widespread (Germany, 1890)
+*Orconectes rusticus* (Girard) (Cambaridae)	USA	France (France, 2005*)
+*Orconectes virilis* (Hagen) (Cambaridae)	North America	The Netherlands (The Netherlands, 2005*)
+*Pacifastacus leniusculus* (Dana) (Astacidae)	North America	Widespread (Sweden, 1960s)
+*Procambarus clarkii* (Girard) (Cambaridae)	USA	Widespread (Spain, 1970s)
+*Procambarus* sp. (Cambaridae)	USA	Germany, The Netherlands (Germany, 2003)

* reported in that year but probably present earlier

Table 3 Other non-indigenous crustaceans in European inland waters (those with a + are considered to be highly invasive).

Scientific name, authority, (family in brackets)	Natural range	Introduced range
Branchiopoda, Cladocera		
+*Bythotrephes longimanus* Leydig (Cercopagididae)	Widespread in Europe	Widespread – further invasions in Europe
+*Cercopagis pengoi* (Ostroumov) (Cercopagididae)	Ponto–Caspian basin	Widespread, including Baltic Sea
Cornigerius maeoticus (Pengo) (Podonidae)	Ponto–Azov	Widespread, including Baltic Sea
Copepoda, Calanoida		
+*Acanthocyclops americanus* (Marsh) (Cyclopoida)	North America	Britain (19th century), now widespread in Europe
Apocyclops panamensis (Marsh)	Central America	Italy (1990s)
Boeckella triarticulata (G. M.Thompson) (Calanoida)	Australia	Italy (1992)
Eudiaptomus gracilis (G. O. Sars) (Calanoida)	Europe, but not Italy	Italy (late 1980s)
Branchiura, Arguloida		
Argulus japonicus Thiele (Argulidae)	South-east Asia	Spain (1921), Germany (1935), France, Italy, Poland, UK (1990)
Malacostraca, Isopoda		
Asellus communis Say (Asellota)	USA	England
+*Jaera istri* Veuille (Asellota)	Ponto–Caspian basin	Austrian Danube (1934), Bavarian Danube (1967), Main–Danube Canal (1993), R. Main (1994), R. Rhine delta (1997), R. Rhine (2003), R. Elbe (1999)
Proasellus coxalis (Asellota)	Southern Europe	Widespread
Proasellus meridionalis Racovitza (Asellota)	Southern Europe	Widespread

Table 3 Continued.

Scientific name, authority, (family in brackets)	Natural range	Introduced range
Malacostraca, Mysida		
+*Hemimysis anomala* G. O. Sars (Mysidae)	Ponto–Caspian basin	Baltic Sea countries (1990s), The Netherlands (1998), Austrian Danube (1999), Belgium (2000), England (2004), Germany (2004), France (2006)
+*Katamysis warpachowskyi* G. O. Sars (Mysidae)	Ponto–Caspian basin	Hungarian, Slovakian and Austrian Danube (2001)
+*Limnomysis benedeni* Czerniavsky (Mysidae)	Ponto–Caspian basin	Budapest (1947), Vienna (1973), Bavarian Danube (1993), Main–Danube Canal (1998), R. Rhine (1998), R. Rhine delta (1998)
Paramysis intermedia (Czerniavsky) (Mysidae)	Ponto–Caspian basin	Baltic countries
Paramysis lacustris (Czerniavsky) (Mysidae)	Ponto–Caspian basin	Baltic countries

Davis (2001) call them the Mysida. Martin and Davis (2001) discussed the conflicting views about the terminology used for crayfish and admit that the one they have used is misleading, i.e. Superfamilies Astacoidea and Parastacoidea in the Infraorder Astacidea, as the crayfish are now considered to be monophyletic (Crandall *et al.* 2000, Scholtz 2002) and yet the two superfamilies are given equal rank with the three other superfamilies in the infraorder. K. Crandall (2006, personal communication) is of the opinion that the crayfish should not be elevated to their own infraorder, e.g. the Astacida, as suggested by Scholtz and Richter (1995) (see also Scholtz 2002 and Taylor 2002), until more studies are carried out, and that the original classification of H. H. Hobbs Jr (see, e.g. Hobbs Jr 1988) should be retained for the time being. However, in this review the classification used by Taylor in Holdich (2002a) is used, i.e. the crayfish are in the Infraorder Astacida with two superfamilies as noted above. Ahyong (2006) in a recent analysis of homarid phylogeny also places the crayfish in the Astacida.

INVASIVE CRUSTACEANS – ORIGINS, SPREAD, AND IMPACT

Background

The invasion of European inland waters by crustaceans has been mainly on three fronts: introductions (a) from North America, Australia, and Asia; (b) from one European region to another; and (c) from the Ponto–Caspian Basin by three routes. These are: (1) northern invasion corridor – Volga–Baltic inland waterway; (2) central invasion corridor – Dnieper–Vistula–Oder–Elbe–Rhine; and (3) southern invasion corridor – the Danube River connection with the Rhine basin (Fig. 1). Many of the species using these invasion corridors have become established in the low salinity Baltic Sea and its associated gulfs, but have moved by natural diffusion or aided by ships through these freshwater corridors to get there.

Invasive crustaceans have either been introduced intentionally or unintentionally, or in some cases have made their own way from one region to another via canals and rivers, and during floods. Van der Velde *et al.* (2000) and Bernaurer and Jansen (2006) note that the River Rhine has many invasive crustaceans (e.g. mysids, amphipods, isopods, and decapods) that have migrated there via the Main–Danube Canal from the River Danube, which itself contains a number of Ponto–Caspian species. Anthropomorphic effects in the R. Rhine has raised salt and temperature levels, thus making conditions favourable for species that originally lived in estuarine or brackish water. However, Kelleher et al. (2000b) point out that water quality in the lower R. Rhine has in fact improved since the restoration plan initiated after the Sandoz chemical spill in 1986, and whilst this is making conditions favourable for the return of some indigenous species, it is also attracting increasing numbers of NIS. Similarly, the

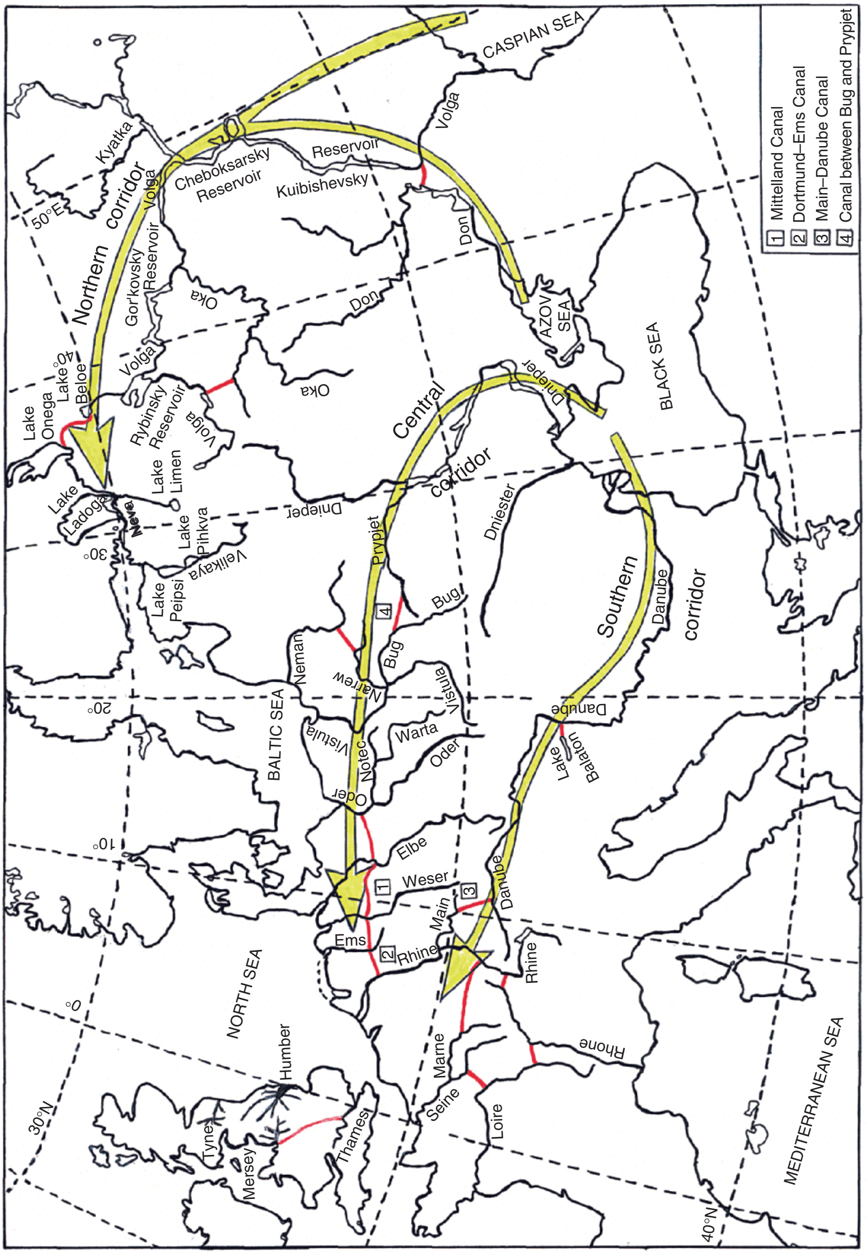

Fig. 1 Map of Europe showing the main inland waterways (rivers and canals), and the three main migration corridors (arrows), i.e. northern, central, and southern, used by Ponto–Caspian species. (Redrawn from Jazdzewski 1980, Bij de Vaate *et al.* 2002)

ability of many freshwater crustacean species, including crayfish (Firkins and Holdich 1993, Holdich *et al.* 1997), to tolerate elevated temperature and salt levels increases their chances of becoming established in new areas. Jaźdźewski and Konopacka (2002) suggest that the recent massive invasion of Ponto–Caspian species into central and western Europe may be due to the increasing ionic content of large European rivers, caused by agricultural and industrial inputs.

Intentional introductions include those for aquaculture (e.g. crayfish), human food (e.g. crabs and crayfish), fish food (e.g. mysids, amphipods, crayfish), pet trade (e.g. crayfish), management (e.g. crayfish for weed clearance), and stock enhancement (e.g. crayfish). Unintentional introductions have occurred via ballast water (e.g. branchiopods, copepods, isopods, amphipods, mysids, decapods), stocking of fish (e.g. branchiurans, decapods), attachment to mobile surfaces such as ships' hulls (e.g. tube-dwelling amphipods), entanglement in nets (e.g. decapods), floating weed and fouled mobile surfaces (a possible route for many species), fish bait (e.g. decapods), dumping of pets or excess stock (e.g. decapods), and perhaps even via predators such as birds, including waterfowl (Niethammer 1950, Segerstrale 1954). Anglers often use invasive crayfish species as bait and this can result in what is known as 'bait-bucket' introductions, which is a particular problem in North America, where the invasive rusty crayfish, *Orconectes rusticus*, has been spread northwards into Canada by this means, displacing indigenous crayfish species along the way (Lodge *et al.* 2000a, b). In Europe recreational anglers sometimes introduce crayfish such as the North American spiny-cheek crayfish, *Orconectes limosus*, in the belief that it will increase fish production (Holdich and Black 2007). This may be the case, but after a time the presence of large numbers of crayfish can have a detrimental impact on the fishing activity itself as well as on the freshwater environment (see below). Examples of those making their own way can be found in most of the invasive crustacean groups, but because they are relatively large, perhaps most noticeable are the decapods (e.g. the Chinese mitten crab, *E. sinensis*, and the narrow-clawed crayfish, *Astacus leptodactylus*).

Many other accidental introductions must also have occurred, but they have either not become established, or not had any noticeable impact. In some cases the introduction becomes established, but remains very localized, even though it may have been present for decades, as in the case of the North American isopod, *Asellus communis*, which only occurs in one isolated lake in England (Gledhill *et al.* 1993, Harding and Collis 2006). The situation is very fluid, with new records for non-indigenous invasive species being discovered on a frequent basis. For example, the Ponto–Caspian mysid, *Hemimysis anomala*, which has been introduced into a number of European countries as fish food, has suddenly appeared in central England (Holdich *et al.* 2006). Also, populations of the North American crayfish, *Orconectes virilis*, have been found recently in the Netherlands, and populations of *O. rusticus* have appeared in one region of France (Souty-Grosset *et al.* 2006).

Some crustaceans introduced via the various routes mentioned above have done equally well or better in their new environments, once they have become established. In some cases there have been positive effects through aquaculture, stock enhancement, and recreational activities (e.g. crayfish, see Ackefors 1999, Westman 2002), and this has encouraged secondary introductions (e.g. the North American red swamp crayfish, *P. clarkii*, and signal crayfish, *Pacifastacus leniusculus*). In others there have been negative effects through competition with indigenous species (e.g. branchiopods, copepods, mysids, amphipods, crayfish), transmission of disease (e.g. crayfish plague), and physical damage to the freshwater environment and its biota (e.g. crabs and crayfish, see Holdich 1999).

The majority of crustacean groups have invasive representatives in European inland waters, although amphipods provide the greatest number. In terms of publications, the majority are on amphipods and branchiopods (J. T. A. Dick 2006, personal communication), although invasive brachyuran crabs and crayfish have attracted a lot of attention in recent years (Gherardi and Holdich 1999, Gollasch 1999, Herborg *et al.* 2003). In their review of the anthropogenic dispersal of decapod crustaceans in the aquatic environment, Rodríguez and Suárez (2001) list 58 marine species that have been dispersed from their natural distribution areas, with 51 of these occurring in European waters. They list an additional eight freshwater and estuarine non-crayfish decapod species, only two of which (*E. sinensis* and *Rhithropanopeus harrisii*) have become established in European waters. They also list 20 crayfish species, including six that have become established in Europe, although this number has now increased (Souty-Grosset *et al.* 2006).

Taxonomic survey

Amphipoda (Table 1)

During the last few decades, numerous previously unrecorded amphipod species have been observed in European inland waters, but there is not enough space in this book to give all the immigration details for each of these species. Therefore only those that have had major effects in their new territories, by displacing indigenous species and/or changing the aquatic community including food web interactions, are dealt with below.

Amphipods have been introduced deliberately to boost secondary productivity and hence yields for the fishing industry. Leppäkoski *et al.* (2002a, b) state that more than 30 amphipod species from the Caspian complex have been introduced for this purpose. Especially in the former Soviet Union, new reservoirs, lakes, and any kind of waterbody were inoculated with species that promised high reproductive capacity. Canals that connected previously separated catchments offered an opportunity to invade new territories by passive and active anthropogenic vectors like navigation and transport in ballast water tanks. Some amphipods can leave the water and migrate at least a short distance over land (e.g. *Gammarus duebeni* Lilljeborg, Gledhill *et al.* 1993), like invasive North American crayfish in Europe. Nevertheless, the occurrence of amphipod species in many isolated waterbodies had been a mystery until Niethammer (1950) and Segerstrale (1954) proved the role of waterfowl in the transport of gammarids and other freshwater invertebrates. The latter showed experimentally that *Gammarus lacustris* Sars could become attached to the plumage and feathers of a mallard and remained in this position even after the wing has been taken out of the water. The attachment is mainly effected by pereopods 3–7, the last, claw-like segment of which is hooked into the plumage. The curved position, typical of the amphipod when out of water, prevents rapid desiccation of the gills. Thus, it may be possible for amphipods to be carried huge distances over land by this means and reach isolated bodies of water.

Most of the non-indigenous amphipod species in Continental Europe originate from the Ponto–Caspian basin. However, two well-established species in western Europe, *Gammarus tigrinus* and *Crangonyx pseudogracilis*, originated from the USA. A third species complex, the Mexican freshwater shrimp, *Hyalella azteca*, from the USA, Mexico, Central America, and the Caribbean, is sold intensively in the aquarium trade: it is kept by many aquarists and in garden ponds (Proßeckert 2001), and it is just a matter of time before it establishes self-sustaining populations in the wild. In Lake Ladoga, Lake Onega, Lake Peipsi, and the Neva estuary (Russia), *Gmelinoides fasciatus* from the Siberian Lake Baikal established dense populations as a result of introduction trials that had been very common in Soviet Fisheries management programmes. *Gammarus roeseli* that originates from the Balkan Peninsula and Asia Minor invaded larger rivers of the lower parts of central Europe, its western border being the eastern parts of France. *Echinogammarus berilloni* originated from the Iberian Peninsula and has invaded France, Belgium, the Netherlands, Luxembourg, and parts of Germany.

Although *Gammarus pulex* is indigenous to Europe, it has a very wide geographical range, stretching from eastern Siberia and China westwards to the British Isles, although it is absent from Norway (Pinkster 1972) and parts of Scotland (Gledhill *et al.* 1993). It has been introduced into some waters in Northern Ireland (where it is not indigenous) and more widely in Britain, supposedly to stock angling waters to enhance fish production (Strange and Glass 1979). It has also recently been introduced to the Irish Republic (McLoughlin *et al.* 2000). At several sites on the western seaboard of Britain, the indigenous *Gammarus duebeni celticus* Stock and Pinkster was supposed to have been displaced by competition with incoming *G. pulex* (Hynes 1954), but Sutcliffe (1967) found no evidence to support this. In Germany, fishery managers favoured the spreading of *G. pulex* (Haempel 1908) and *Gammarus fossarum* Koch (which had been regarded as a subspecies of *G. pulex* by many workers at these times) in any suitable body of water. Lough Neagh in Northern Ireland has been invaded by three non-indigenous amphipods: *G. tigrinus* and *C. pseudogracilis* from North America, and *G. pulex* from Europe, which have come into contact with the sole indigenous species, *G. duebeni celticus*, that is still present. Various studies have shown that *G. pulex* in Ireland is capable of replacing *G. duebeni* by competitive exclusion (Dick *et al.* 1990a, b, 1993, Dick 1996, MacNeil *et al.* 1999, McLoughlin *et al.* 2000, J. D. Reynolds 2006, personal communication). *Gammarus duebeni* is also common in parts of NW France, but is now extinct in Normandy due to interactions with the expanding *G. pulex* (Piscart *et al.* 2006). In Brittany, a recent study has revealed a decline of the endangered *G. d. celticus* since 1970 due to changes in environment and interference from indigenous *G. pulex*, which is expanding its range (Piscart *et al.* 2007).

Since its discovery in the London area in the 1930s, *C. pseudogracilis* has become widespread in most of England and Wales, and has spread northwards into Scotland (Gledhill *et al.* 1993). Similarly, since *C. pseudogracilis* was recorded from a pond in Dublin (Holmes 1975), it has become widespread in both Northern Ireland and the Irish Republic (Dick *et al.* 1999). It was discovered in the Netherlands in 1979 (Platvoet *et al.* 1989). It is likely that it will spread further in continental Europe – it was discovered in the R. Rhine in 1992 (Bernaurer and Jansen 2006). Notes on the ecology of this species are given in Gledhill *et al.* (1993). The species inhabits any kind of waterbody, from fresh to brackish and clean to organically enriched.

Gammarus tigrinus, which originates from the Atlantic seaboard of North America, was introduced by unknown means into Britain, perhaps early in the 20th century (Sexton 1939), where it thrived in areas where the water was salty due to mining pollution. In 1957, specimens from Wyken Slough near Coventry were deliberately introduced into the Rivers Weser and Werra (also the Elbe, Ems, and Schlei) in Germany where indigenous gammarids have disappeared due to pollution (Bulnheim 1985). *Gammarus tigrinus* thrives in polluted, slightly saline waters and is a source of food for fish. By 1964 it had become common in the IJselmeer and northern parts of the Netherlands (Pinkster *et al.* 1977). It is now widespread throughout the lowlands of western Europe and has become one of the dominant macroinvertebrates in many catchments, where it has outcompeted indigenous species (Fries and Tesch 1965). It is also known from coastal lagoons in the southern Baltic (Leppäkoski *et al.* 2002a). Its distribution in Britain is summarized by Gledhill *et al.* (1993), and its spread through the Netherlands is documented by Pinkster *et al.* (1977, 1980, 1992), Pinkster and Platvoet (1983), and Platvoet *et al.* (1989). During rapid colonization in the 1960s and 1970s, *G. tigrinus* displaced the indigenous *G. pulex* from many freshwater habitats, and the indigenous *G. duebeni* and *Gammarus zaddachi* Sexton from brackish water habitats. When the salt-enriched River Erewash was breached near a series of water-filled gravel pits in the English Midlands in the 1980s to allow further gravel extraction, *G. tigrinus* quickly colonized the gravel pits and became the dominant macroinvertebrate amongst the marginal vegetation for a number of years. However, due to a decline in the coal mining industry in the area, the river became less saline and so did the gravel pits, resulting in a dramatic (although not complete) decline in the NIS (D. M. Holdich 1995, personal observation).

Fig. 2 The tube-dwelling Ponto–Caspian amphipod, *Chelicorophium curvispinum*, from the Morava River, the border stream of Austria and Slovakia, between Zwerndorf and Baumgarten, Lower Austria. (Photo: W. Graf and A. Schmidt-Kloiber)

The tube-dwelling amphipod *Chelicorophium curvispinum* (Fig. 2) originates from large rivers discharging into the Black and Caspian seas, e.g. Volga, Dnieper, Dniester, Danube, etc., and clearly dispersed through the central corridor into the Baltic and North Sea drainage systems. The earliest report (1912) of the corophiid outside its natural range was from the Spree–Havel system near Berlin where it was described as *Corophium devium* (Wundsch 1912). It was also found in the Mittelland Canal and Dortmund–Ems Canal in 1956 and 1977, respectively (Van den Brink *et al.* 1989). *Chelicorophium curvispinum* was first recorded in Britain in the early 1930s by Crawford (1935) from the River Avon at Tewkesbury, and from then onwards it was reported widely as occurring in the interconnected canals and rivers of the English Midlands, as well as in other river systems, e.g. the R. Stour in SE England (Buckley *et al.* 2004). It was most likely introduced to Britain by ships sailing from ports of the Elbe estuary (Harris 1991). It is now present in Ireland in the R. Shannon and R. Erne systems (Lucy *et al.* 2004). In the Austrian Danube it has been known at least from the 1960s as far as the German border at Passau (Vornatscher 1965). The Main–Danube Canal where it was found in 1993 has been colonized by *C. curvispinum* from two directions, i.e. from the rivers Rhine (1987) and Main (1988) and from the Upper Danube (1959). The adults range in length from 2.5 to 7.0 mm. They filter suspended particles from the water column for the construction of tubes on solid substrates in which they live, giving them some shelter against predation. Soon after being recorded in the middle and lower Rhine in 1987 (Van den

Brink *et al.* 1989, Schöll 1990a), its numbers have increased explosively, and densities of well above 100,000 m^{-2} (maximum approximately 750,000 m^{-2}) have been recorded, which is much higher than numbers recorded in other rivers. The overgrowth of stones by the tubes of these animals can bind mud with a dry weight of up to 1.044 g m^{-2} and thus completely change the habitat (Van der Velde *et al.* 1998), causing direct environmental impacts over a distance of 200–500 km in the Rhine (Van den Brink and Van der Velde 1991) due to: (a) competition for space; (b) competition for food; and (c) changes in food web interactions. Larva of the zebra mussel *Dreissena polymorpha* Pallas, also a successful invader from the Ponto–Caspian basin, need bare hard substrates on which to settle, which may not be available because of the tube-building activities on such surfaces by the corophiid invader. Other filter feeders, such as the invading *D. polymorpha* and the indigenous species such as *Hydropsyche contubernalis* McLachlan (a caseless caddisfly larvae), chironomid larvae, and zooplankton species may be outcompeted. Eel and perch were found to shift their diet because of the invasion by *C. curvispinum*, which provided a new source of food (Kelleher *et al.* 1998). Dutch workers have found that *C. curvispinum* breeds from April to September, producing three generations a year – one more than related corophiid species (Rajagopal *et al.* 1998).

Specimens of *Chelicorophium robustum* were sampled in the R. Main in 2003 in the States of Bavaria and Hessen, being the first records of this species in Germany (Bernerth and Stein 2003, Berthold and Kaiser 2004). It was also recorded in the R. Rhine in 2004 (Bernaurer and Jansen 2006). Compared with *C. curvispinum*, the newly recorded species is easily detected by the large body size of adult specimens, i.e. 9 mm. A further spread in European inland waters is expected.

Migration patterns of *Corophium sowinskyi* are unclear because it is difficult to distinguish it from *C. curvispinum*. The species originates from the Danube, Dnieper, Volga, Don, and Dniester rivers (Mordukhai-Boltovskoi 1979). Records of this species in the Czech Republic indicate that the southern corridor could become the most obvious route for its range extension.

Dikerogammarus haemobaphes, originating from the Ponto–Caspian basin, was reported in the early 1960s from the Austrian Danube near Vienna by Vornatscher (1965) and in 1992 for the Bavarian stretch of the Danube (Tittizer 1996). During the 1980s it was the most abundant species in stony sediments (Pöckl 1988, 2002). It was probably the first amphipod species to invade the R. Rhine system via the southern corridor (Schleuter *et al.* 1994). For the first time in the Baltic Sea basin, the species was recorded in Poland in 1997, and its range expansion was reported by Jaźdżewski and Konopacka (2000). Its life history is presently being studied in the Vistula River where it is multivoltine, with three generations per year and high fecundity (Bacela and Konopacka 2005b).

Specimens of *Dikerogammarus villosus* (Fig. 3), which can reach a male maximum length of almost 30 mm, were not found in the Austrian Danube

Fig. 3 The Ponto–Caspian amphipod, *Dikerogammarus villosus*, from the Austrian Danube at Linz, Upper Austria. Although this species dominates the community by number and biomass, other amphipod species do occur. (Photo: W. Graf)

before 1989 (Nesemann *et al.* 1995), and examples for different colour variants in live animals are given in that paper. It was demonstrated, however, that the different colour types cannot be differentiated at the allozyme level (Müller *et al.* 2002). The species was not found in the Bavarian Danube before 1992. It used the southern corridor and was sampled from the lower Rhine in the Netherlands (Bij de Vaate and Klink 1995). *Dikerogammarus villosus* is reported to be a successful invader by competition and predation: *D. haemobaphes* is rarely found in the Rhine system since the arrival of *D. villosus*, which has successfully invaded via the Rhône system (Müller and Schramm 2001) and the large rivers in northern Germany (Grabow *et al.* 1998), as well as the Moselle and other French hydrosystems (Devin *et al.* 2001). *Dikerogammarus haemobaphes* on the other hand is actively expanding in Poland (Jaźdźewski and Konopacka 2000). In the Netherlands, Dick and Platvoet (2000) have found that *D. villosus* is having a marked impact on the indigenous *G. duebeni*, as well as the non-indigenous *G. tigrinus*, and they predict that it will further reduce amphipod diversity in a range of freshwater habitats in Europe. *Dikerogammarus villosus* also occurs in several lakes, e.g. Traunsee and R. Traun, Austria (O. Moog 2003, personal communication), Lake Constance, Germany (K. O. Rothhaupt 2003, personal communication), Lake Garda, Italy (Casellato *et al.* 2005), where it is partially replacing the indigenous *Echinogammarus stammeri*

(Karaman). *Dikerogammarus villosus* preys heavily on other amphipod species, which it is thought to replace, as well as on *Asellus aquaticus* Linnaeus, insect larvae, and fish eggs (Chapter 27), and even small fish are reported to be attacked (Dick *et al.* 2002, La Piana *et al.* 2005). However, Platvoet (2005) also showed that the species is able to nourish itself by a wide range of feeding methods, such as shredding, grazing, collecting micro- and macro-algae, coprophagy, and carnivory, and that the feeding habits are dependent on water temperature and the micro-distribution of food organism. *Dikerogammarus villosus* is apparently less predatory when a population is well established in comparison to the phase when it is rapidly increasing its individual numbers in a new habitat (Van Riel *et al.* 2005). The life history and population dynamics of *D. villosus* have been studied intensively by one of us (M. Pöckl) in the Austrian Danube during 2002–2004, where the variability in life history and reproductive output with a mean fecundity of 43 eggs and a maximum of almost 200 were found to be unique in freshwater amphipods (Pöckl 2007). The reputation given in the literature of *D. villosus* as a ''killing machine'' was not confirmed by these studies. Oxygen consumption, temperature, and salinity tolerance of the invasive amphipod *D. villosus* have been studied in the laboratory by Bruijs *et al.* (2001), who found that the species has wide capacities for adaptation and could possibly survive ballast water exchange and thus develop large populations in temperate areas on a global scale.

Müller and Schramm (2001) reported that a third riverine *Dikerogammarus* sp., *D. bispinosus*, has colonized the middle and upper R. Danube (Austrian stretch at Linz from 1998). Their genetic analyses demonstrate the clear species status of this taxon, which formerly had been described as a subspecies of *D. villosus* by Martynov (1925) from the lower Dnieper. The lack of hybrid genotypes indicates a reproductive isolation among *D. haemobaphes, D. villosus*, and *D. bispinosus* in a syntopic population from the Hungarian Danube near Szob (Müller *et al.* 2002). The dispersal behaviour of *D. bispinosus* may be species-specific as with *D. haemobaphes* and *D. villosus*.

Echinogammarus ischnus belongs to the group of Ponto–Caspian amphipods that have advanced farthest north-westwards, reaching the systems of the North and Baltic seas. In 1928, it was recorded for the first time from the Vistula below Warsaw (Jarocki and Demianowicz 1931), and has probably passed through the Rivers Dnieper, Pripet, the Pripet-Bug Canal, and the R. Bug. Using a similar pathway, the Neman–Pripet canal, *E. ischnus* had reached the lower R. Neman by about 1960 (Gasjunas 1965, 1968 in Jażdżewski 1980). Herhaus (1978) discovered the species in the Dortmund–Ems canal. The well-developed canal systems joining the Vistula, Oder, Elbe, and Weser rivers seem to have been its most probable route (Jażdżewski 1980). Between 1979 and 1981 specimens of *E. ischnus* were sampled in the Mittellandkanal (Herbst 1982). In the late 1980s the species was observed from the Rhine–Herne Canal and the Weser–Dattel Canal (Schöll 1990b). At about the same time, *E. ischnus* was also found in the Mecklenburgian and Pommeranian lakes (Jażdżewski and Konopacka 1990, Köhn and Waterstraat

1990), indicating that in western Europe it is colonizing habitats that are comparable to those of its natural Ponto–Caspian distribution area, where it occurs in several inshore Black Sea lakes (Jaźdźewski 1980). From the lower Rhine in Germany, a density of 100 m^{-2} of hard substrate has been reported (Schöll 1990b), and in 1991 and 1992 specimens were recorded from the lower Rhine delta in the Netherlands (Van den Brink *et al.* 1993). The development of a dense population of *E. ischnus* in the Rhine may have been hindered by *G. tigrinus*, as well as the mass abundance of *C. curvispinum* and *D. villosus*. In the Austrian stretch of the Danube, *E. ischnus* had not been reported to occur in the 1960s (Vornatscher 1965), but during the 1980s dense populations were encountered on stony substrate (Pöckl 1988). Via the Bavarian Danube (1989) the species migrated to the Main–Danube Canal (1995) (Van der Velde *et al.* 1998). Köhn and Waterstraat (1990) suggested that *E. ischnus* is closely associated with clumps of *D. polymorpha* in Lake Kummerow, Germany.

Echinogammarus berilloni originates from Mediterranean rivers, and adult males can reach a body length of 22 mm. When true estuarine species are absent (e.g. *G. zaddachi*, *Gammarus chevreuxi* Sexton), as in north-western Spain, it is able to penetrate into estuarine regions. According to Pinkster (1993), it is a typical species of middle courses of streams and rivers, and has never been found in the upper reaches. It is an active migrant, which has made use of canals to reach a large area of western Europe. Presently, it is found in the Rhine from Düsseldorf to Basel where it occurs in low densities, and in the Mosel (Moselle), a tributary of the Rhine. Meyer *et al.* (2004) reported that in temporary waters of a karstic system in western Germany, *Gammarus* species dominated, but in permanent downstream sections *E. berilloni* almost completely replaces *G. pulex* and *G. fossarum*. The occurrence of *E. berilloni* in the estuarine parts of some river systems in north-western Spain indicates that the species can stand high salinities as well as considerable changes in salinity. It also can withstand a high amount of organic pollution and high temperatures, and has been sampled in some parts of Spain at temperatures of up to 31°C (Pinkster 1993).

Outside its original natural distribution area in the Ponto–Caspian basin, *Echinogammarus trichiatus* was recorded for the first time in 1996 in the Bavarian Danube (Weinzierl *et al.* 1997), and three years later at a distance of 120 km from the first record in the Upper Danube. In 2000 and 2001, the species was sampled in the Upper and Lower Rhine, respectively (Podraza *et al.* 2001), which means that it must have spread through the Main–Danube Canal, using the southern invasive corridor. In 1998, *E. trichiatus* was also found in the Austrian Danube (H. Nesemann 1999, personal communication), which is later than the German record. Distribution with the stream flow is obviously easy, but the distribution of this species is still largely unknown and may be scattered.

Echinogammarus warpachowskyi originates from the brackish parts of the Caspian Sea and the deltas and estuaries of many Ponto–Caspian rivers. Some 40 years ago the species became one of the main objects of Soviet acclimatization enterprises. It was introduced into reservoirs and lakes in the Ukraine, and in Lithuania in the Neman River drainage area (Kaunnasskoe Reservoir). It penetrated into artificial reservoirs in the Dnieper River and into the Kuronian Lagoon (Jaźdźewski 1980). This small species (adult males reaching a maximum of 6.5 mm) is very tolerant to both varying salinity and temperature conditions and has spread over large parts of eastern Europe.

Since 1994, the stout and small *Obesogammarus obesus* from the Ponto–Caspian basin, which swims in an upright position (it is not laterally compressed like most gammarids), is known to occur in the Austria Danube, and has in some parts developed high densities (M. Pöckl 1994, personal observation), occupying a position after *C. curvispinum*, *D. villosus*, and *E. ischnus* in abundance. In 1995 it was recorded from the Bavarian Danube (Weinzierl *et al.* 1996), and an estimated density of 3,300 m^{-2} was reported. The invasion of the R. Rhine is expected to occur via the Main–Danube Canal in the near future. In October 2004, the species was recorded in the R. Rhine near Koblenz, Germany. The sampling site was located approximately 0.5 km away from the main river, quite close to a sports boat marina. Additional records from the same location in 2005 and 2006 indicate that this species may have become established in the central section of the R. Rhine (Nehring 2006). It can be speculated that *O. obesus* will extend its range within the European river and canal system in the near future.

Obesogammarus crassus was intentionally introduced in the 1960s into the Kaunas Reservoir (Lithuania), in the Neman River, and in several aquatic habitats along the Baltic coast of the former Soviet Union (Jaźdźewski 1980). From the Neman River, the species colonized the Kuronian Lagoon. Recently, *O. crassus* was observed from the Vistula Lagoon (Jaźdźewski *et al.* 2002). Westward dispersal has been the result of offshore transportation (in ballast water) via the Baltic Sea, indicating the northern dispersal route. However, part of the central corridor is considered to be a potential second corridor.

The first record of *Pontogammarus robustoides* in Germany dates from 1994 when it was found in the Peene (Rudolph 1997). From there it may have used the Hohenstaaten–Friedrichthaler Wasserstraße, the R. Oder, the Oder–Havel Canal, the Havel Canal, and the R. Elbe to reach the Mittellandkanal where it was sampled at Wolfsburg in 1998 (Martens *et al.* 1999, Tittizer *et al.* 2000). Like the other Ponto–Caspian species, *C. curvispinum*, *E. ischnus*, and *P. robustoides* probably also used the central corridor to penetrate westwards, and clearly not the southern one via the R. Danube. The average body length of mature specimens was 11.15 mm, ranging from 4.5 to 21.0 mm, and the smallest ovigerous females were 8.5 mm long. The mean brood size for all gravid females was 64.5 and varied from 11 to 185, and the egg number was exponentially correlated to female body length. These traits in life history determine the success of *P. robustoides* as a potential invader (Bacela and Konopacka 2005a).

Before the 1960s, the distribution area of the Baikalian amphipod, *G. fasciatus*, was limited to basins of Siberian Rivers (Angara, Lena, Yenisay, Irtysch, Pyasina, Tunguska, Selenga, Barguzin). In the former Soviet Union it was considered to be a suitable species for intentional introduction to enhance fish production in lakes and reservoirs, because of its high environmental plasticity and general high abundances within its native range. During the 1960s and 1970s, hundreds of millions of *G. fasciatus* specimens were introduced into 22 lakes and reservoirs outside its native range in Siberia and European Russia (Panov and Berezina 2002). In European Russia, *G. fasciatus* was introduced intentionally into Gorkovskoe Reservoir in the R. Volga basin, several Karelian Isthmus lakes located close to the western shore of Lake Ladoga, and Lake Ilmenin in the Lake Ladoga basin. *Gammarus fasciatus* invaded the western and northern shores of Lake Ladoga, some 18,400 km^2 in area, in the late 1980s (Panov 1996) and by the 1990s it had successfully colonized the whole littoral zone of this largest European lake. In the 1990s, from Lake Ladoga via the R. Neva, *G. fasciatus* penetrated into the Neva estuary, the largest estuary in the Baltic Sea (3,600 km^2). In 1996, the species was found in the Neva Bay and by 2001 it had established successfully in the coastal zone of the estuary (Berezina and Panov 2003). In 2001, *G. fasciatus* established self-sustaining populations along the western shore of Lake Onega. Berezina (Chapter 26) discusses the changes in the littoral communities of large lakes caused by introduction of *G. fasciatus*. In Lake Peipsi, *G. fasciatus* was introduced accidentally at the beginning of the 1970s during several attempts to enrich the native population of *G. lacustris* G.O. Sars by addition of specimens of this species from Siberian populations. These introductions were "contaminated" because the material released (several million specimens) contained a mixture of *G. fasciatus* (1–2% in density) and *G. lacustris*. The accidentally introduced *G. fasciatus* survived and were first observed in Lake Peipsi in 1972. By 1990 it had become established in the whole littoral zone of this lake (Berezina 2004). Two decades ago, the indigenous amphipod species *G. lacustris* was common in Lakes Ladoga and Onega as well as the freshwater parts of the Neva estuary. After invasion by the Baikalian amphipod, the indigenous *G. lacustris* has disappeared from many habitats. Moreover, the density of the freshwater isopod, *Asellus aquaticus*, was found to be dependent on the density of the Baikalian amphipod, decreasing significantly at localities with more than 500 *G. fasciatus* m^{-2}.

Astacida (crayfish) (Table 2)

Approximately 600 species of freshwater crayfish belonging to three families (Astacidae, Cambaridae, and Parastacidae) have been described and new species are being described on a regular basis, particularly from the Americas and Australasia (Taylor 2002, Fetzner 2005). However, there are only five indigenous crayfish species in Europe, all belonging to the Astacidae (Holdich 2002b, 2003, Souty-Grosset *et al.* 2006). After the last glaciation some 10,000 years ago, these crayfish species gradually colonized Europe by natural diffusion, either from glacial refugia or from the Ponto–Caspian basin. Subsequently, at least four of the five species have been translocated by man, or have migrated via man-made structures such as canals, to an extent that often makes it difficult to determine their origins. However, molecular genetic studies are being used to gradually unravel their origins, and what some countries consider to be their indigenous species appear to have been probably introduced. For example, the white-clawed crayfish, *Austropotamobius pallipes* (Lereboullet) *sensu lato*, in England and Ireland has been introduced on several separate occasions from France (Grandjean *et al.* 1997, Gouin *et al.* 2003), and the same species was introduced into Spain from Italy (Machino and Holdich 2006). When these events occurred, however, is not known, though probably in the last 1,000 years. Similarly, the noble crayfish, *Astacus astacus* (Linnaeus), which is now a treasured gastronomic icon, was introduced into Sweden and Norway in the Middle Ages (Machino and Holdich 2006).

When these species were introduced into the fresh waters of new areas and became established they must have been invasive and had an impact on the pre-existing biota. This is often a fact that is overlooked and is particularly relevant to such a keystone species as a crayfish, which can have a considerable impact when introduced into a waterbody that has not experienced it before. A case in point is *A. leptodactylus sensu lato*, which is indigenous to the Ponto–Caspian basin, but which has spread naturally via rivers and canals into northern and eastern Europe, and has been introduced into western Europe for commercial purposes. This crayfish is highly fecund and can grow to a very large size (up to 500 g wet weight) and reach very high densities. As a consequence of this, it can become the dominant animal in a waterbody, displacing other crayfish species if they are present (Souty-Grosset *et al.* 2006). As with other European crayfish it does not carry crayfish plague, but is susceptible to it (see below).

From the middle of the 19th century, a disease now commonly known as crayfish plague entered the waters of the Po Valley in Italy and gradually spread throughout Europe, killing off many populations of indigenous crayfish (Holdich 1999, 2003). The ranges of indigenous crayfish such as *A. astacus* and *A. pallipes* in western Europe were particularly affected and are still being compromised today (Souty-Grosset *et al.* 2006). Crayfish plague is indigenous to North America, and all those North American crayfish that have been studied are carriers of the oomycete causing it.

As crayfish were a valuable commodity in Europe in the 19th century, to boost European stocks steps were taken to introduce a North American crayfish species that was immune to the disease, i.e. *O. limosus* (see below). Two further species, i.e. *P. leniusculus* and *P. clarkii*, were introduced in the 1960s and 1970s respectively, to improve stocks further (see below). Their spread throughout Europe (see below) has only made the situation worse for the indigenous species, particularly as they are superior competitors (Holdich 1999), although there have also been some commercial, management, and recreational benefits (Ackefors 1999). These three species are further dealt with below as they have the widest distribution of invasive crayfish occurring in European inland waters. The Australian crayfish, *Cherax destructor*, was also introduced for commercial purposes in the 1980s, but it is restricted to Spanish waters, although it is imported live for restaurants in other countries and is cultivated in Italy (Souty-Grosset *et al.* 2006).

A second wave of crayfish introductions occurred in the late 20th and early 21st centuries (see Table 2), but unlike the four species mentioned above it seems likely that most were imported for the pet trade, and were subsequently released or escaped into natural waters. At the present time, although they can be considered invasive, their range is very limited (see Souty-Grosset *et al.* 2006 for further details). Of particular concern is the marbled crayfish, *Procambarus* sp., of unknown origin and species, which has been made widely available through the aquarium trade in recent years, and which now occurs in the wild in Germany and the Netherlands. This crayfish is parthenogenetic and can produce large numbers of offspring in a short space of time (Vogt *et al.* 2004, Seitz *et al.* 2005, Souty-Grosset *et al.* 2006). Considering the number of crayfish species available through the aquarium trade this source of invasive crayfish is likely to be a continuing problem as owners want to get rid of their pets as they grow too large or breed too rapidly.

As mentioned above, the first non-indigenous crayfish to be introduced into Europe from another continent was *O. limosus* (Fig. 4). After its introduction to Germany in 1890, secondary introductions were made into other parts of Germany and into Poland and France, in an attempt to make up for losses of

Fig. 4 The North American spiny-cheek crayfish, *Orconectes limosus*, and its burrows. This has become well-established in continental Europe since its introduction into Germany in 1890, but has only recently invaded England. Adults from Clifton Pond, Nottingham, England. (Photo: J. Black)

A. astacus through crayfish plague (Souty-Grosset *et al.* 2006). It also spread naturally through rivers and canals and is now probably the commonest crayfish in continental Europe, occupying at least 20 countries. Out of 300 lakes recently examined in NE Germany, 214 were found to have *O. limosus*. In Poland, populations of *O. limosus* increased from 57 in 1959 to at least 1,383 by 2004. It is gradually spreading eastwards in Europe and recently has been found in Croatia (Maguire 2003) and Serbia (Karaman and Machino 2004); it is likely to spread into Bulgaria, Romania, and the Ukraine via the R. Danube before long (Machino and Holdich 2006). It has been implicated in the demise of indigenous crayfish populations through competition and crayfish plague. Its large numbers and burrowing activity are likely to have a marked effect on the freshwater environment. However, *O. limosus* has never fulfilled its role as a replacement for *A. astacus* from the gastronomic point of view, as other species are much preferred. It is commonly used as fish bait and this has led to its introduction into new sites and countries such as England, where it has built up large populations in a short space of time (Holdich and Black 2007).

As indicated by the number of contributions relating to its biology in this volume, *P. clarkii* attracts a lot of attention because of its invasive capabilities. It was introduced to southern Spain in 1973 for aquacultural purposes but soon became widely established in the wild and is now present in 13 European countries, including islands in the Azores and Canaries (Holdich 2002b, Souty-Grosset *et al.* 2006). Although it has brought undoubted benefits to the Spanish economy through its harvesting and export, mainly to Scandinavian countries (Ackefors 1999), its environmental impact caused by burrowing and high consumption of both plant (including rice seedlings) and animal matter can be striking. For example, prior to 1996, Chozas Lake in NW Spain used to harbour a rich community in its clear, shallow waters. *Procambarus clarkii* was then introduced and its activities caused the waters to become turbid (Rodriguez *et al.* 2005). This was followed by a 99% reduction in plant cover, 71% loss of macroinvertebrates, 83% reduction in amphibian species, 52% reduction in waterfowl, and plant-eating birds such as ducks were also reduced by 75%. However, carnivorous birds increased their presence after the introduction of the crayfish. In addition to such effects, *P. clarkii* is also a carrier of crayfish plague and is thought to be responsible for the decline in indigenous crayfish species in a number of countries, e.g. Italy and Spain.

Pacifastacus leniusculus, is the only member of the Astacidae to be introduced into Europe (Lewis 2002). As the indigenous crayfish fauna in Europe all belong to this same family, many aspects of their biology are similar. *Pacifastacus* is the only genus of the Astacidae in North America, but like members of the other family, the Cambaridae, it too carries crayfish plague. *Pacifastacus leniusculus* was first released into Swedish waters in 1960, to replenish stocks of crayfish with an ecological and gastronomic homologue replacing *A. astacus*, which had been badly affected by crayfish plague. It soon became a popular species for stocking and culture, and as a result of secondary introductions (both from Sweden and North America) had become established in 24 European countries, from the UK across to eastern Europe by 2005, making it the most widespread non-indigenous crayfish (Souty-Grosset *et al.* 2006). In most of the countries into which it has been introduced, it has become established in the wild either as a result of escapes or deliberate seeding of waters. *Pacifastacus leniusculus* is most established in Sweden where it occurs in approximately 3,000 localities. Although it was welcomed in many countries by aquaculturists, particularly in Sweden and Finland, conservationists were concerned about the dangers of introducing a large, aggressive, highly fecund, fast-growing species into the freshwater environment, especially where indigenous crayfish, which are susceptible to the effects of crayfish plague, were still present. The fears of conservationists have proved true, whilst *P. leniusculus* has not provided the huge improvement in stocks that was predicted. Ironically, it is in the UK, which does not have a modern tradition for eating crayfish and which had good healthy stocks of its so-called (see above) indigenous species, *A. pallipes*, where problems are most acute since the introduction of *P. leniusculus* for aquacultural purposes in the 1970s. Despite a raft of legislation being drafted to protect the indigenous species and measures taken to try and stop the spread of the NIS, *A. pallipes* may well become extinct in a few decades (Sibley 2003, Holdich *et al.* 2004, Holdich and Pöckl 2005). This is due to a combination of the effects of crayfish plague and the superior competitive abilities of *P. leniusculus*. In addition, the burrowing activity (Fig. 5) of *P. leniusculus*, coupled with its insatiable appetite, is

Fig. 5 River bank collapse caused by the burrowing activities of the North American signal crayfish, *Pacifastacus leniusculus*, in the Gaddesby Brook, Leicestershire, England. (Photo: P. J. Sibley)

having both a physical and biological impact on both lentic and lotic environments (Guan and Wiles 1997, Sibley 2000). Attempts at eradicating *P. leniusculus* have so far proved futile despite the removal of many thousands of adults at a number of sites, e.g. in Scottish rivers (Collins 2006). As Holdich *et al.* (1999) predicted in their review of eradication methods, the only sure way is to use biocides, and this method has been successfully trialled in the UK, but it is only of use in enclosed waterbodies (Peay *et al.* 2006).

Caridea (Table 2)

Van der Velde *et al.* (2000) note that the freshwater river prawn, *Ataephyra desmaresti* (Atyidae), which originates from southern Europe, has spread widely throughout Europe via canals that connect European river basins. It was first observed in 1843 near Paris, 1888 in Belgium, 1916 in the Netherlands, 1925 in Metz, and 1929 in Strasbourg (Thienemann 1950). The first German record dates from 1932, from a backwater of the Lower R. Rhine near Rees. Thereafter it occurred at several sites of the dense canal network in north-western Germany, and after passing the Mittellandkanal it was found near Hannover in 1936. Several records were noted from the Rhine–Rhône Canal, the R. Saar at Saarbrücken, and the R. Mosel at Merl (summarized by Kinzelbach 1972). It was observed in the Lower R. Main in 1983 (Nesemann 1984), from where it migrated upstream in this river, entered the Main Canal (Heuss *et al.* 1990), passed the highest point of the Main–Danube Canal (Wittmann 1995), went downstream, was recorded in 1997 in the Bavarian Danube (Weinzierl *et al.* 1997), and in 1998 in the Austrian Danube (Moog *et al.* 1999). It therefore can be expected to occur in Slovakia, Hungary, and further downstream in the R. Danube in the near future. It feeds on micro-organisms, algae, plants, detritus, live and dead animals. *Ataephyra desmaresti* has a wide tolerance to temperature and salinity ranges, and lacks planktonic larvae, which are all useful attributes to possess when colonizing new habitats (Steffen 1939, Fidalgo 1989b). Adult males can reach a body length of 16–27 mm, females a maximum of 35 mm. The number of eggs is reported to vary between 100 and 1,400 (Fidalgo 1989a, b). Normally, the lifespan is 12–14 months, but under unfavourable conditions juveniles grow at a slower rate, reach sexual maturity in the second year and can live for three years. It is not known how many successive broods can be produced by an individual female.

The first record for the oriental prawn, *Palaemon macrodactylus* (Palaemonidae), for Europe was reported by Ashelby *et al.* (2004). Although this introduced species is widespread in the western USA, it has only colonized one location in Europe so far. It is thought to have been introduced into the R. Orwell estuary on the eastern coast of England some time between mid-2000 and late-2001, where it is now common and breeding. Transport in ballast water seems the most likely route of its introduction. It has since been found in the adjacent R. Stour estuary (Ashelby *et al.* 2004). *Palaemon macrodactylus* is extremely hardy and is known to live in salinities as low as 1.0 ppt in California. It is probable that aided by shipping this species will spread in European coastal waters and could enter inland waters.

Brachyura (Table 2)

The indigenous freshwater crab, *Potamon fluviatile*, occurs in Italy, the Balkans and Greece. Its behaviour has been studied by Italian workers (Barbaresi and Gherardi 1997, Gherardi *et al.* 1999). In competitive situations with the white-clawed crayfish, *A. pallipes*, it is usually the crab that wins as it has higher levels of aggression and strength. At present the two species have mainly different distributional ranges but where these overlap they never share the same water-body. They may have had a common distribution in the past, but competitive exclusion by the crab has meant that the crayfish has been pushed into less favourable habitats (Barbaresi and Gherardi 1997). The same may happen with some populations of indigenous crayfish species in France, where three non-indigenous *Potamon* species (see Table 2) have been introduced and become established there, one since the early 19th century (see Chapter 3).

The catadromous North American blue crab, *Callinectes sapidus* Rathbun, is euryhaline and eurythermic, and in its natural range migrates down rivers to reproduce in the sea. It was introduced into the Netherlands in 1932, probably in ballast water (Adema 1991). It has been recorded in a number of other European countries, e.g. France (Goulletquer *et al.* 2002), and is breeding in the eastern Mediterranean (Froglia 2005). It has also been recorded in the Marmara (Ozturk 2002), Black and Azov seas (Gomoiu *et al.* 2002). It does not appear to have extended its range into inland waters very far. Often, only single specimens are found, e.g. one was recorded from a river on the eastern coast of England in 1982 (Gledhill *et al.* 1993).

One of the commonest non-indigenous crab species is the North American mud crab, *R. harrisii*, which is found in a number of estuaries and coastal lagoons throughout Europe, including in the Mediterranean and Adriatic (Froglia 2005), as well as the Black and Azov seas since 1932 (Gomoiu *et al.* 2002), and also the Caspian Sea (Aladin *et al.* 2002). It is also present in Wales (UK) (Minchin and Eno 2002). It is thought to have been introduced via ballast water into the Netherlands in the 19th century (Adema 1991). It has been recorded in the lower R. Rhine, but only in low numbers (Van der Velde *et al.* 2000). In Poland, Jaździewski and Konopacka (2000) noted that this species attained very high densities in brackish waters in the 1950s and 1960s and became a major component of the zoobenthos, although its numbers decreased after that time. It does not appear to penetrate far into inland waters.

The most invasive of the non-indigenous crabs is the catadromous Chinese mitten crab, *E. sinensis* (Fig. 6), from SE Asia, where it has been recorded as far as 1,400 km upstream in China (Gollasch 1999). It is considered a delicacy in the Far East where it supports a billion dollar industry (Herborg *et al.* 2005), but

Fig. 6 An ovigerous female Chinese mitten crab, *Eriocheir sinensis*, from the River Thames (November 2005), London, England. *Eriocheir sinensis* was first recorded in Germany in 1912 and is now widely spread in European inland waters and estuaries. (Photo: P. Hurst)

in Europe it only tends to be eaten by Chinese immigrants. It is thought to have reached Europe via ballast water and was first recorded in the River Aller (a tributary of the R. Weser in Germany) in 1912 (Peters and Panning 1933, Gollasch 1999). Like the blue crab it migrates down rivers to breed after which it dies, and then as juveniles migrates upstream again in large numbers, taking 3–5 years to become sexually mature in Europe (Schubert 1935 in Herborg *et al.* 2005). In its migrations it can move across land to get around weirs (Rettig 2000 in Puky *et al.* 2005, Herborg *et al.* 2003). It is euryhaline and eurythermic and is capable of moulting in freshwater.

Despite being introduced in 1912, the range expansion of *E. sinensis* was not reported until 1927 when it migrated from Germany via the Kiel Canal into the Baltic Sea (Peters 1938 in Herborg *et al.* 2003), from where it reached Russia and Finland by 1933. It reached the Netherlands in 1929 and spread throughout the country (Van der Velde *et al.* 2000), France in 1930, Belgium in 1933, and England in 1935. It had migrated 700 km up the R. Elbe to Prague and 512 km along the R. Rhine by 1932, and by 1934 it occurred 464 km up the R. Oder as far as Breslau (Robbins *et al.* 2000, Herborg *et al.* 2003). Although it was known from the French coast as far as Le Havre in 1943, there appears to have been a secondary introduction, probably via ballast water or associated with oyster cultivation, to the R. Gironde region (1954–1960), from where *E. sinensis* reached the Mediterranean coast via canals in 1959 (Herborg *et al.* 2003). It is known from the Austrian (Rabitsch and Schiemer 2003) and Serbian (Karaman and Machino 2004) stretches of the Danube and has recently (2003) been found in the Hungarian part (Puky *et al.* 2005). It has also been reported from the White Sea (Berger and Naumov 2002) and the first record for Europe's largest lake, Lake Ladoga in Russia, was found in 2005 (Panov 2006). It was discovered in the Black Sea (Gomoiu *et al.* 2002) and Azov Sea in 1997 (Murina and Antonovsky 2001 in Herborg *et al.* 2003), and from the River Tazeh Bekandeh that drains into the Caspian Sea, Iran in 2002 (Robbins *et al.* 2006). Recently, in the west, it has been found in Waterford Harbour on the south-eastern coast of the Irish Republic (J. D. Reynolds 2006, personal communication).

According to Jaźdźewski and Konopacka (2000), *E. sinensis* is less of a problem in most of Europe than it used to be in the 1920–1940s. In the 1930s and 1940s lack of competition and an abundant food supply led to them becoming so abundant in Germany that millions of juveniles were caught during their upstream migration in 1936, but subsequently pollution led to a reduction in the crab's food supply and the crab itself (Gollasch 1999). Due to recent improvements in the water quality and a consequent increase in food supplies of some European rivers, *E. sinensis* is becoming abundant again and, in 1998, 75,000 crabs were taken by hand in only two hours in the River Elbe, where it is once again causing problems due to its migratory habit (Gollasch 1999, S. Gollasch 2006, personal communication). The main problems associated with *E. sinensis* are its burrowing habit that may endanger flood defences, and the fact that it reaches high densities, thus competing with indigenous species for food, including crayfish (Robbins *et al.* 2000), as well as endangering navigation. It also interferes with recreational and commercial fishing by taking bait and interfering with nets (Herborg *et al.* 2003, 2005).

Recent studies have mainly dealt with its spread in the UK, where it was first observed in the River Thames in 1935 but remained at low numbers until the 1990s when numbers escalated (Robbins *et al.* 2000), possibly as a result of improving water quality (Herborg *et al.* 2005). In England, *E. sinensis* spread along the coasts at an average rate of 78 km per year in the period 1976–1999, but this increased dramatically to 448 km per year in the period 1997–1999, which is similar to the rate of spread along the Baltic coast in 1928–1935 (Herborg *et al.* 2005). The upstream spread was 16 km per year in 1973–1998 with a marked increase to 49 km per year in 1995–1998. There are concerns about the impact that it will have on the structure of river banks and the indigenous fauna, including crayfish.

Other taxa (Table 3)

Space does not permit a full review of the other taxa of Crustacea that have invaded European inland waters, but brief details are given below and a tentative list is given in Table 3.

Branchiopoda. The spiny water flea, *Bythotrephes longimanus*, is indigenous to lakes throughout the Palearctic, ranging from the British Isles to the Bering Sea. Sikes (2002) has summarized what is known of this species as an invader. *Bythotrephes longimanus* has been found in areas where it was not previously known, including the North American Great Lakes in 1982, where it is thought to have been introduced with ballast water from a transoceanic ship originating from St. Petersburg harbour (Russia), where it is common in the nearby Lake Lagoda. *Bythotrephes longimanus* reproduces rapidly by parthenogenesis and its ability to produce sexual eggs allows it to survive adverse environmental conditions. It is a dominant predator of zooplankton in the summer months. Van der Velde *et al*. (2000) have found that *B. longimanus* is common in water storage reservoirs, lakes, and rivers in the Netherlands, and that it has a marked effect on other zooplankton. They also mention that it is found in the catchment area of the R. Rhine in the Alps, north-eastern Germany, Poland, Belarus, the Baltic States, Scandinavia, and the British Isles. They suggest that it has reached the Netherlands and other countries by long distance dispersal through the transport of resting eggs by rivers and/or birds. Panov *et al*. (2006) stated that the predatory Ponto–Caspian cladocerans, *C. pengoi*, *E. anonyx*, and *Cornigerius maeoticus* have moved through to the Baltic via the Volga–Baltic waterway (northern invasion corridor), probably in ships' ballast water, and that, although they are warm-water species, they have the potential to become established in a wide range of inland and coastal water ecosystems in temperate zones. Rodionova and Panov (2006) noted that *E. anonyx* increased ten fold in the eastern Gulf of Finland between 2000 and 2004. Litvinchuk and Maximova (2005) have studied the biology of *E. anonyx* and *Cornigerius maeoticus maeoticus* Pengo in the Baltic Sea and found them living with the indigenous branchiopod fauna. *Cercopagis pengoi* and *C. maeoticus* are known to occur in freshwater reservoirs in the Ponto–Caspian basin as well as those associated with the R. Volga, and it is probably only a matter of time before they are recorded from similar habitats further west. According to Panov *et al*. (2006), most Ponto–Caspian onychopod cladocerans are euryhaline and can survive in relatively high salinities as well as in freshwater (with the exception of *E. anonyx*). The invasion of the Baltic by these species has been helped by climate changes and the intensive shipping activity along the corridor. They suggest that Ponto–Caspian cladocerans should be considered as ''high risk'' invasive species because of their potential for range expansion and the impact they have on the recipient ecosystem. Indeed, Telesh and Ojaveer (2002) have found that *C. pengoi* in the Baltic Sea has a marked impact on the zooplankton community as well as pelagic food webs involving planktivorous fish species. They suggest that the dietary overlap with young planktivorous fish may lead to a decline in food sources for fish such as herring and sprat, although this is compensated to some extent by the fact that the fish can feed on the branchiopod.

Copepoda. Until recently few invasive Copepoda had been reported, but N. Riccardi and G. Rossetti (2006, personal communication) have found the calanoid, *Eudiaptomus gracilis*, in lowland waters of northern Italy. Although this species is indigenous and widespread in Europe, it was not known in Italy until the 1980s and it now appears to be having an adverse effect on the indigenous *Eudiaptomus padanus* Burckhardt in northern Italy at least. Ferrari *et al.* (1992) have recorded the Australian calanoid, *Boeckella triarticulata*, from fishponds in northern Italy, and Baldaccini *et al.* (1997) have reported the occurrence of the Central American cyclopoid, *Apocyclops panamensis*, from Lake Massaciuccoli (a brackish shallow lake) in Tuscany (Italy). Alekseev *et al.* (2002) have reported that a cyclopoid, *Acanthocyclops americanus*, now occurs in Belgium at densities of 40,000 m^{-2}. They mention that this species rapidly expanded across Europe and Asia in the 20th century after its introduction from North America into Britain in the 19th century. It is now found as far east as reservoirs on the Rivers Volga and Dnieper, where it is the dominant pelagic animal in the summer months (Alekseev and Kosova 1977 in Alekseev *et al.* 2002).

Branchiura. The fish-louse, *Argulus japonicus*, has a worldwide distribution having being moved with farmed fish stocks, e.g. koi carp, *Cyprinus carpio* Linnaeus from the Orient (Rushton-Mellor 1992, Lester and Roubal 1999). It is common wherever goldfish are found. Its distribution overlaps that of *Argulus foliaceus* Linnaeus but generally occurs in warmer water. *Argulus japonicus* was first discovered in Europe in 1921 (Spain) and has since been found in Germany, France, Italy, Poland, and Slovakia (G. Boxshall 2006, personal communication) on many fish, including species *Carassius*, *Cyprinus*, *Esox*, *Perca*, *Tinca*, and *Scardinius*. The first record for the UK was in 1990 on koi and mirror carp in English ponds (Rushton-Mellor 1992), and it has since spread to indigenous fish populations in southern England (G. Boxshall 2006, personal communication).

Isopoda. Only isopods belonging to the Asellota have invaded European inland waters. *Asellus communis* from North America was mentioned earlier. *Proasellus coxalis*, originating from the western Mediterranean, southern Italy, Sicily, and the Aegean Sea, reached the R. Rhine via southern France, through the Rhône, Saône, Doubs, and the Rhine-Rhône Canal. It is chiefly distributed in streams and rivers of northern Germany: Ems, Saale, Ruhr, Weser, Aller, and Elbe. It is seldom found in the upper Rhine in southern Germany. *Proasellus meridionalis* was previously distributed in western Europe, and was recorded in the 1930s and 1940s in France and England. It made use of the Rhône-Saône-Seine Canal and the Rhine-Rhône Canal for its further spread. The density of this isopod in the Rivers Saar and Rhine, however, is not high. Van der Velde *et al.* (2000) list *P. coxalis* and *P. meridionalis* as having invaded the R. Rhine in the Netherlands.

The isopod genus *Jaera* Leach (Family Janiridae) has been revised by Veuille (1979) who described *Jaera istri* as a new species using morphological characters. The type locality was near Kladovo on the R. Danube near the Iron Gate. At that time, *J. istri* was endemic to the R. Danube from Romania to the Austrian–German border. The distribution of *Jaera sarsi* (Valkanov) is limited to brackish waters in Bulgaria, where it colonizes the supra-littoral zone of the

Black Sea and adjacent areas. It has been described from Lake Gebedze and Lake Schabla. The literature before the revision of Veuille (1979) has obviously listed only *J. sarsi* but it is certain that the purely freshwater populations from the middle and upper stretches of the R. Danube can be referred to as *J. istri*. The oldest Austrian record of the species is from the R. Danube in Vienna, dating back to the year 1934 (Strouhal 1939). In the Bavarian section of the R. Danube, *J. istri* was observed in 1967 (Kothé 1968). After the opening of the R. Danube-Main-R. Rhine Canal, thus joining two previously separated catchments to create a new navigation route between the North Sea and the Black Sea in 1992, *J. istri* has taken the southern corridor to invade many waters in the west of the European Continent. Muskó *et al.* (2005) stated that the littoral zone of Lake Balaton in Hungary has been invaded by *J. istri*. It was found in 1993 in the Main-Danube Canal (Tittizer 1997), in 1994 in the R. Main (Schleuter and Schleuter 1995), and in 1996 in the middle section of the R. Rhine (Schöll and Banning 1996). The Rhine delta was colonized in 1997 (Kelleher *et al.* 2000a), where this lithophilous isopod species inhabits solid substrates. In 1999, *J. istri* was found in the R. Elbe, having used the central corridor for further range extension into the north-eastern part of Europe (Schöll and Hardt 2000). The species, which is salt tolerant, may be spread by means of vessels. The food of this small (1.98 mm) isopod, which can reach mean densities of 2,814 m^{-2}, and highest maximum densities of 5,110 m^{-2} (Kelleher *et al.* 2000b), consists of algae, plant remains, and detritus. Its abundance on all sides of a stone, either sheltered or unsheltered, is fairly similar, in contrast to amphipods such as *E. ischnus* and *D. villosus*, which are found mainly on more sheltered areas and crevices of stones. The life history and reproductive behaviour have not been studied.

Mysida. Species belonging to the mysid genera, *Hemimysis*, *Limnomysis* and *Paramysis* are amongst those crustaceans that have been deliberately introduced from the Ponto–Caspian basin to eastern European countries as fish food (Borodich and Havlena 1973, Ketelaars *et al.* 1999, Arbaciauskas 2002). *Limnomysis benedeni* is a euryhaline mysid species and tolerates a salinity of 6.5‰. Lentic environments with aquatic vegetation and tree roots are preferred. Originally, the species was endemic to the coastal waters of the Black and Caspian seas and can be found several hundred kilometres upstream in rivers discharging into both seas. The species have been intentionally introduced into several habitats along the Baltic coast of the former Soviet Union, and in Lake Balaton, Hungary, for the enhancement of fish production (Bij de Vaate *et al.* 2002). However, Muskó *et al.* (2005) noted that it is only found sporadically in that lake. In 1947, *L. benedeni* was found in the R. Danube in the vicinity of Budapest (Dudich 1947), in 1973 in an ox bow lake of the Austrian Danube near Schönau (Weish and Türkay 1975), in 1993 in the Bavarian Danube (Wittmann 1995), and in 1998 in the Main–Danube Canal (Reinhold and Tittizer 1998). However, by 1998 the species had already reached the middle R. Rhine and the Rhine delta (Kelleher *et al.* 1999, Ketelaars *et al.* 1999). This

Fig. 7 The Ponto–Caspian mysid, *Hemimysis anomala*. Widely spread in continental Europe as a result of stockings to enhance fish production since the middle of the 20th century, but a recent invader in central England. Specimen figured taken from a large swarm in the National Water Sports Centre, Holme Pierrepont, Nottingham, England. (Photo: M. Winter and L. Rippon)

well documented immigration clearly indicates the southern corridor of the migration route for the westward range extension of *L. benedeni*. As Wittmann (1995) has most frequently caught the species in harbours, he suggests that the major vector of migration is shipping. *Hemimysis anomala* (Fig. 7) is a euryhaline mysid from the coastal regions and lagoons associated with the Black, Azov, and Caspian seas, as well as extending upstream into rivers. In the middle 20th century it was introduced into a number of reservoirs in the former USSR, and from these to Lithuania from where it spread to the Baltic Sea (Ketelaars *et al.* 1999). Subsequently, it was recorded from the R. Rhine catchment in 1997, then in the R. Main in 1998. In 1999, it was recorded from the R. Danube (Wittmann et al. 1999). It reached the Netherlands via the Main–Danube Canal or invaded from the Baltic via ballast water (Faasse 1998, Van der Velde *et al.* 2000). It has also been recorded in Belgium (Verslycke *et al.* 2000) and most recently in France (Dumont 2006) and Germany (Bernauer and Jansen 2006). It is a voracious predator and also an omnivorous feeder, and its adverse impact on zooplankton and algae in a freshwater storage reservoir in the Netherlands has been documented by Ketelaars *et al.* (1999). This species has made a sudden appearance in central England, although it is not known how it entered the country. It is presently most common in a large recreational lake that hosts international rowing events (Holdich *et al*. 2006). In 2001, *Katamysis warpachowskyi*, a further mysid shrimp from the Ponto–Caspian basin, was recorded for the Hungarian, Slovakian, and Austrian stretches of the R. Danube (Wittmann 2002). Although the relict mysid, *Mysis relicta* Lovén, is indigenous to Europe it was introduced into lakes in Norway and Sweden as fish food. Subsequently, in Swedish lakes many cladocerans disappeared and this led to reduced growth of Arctic char (*Salvelinus alpinus* Linnaeus) (Langeland *et al*. 1991 in Ketelaars *et al*. 1999). The dramatic impact that the stocking of *M. relicta* in Flathead Lake (North America) has had at all trophic levels, including top carnivores, is provided by Spencer *et al*. (1991).

CONCLUSIONS

As noted by Aladin *et al*. (2002) in relation to the Caspian Sea, all resident species can be described as invaders, the only difference being the time of introduction, with the most ancient invaders now being regarded as indigenous. The same can be said for the inland waters of Europe, which were invaded by a wide variety of species after the last glaciation some 10,000 years ago or were colonized by glacial relics. In this review of invasive crustaceans, only recent invaders are considered. Leppäkoski *et al*. (2002a) noted that the "North American" barnacle, *Balanus improvisus* Darwin, was first recorded in Europe in 1844, although P. Rainbow (2006, personal communication) doubts that it is a North American species, but occurs naturally on both sides of the Atlantic. The Chinese mitten crab, *E. sinensis*, is considered to be the first recorded case (1912) of a species being transported between continents in ballast water (Carlton 1985). The narrow-clawed crayfish, *A. leptodactylus*, might well be the first recorded case of a Ponto–Caspian crustacean invading northern Europe. Huxley (1881) stated that, "the invading *Astacus leptodactylus* is everywhere overcoming and driving out *Astacus nobilis* in the struggle for existence, apparently in virtue of its more rapid multiplication." He was referring to the displacement of *A. astacus* in the White Sea region of Russia, and the fact that *A. leptodactylus* had probably reached this region via canals connecting its rivers to the R. Volga. The spiny-cheek crayfish, *O. limosus*, introduced into Germany in 1890, is certainly the first example of a crustacean being introduced from North America for stocking purposes (Holdich 2002b, Machino and Holdich 2006, Holdich and Black 2007).

Introductions usually increase biodiversity, but this can be at a cost to the indigenous fauna. For example, the UK had a single indigenous species of crayfish before the 1970s, but by 2004 there were five other established crayfish species, imported deliberately for aquaculture, restaurant, bait, and pet trades, and all with the potential to harm the indigenous species through competition, and transmission of disease in the case of North American species (Holdich *et al.* 2004, Holdich and Pöckl 2005). Many countries associated with the R. Danube and R. Rhine and their various connecting canals, have seen a large increase in the number of mostly Ponto–Caspian species, particularly amphipods, cladocerans and mysids, inhabiting their inland waters over the last few decades, e.g. the Netherlands and Germany (Van der Velde *et al.* 2000, Bernauer and Jansen 2006), which have been found to have an adverse impact on the indigenous biota. However, there can also be benefits, e.g. Kelleher *et al.* (2000b), pointed out that many non-indigenous amphipods in the R. Rhine now form a large part of the diet of macrozoobenthivorous fish. These invaders have either diffused naturally or been aided by human activities such as shipping and inoculation of waters to enhance fish production.

For crustaceans, the trends outlined in this review are set to become worse. A case in point is the R. Rhine, which amongst European rivers is probably the best documented (see above). Most recently, Bernauer and Jansen (2006) reported that NIS made up 74% of the total number of organisms collected from ship-based samples and 85% from cooling water intake (of which 64% were *D. villosus*). They recorded 17 species of non-indigenous crustaceans in the upper R. Rhine, which was just over 50% of the non-indigenous macroinvertebrate species found there. It is thought that most of these species have made their way into the R. Rhine via the Main–Danube canal, which first opened in 1992. Bernauer and Jansen (2006) have shown that the macroinverebrate community of the upper R. Rhine has been severely altered by the invasion of several highly successful NIS (mostly crustaceans) that has resulted in the elimination or population decline of some of the indigenous species.

The largest crustacean invaders, the Chinese mitten crab and the North American crayfish, still have parts of Europe to conquer. The former is gradually moving round Britain, and has recently entered Irish waters, as well as spreading into eastern Europe and the Near East, whilst the latter is moving into eastern Europe, often aided by humans with aquacultural interests. Ireland is of particular interest when considering invasive species (J. D. Reynold 2006, personal communication). It was cut off from continental Europe before 9000 BP, and as a consequence freshwater species had special difficulties in bridging the more saline seas. The amphipod *G. duebeni* perhaps invaded from the sea in peri-glacial times of low salinity to become widespread in freshwaters, with *G. lacustris* invading large lakes. Most of the invasive species in continental European inland waters have yet to arrive in Ireland, and for larger species such as crayfish this is in part due to strict legislation on imports (Reynolds 1997).

It is virtually impossible to eliminate an established non-indigenous aquatic macroinvertebrate in anything but a small, enclosed waterbody (Holdich *et al.* 1999, Peay *et al.* 2006). The aim of eradication is to completely remove the invasive species, whereas control aims for its reduction over time. Eradication is best attempted in the early stages of invasion. However, many invasive species are not noticed until they become established, e.g. the case of the crayfish, *O. virilis*, in the Netherlands (Souty-Grosset *et al.* 2006) and the mysid, *H. anomala*, in England (Holdich *et al.* 2006). Unless an invasive species can be seen by the relevant authorities to be causing economic or physical harm to the aquatic environment, then they are unlikely to be prepared to spend large sums of money on eradication programmes. Control is also very difficult if only trappable crustaceans are removed as the lack of large individuals may result in smaller cohorts growing more rapidly. Hundreds of thousands of non-indigenous crayfish have been removed from some rivers in Britain at great expense but this has had little impact (Collins 2006). No amount of legislation (Holdich and Pöckl 2005) will prevent a child tipping a pet crayfish into a lake after it has outgrown its tank. If such a crayfish is parthenogenetic, as has been found in the case of *Procambarus* sp. (Scholtz *et al.* 2003, Vogt *et al.* 2004, Seitz *et al.* 2005), then it only needs one individual to start a population. It is also very difficult to get the message over to recreational anglers that introducing live non-indigenous crustaceans as food to increase fish production is not a good idea. One huge problem concerns the pet trade, which some European countries appear unwilling to do anything about (Holdich and Pöckl 2005). Extensive lists of North American crayfish are available to European aquarists. Potentially invasive crustaceans are even traded on eBay!

As pointed out by Gollasch and Leppäkoski (1999), all invasive species should be treated as "guilty until proved innocent", as there is no way of exactly predicting how a NIS will behave in a new habitat (Leppäkoski *et al.* 2002b). However, it seems to be the case that the majority of introduced crustaceans have some of the characteristics of *r*-selected species (short life cycles, high fecundity, fast growth), whilst the established indigenous species are more K-selected (Lindqvist and Huner 1999, Van der Velde *et al.* 2000). Hopefully, continued education, vigilance, and prosecutions may eventually lead people to realize the dangers of intentional introductions of invasive species, but unintentional introductions will be impossible to stop. All that can be hoped for is that education will lead to increased vigilance, so that when NIS are reported to the relevant authorities they may try and do something about them rather than procrastinating for years until it is too late, as is usually the case (Holdich and Pöckl 2005). Certainly, in the UK, press and TV coverage have raised public awareness of the dangers of introduced crustacean species. In recent years, the UK attention has been on crayfish, but currently it has become focused on the Chinese mitten crabs with headlines such as "Crab that eats riverbanks brings flood threat" (Daily Mail, 17 November, 2005).

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