

## PERSPECTIVE

# Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe<sup>1</sup>

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**Abstract:** Range extensions of aquatic Ponto-Caspian macroinvertebrate species in Europe have mainly been facilitated by the interconnection of river basins through man-made canals and intentional introductions. Three inland migration corridors can be distinguished: (i) a northern corridor: Volga → Lake Beloye → Lake Onega → Lake Ladoga → Neva → Baltic Sea, (ii) a central corridor connecting the rivers Dnieper → Vistula → Oder → Elbe → Rhine, and (iii) a southern corridor connecting the Danube and Rhine rivers. Important trade harbours in Europe were connected via these corridors allowing further range extensions of macroinvertebrate species attached to a vessel's hull or in ballast water. The central corridor was the main migration route before 1992, after which the southern corridor became the most important migration route for the range expansions to the west because of the reopening of the Main–Danube Canal, connecting the Rhine and Danube basins. Especially the water level maintenance in the upper part of the canal, with water supply from the Danube basin, facilitated migration of mobile animals (e.g., crustaceans) from the Danube basin towards the Rhine basin; however, contribution of other transport mechanisms (e.g., shipping) is expected in the near future.

**Résumé :** L'extension vers l'Europe des aires de répartition des espèces pontocaspiennes de macroinvertébrés aquatiques a été facilitée principalement par l'interconnection des bassins hydrographiques par la construction de canaux, ainsi que par des introductions délibérées. On peut reconnaître trois corridors de migration à l'intérieur du continent: (i) un corridor boréal: Volga → lac Blanc → lac Onega → lac Ladoga → Néva → mer Baltique, (ii) un corridor central reliant les fleuves Dnieper → Vistule → Oder → Elbe → Rhin et (iii) un corridor austral joignant le Danube et le Rhin. D'importants ports commerciaux européens sont reliés par ces corridors, ce qui permet des extensions d'aires supplémentaires d'espèces de macroinvertébrés attachées aux coques des navires ou contenues dans l'eau de ballastage. Le corridor central constituait la voie principale de migration avant 1992, après quoi la voie australe est devenue la route privilégiée d'extension des aires vers l'Occident à cause de la réouverture du canal Main–Danube, reliant les bassins du Rhin et du Danube. En particulier, le maintien des niveaux d'eau dans la partie supérieure du canal par apport d'eau provenant du bassin du Danube favorise la migration d'animaux mobiles (e.g., les crustacés) du bassin du Danube vers celui du Rhin. Néanmoins, l'importance d'autres mécanismes de transport (e.g., le commerce maritime) augmentera, sans doute, dans un avenir rapproché.

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## Introduction

The introduction of aquatic organisms outside their native ranges has occurred intentionally and unintentionally for

connecting river basins, or as nontarget species associated with intentionally introduced ones (Jazdzewski 1980). Important reasons for the intentional introduction of aquatic species

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**Table 1.** Biological attributes associated with successful Ponto-Caspian invaders into Europe. Table 1 continues on following pages.

Attribute	<i>Cordylophora caspia</i>	<i>Dendrocoelum romanodanubiale</i>	<i>Hypania invalida</i>	<i>Caspiobdella fadejewi</i>	<i>Lithoglyphus naticoides</i>	<i>Dreissena polymorpha</i>	<i>Caspihalacarus hyrcanus</i>
Relatively short life span and generation time		+	+				
Rapid growth with early sexual maturity						+	
High fecundity						+	
Dispersal by larvae	+					+	
Protection of juveniles							
Larger than closely related species or much smaller							
Euryoecious							
Euryhaline	+	+	+		+	+	+
Nonspecific food preference		+	+		+	+	+
Suspension feeding						+	
Special adaptations	+			+		+	
Gregarious behaviour	+					+	+

include (i) aquaculture, (ii) the improvement of wild stocks, and (iii) the control of unwanted organisms (Welcome 1988; Williamson 1996).

The transport of large quantities of water in ballast tanks from one biogeographical region to another is considered to be one of the most important sources of unintentional inter-continental introductions (e.g., Gollasch 1996). Recently, it was estimated that the world's major cargo vessels transfer 8–10 billion tons of ballast water per year (Carlton and Geller 1993), and that on average 3000 to 4000 species are transported by ships each day (Carlton and Geller 1993; Gollasch 1996). However, not only transport of macro-invertebrates by seagoing vessels is important for their spread, but also the construction of canals, connecting previously separated biogeographic regions. The interconnection of river basins has facilitated the range expansions of many species in Europe (e.g., Jazdzewski 1980). Numerous canals have been constructed during the last two centuries in Europe as a result of industrial and economic activities. In Germany for example, approximately 1770 km of all inland waterways are man made (Tittizer 1996). Also, intentionally released or escaped specimens have taken advantage of interconnected river basins.

In this paper, range expansion to the west of 22 Ponto-Caspian macroinvertebrate species is reviewed to make clear their expansion routes. Knowledge of these routes and their mechanisms of spread are important to assess the expansion potential of these animals in and outside Europe. In addition, biological attributes to make them successful invaders are discussed.

## Invasion success

The introduction of a species will be successful if all abiotic and biotic factors in its new environment are tolerable. That means it has to arrive in sufficient numbers at the right time. Successful invasions usually proceed through a number of successive stages. After its initial introduction, an invasive species must be able to adapt to its new habitat. Subsequently, the species must be able to reproduce and complete its life cycle. Finally, it will disperse within the new range, usually by gradual local dispersal, but also by

jumps often aided by human transport (secondary introductions). It will exhibit exponential population growth, sometimes to densities higher than those in its native range, followed by somewhat lower steady-state numbers.

In spite of the increased opportunities for the immigration of nonindigenous species, not all of these species are successful invaders. To explain this phenomenon, the rule of 10 was formulated. This rule states that only 10% (in practice between 5 and 20%) of the established immigrant species are able to develop populations dense enough for them to be regarded as pests (Williamson 1996). Examples of species considered to be pests are the Ponto-Caspian bivalve *Dreissena polymorpha*, which already spread across western Europe in the 19th century (Kinzelbach 1992), and the Ponto-Caspian amphipod *Chelicorophium curvispinum*, which spread via river basin connecting canals draining westward (Jazdzewski 1980), and into brackish areas of the Baltic Sea (Gollasch and Leppäkoski 1999). Both species were also transported in ballast water (e.g., to Great Britain).

Immigrant species appear to be especially successful in regions with a climate comparable to where they originated from, in combination with biological attributes to make invasions successful (Table 1). Species dispersing or transferred from the Ponto-Caspian area into the Baltic Sea drainage system arrive in an area with many similar habitats. Both seas belong to the east Atlantic boreal climate zone, and salinity gradients are also comparable (Gollasch and Leppäkoski 1999).

Range extensions by nonindigenous species can be aided by anthropogenic modification of habitats as well (Den Hartog et al. 1992). As a result, new species can be pre-adapted because of the similarity of their ancestral habitat, resulting in relatively quick colonization, whereas indigenous species are simultaneously weakened by the modifications. Sometimes new niches are exploited because equivalent indigenous species are not present. Pollution calamities in rivers, for example, can create empty niches, giving invasive species an opportunity to colonize. Persistent pollution can create such empty niches as well (Den Hartog et al. 1992). Water quality improvement subsequently gives newcomers the opportunity to settle.

<i>Astacus leptodactylus</i>	<i>Hemimysis anomala</i>	<i>Limnomysis benedeni</i>	<i>Chelicorophium curvispinum</i>	<i>C. sowinskyi</i>	<i>Dikerogammarus bispinosus</i>	<i>D. haemobaphes</i>	<i>D. villosus</i>	<i>Echinogammarus ischnus</i>
	+	+	+	+	+	+	+	+
			+					
+	+	+	+	+	+	+	+	+
					+	+	+	
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
	+	+	+	+				+
	+	+	+	+				

## Invasion routes

Range extensions of aquatic Ponto-Caspian species in Europe have been mainly facilitated by the interconnection of river basins, beginning in the 17th century. An important phase was the construction of canals that connected the Bug (Vistula basin) and Pripyat (Dnieper basin) rivers, the Vistula and Oder rivers, and the Elbe and Oder rivers in the 18th century. The Volga–Don Canal connecting the Volga and Don rivers, which opened for shipping in 1952, provided a connection between the Caspian and Black seas. Although attempts were already made in the 19th century to connect the rivers Danube and Main (Rhine basin), the canal constructed at that time (Ludwig Canal) only functioned briefly for a relatively small number of cargo vessels. During the Second World War, the link between both rivers was interrupted, and afterwards not restored. However, a new shipping canal (Main–Danube Canal), which officially opened in September 1992, is an important new route for Ponto-Caspian species to migrate from the Danube River to the west (Tittizer 1997).

Intentionally introduced species could also take advantage of the river basin connections. In the former Soviet Union large quantities of crustaceans were used as live food for commercial fish species (Decksbach 1952). The Ponto-Caspian region has been the preferred source for the so-called “acclimatization” of new species to different types of water bodies, especially impoundments on large rivers for the purpose of enriching the fauna and as fish food (Mordukhai-Boltovskoi 1979). The most frequently used Ponto-Caspian invertebrates were mysids of the genera *Paramysis*, *Limnomysis*, and *Hemimysis* and the amphipods *Dikerogammarus haemobaphes*, *Pontogammarus robustoides*, *Obesogammarus crassus*, *Echinogammarus ischnus*, *Echinogammarus warpachowskyi*, and *Chelicorophium curvispinum* (Karpevich 1975; Jazdzewski 1980). All together, nine species of Mysidacea, seven species of Cumacea, and 17 species of Amphipoda were used in the period 1940–1970 (Karpevich 1975).

In general, the interconnection of river basins in Europe resulted in corridors for aquatic animals to migrate actively or passively (e.g., by vessels in humid places or attached to

the ship’s hull) from one geographical region to another. Three important canal corridors for the range extension of Ponto-Caspian species can be identified (Fig. 1).

### Northern corridor

The northern corridor covers the route Volga River → Lake Beloye → Lake Onega → Lake Ladoga → Neva River → Baltic Sea. In the past there was another northern corridor from the Dnieper River to the Kuronian Lagoon in the Baltic Sea (via the Oginskiy Canal and the Neman River), but this corridor does not exist anymore (S. Olenin, Klaipeda University, Manto, Lithuania, personal communication). The bivalve *D. polymorpha* likely used this corridor, which opened by the end of the 18th century, for its range extension (Decksbach 1935).

### Central corridor

The central corridor covers the route Dnieper River → Vistula River → Oder River → Elbe River → Rhine River. Invasive species were able to reach the Baltic Sea and western Europe via this corridor. The amphipod *Chelicorophium curvispinum* was probably the first Ponto-Caspian crustacean that successfully used the corridor for range extension (Jazdzewski 1980; Jazdzewski and Konopacka 2000).

Both the northern and central corridors have been important routes for Ponto-Caspian macroinvertebrates to immigrate to the Baltic Sea. Which one has been the most important could not be determined. Species that reached relatively high densities in the Baltic Sea lagoons, especially in the Kuronian Lagoon, are *D. polymorpha*, *Paramysis lacustris*, *Limnomysis benedeni*, *Pontogammarus robustoides*, *O. crassus*, *E. ischnus*, and *E. warpachowskyi* (Olenin and Leppäkoski 1999).

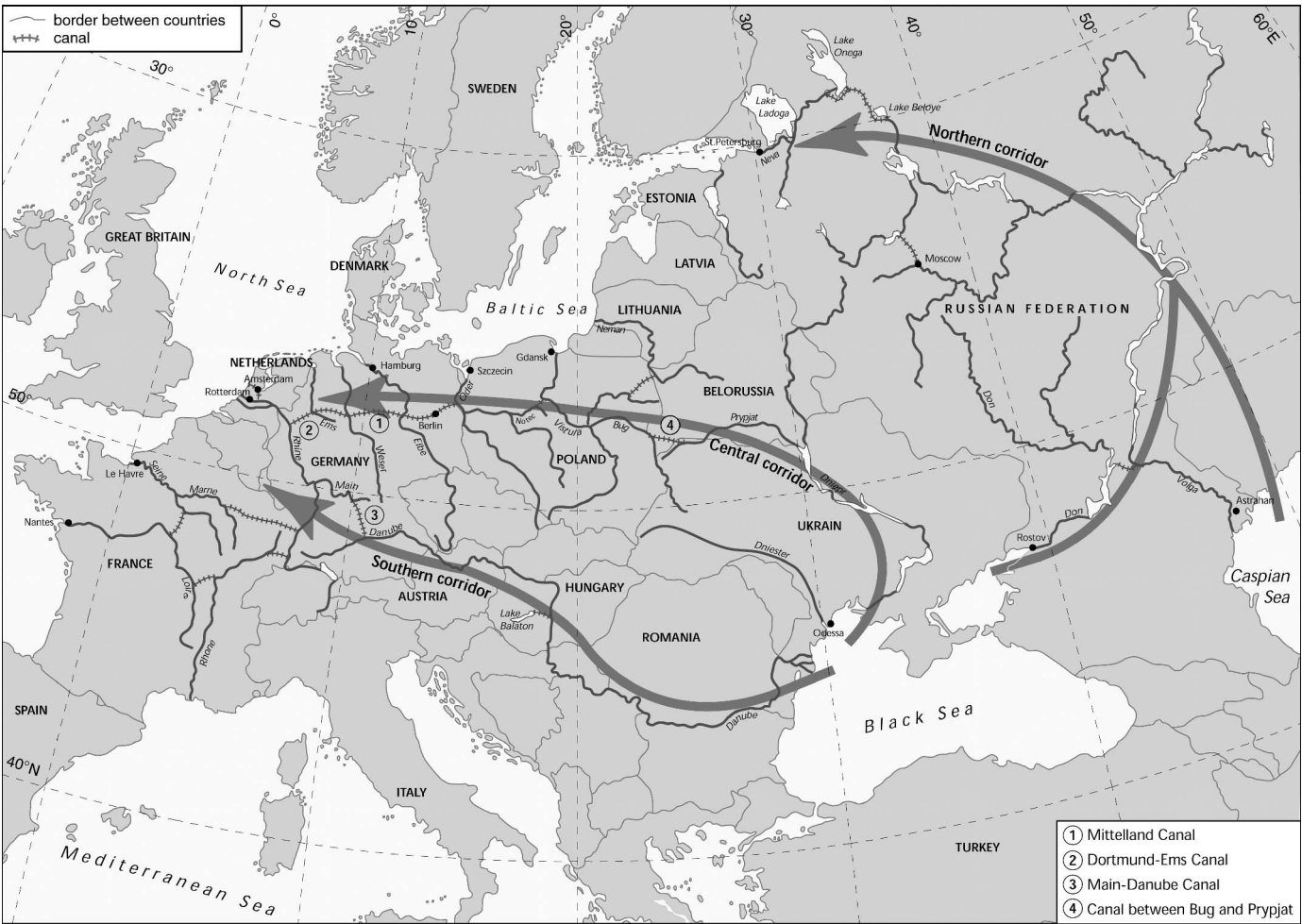
### Southern corridor

The southern corridor covers the route Danube River → Rhine River. As indicated above, the Main–Danube Canal forms the link between these river basins. The water level maintenance in the upper part of the canal, with water supply from the Danube basin, especially facilitates migration of mobile animals (e.g., crustaceans) from the Danube basin

Table 1 (concluded).

Attribute	<i>Echinogammarus ischnus</i>	<i>E. trichiatus</i>	<i>E. warpachowskyi</i>	<i>Obesogammarus crassus</i>	<i>Obesogammarus obesus</i>	<i>Pontogammarus robustoides</i>	<i>Jaera istri</i>
Relatively short life span and generation time	+	+	+	+	+	+	+
Rapid growth with early sexual maturity							
High fecundity							
Dispersal by larvae							
Protection of juveniles	+	+	+	+	+	+	+
Larger than closely related species or much smaller							
Euryoecious	+	+	+	+	+	+	+
Euryhaline	+	+	+	+	+	+	+
Nonspecific food preference	+	+	+	+	+	+	+
Suspension feeding	+	+					
Special adaptations							
Gregarious behaviour							

Fig. 1. The migration corridors of Ponto-Caspian species in Europe.



towards the Rhine basin. Tittizer (1997) estimated that 150 million cubic metres of water from the Danube basin flows into the Rhine River each year. The corridor to the Rhine delta has already been successfully traversed by some amphipod species such as *D. haemobaphes* (Schleuter et al. 1994), *D. villosus* (Bij de Vaate and Klink 1995), and *Echino-*

*gammarus trichiatus* (Podraza et al. 2001), the isopod *Jaera istri* (Schleuter and Schleuter 1995) and the mysid *L. benedeni* (Reinhold and Tittizer 1998), the polychaete *Hypania invalida* (Klink and Bij de Vaate 1996), as well as the planarian *Dendrocoelum romanodanubiale* (Schöll and Behring 1998).

**Table 2.** Ponto-Caspian macroinvertebrate species found in coastal waters of the Baltic Sea.

	Species	Reference
Cnidaria	<i>Cordylophora caspia</i>	Olenin and Leppäkoski 1999
Oligochaeta	<i>Paranais frici</i>	Panov et al. 1997
	<i>Potamothenix heuscheri</i>	Panov et al. 1997
	<i>Potamothenix vejdoskyi</i>	Panov et al. 1997
Mollusca	<i>Lithoglyphus naticoides</i>	Piechocki 1979
	<i>Theodoxus pallasii</i>	Mordukhai-Boltovskoi 1979
	<i>Dreissena polymorpha</i>	Panov et al. 1997
Crustacea	<i>Hemimysis anomala</i>	Salemaa and Hietalahti 1993
	<i>Limnomysis benedeni</i>	Olenin and Leppäkoski 1999
	<i>Paramysis lacustris</i>	Gollasch and Leppäkoski 1999
	<i>Chelicorophium curvispinum</i>	Gollasch and Leppäkoski 1999
	<i>Dikerogammarus haemobaphes</i>	K. Jazdzewski and A. Konopacka, unpublished data
	<i>Echinogammarus ischnus</i>	Jazdzewski 1975
	<i>Echinogammarus warpachowskyi</i>	Olenin and Leppäkoski 1999
	<i>Obesogammarus crassus</i>	Gollasch and Leppäkoski 1999
	<i>Pontogammarus robustoides</i>	Gruszka 1999

**Table 3.** Ponto-Caspian macroinvertebrate species found in the Rhine basin.

	Species	Reference
Cnidaria	<i>Cordylophora caspia</i>	Tittizer 1996
Tricladida	<i>Dendrocoelum romanodanubiale</i>	Schleuter and Schleuter 1998
Polychaeta	<i>Hypania invalida</i>	Klink and Bij de Vaate 1996
Hirudinea	<i>Caspiobdella fadejewi</i>	Geissen and Schöll 1998
Mollusca	<i>Lithoglyphus naticoides</i>	Gittenberger et al. 1998
	<i>Dreissena polymorpha</i>	Bij de Vaate et al. 1992
Acarina	<i>Caspihalacarus hyrcanus</i>	A. Bij de Vaate, unpublished data
Crustacea	<i>Astacus leptodactylus</i>	Holthuis and Heerebout 1986
	<i>Chelicorophium curvispinum</i>	Van den Brink et al. 1989
	<i>Hemimysis anomala</i>	Schleuter et al. 1998
	<i>Limnomysis benedeni</i>	Kelleher et al. 1999
	<i>Dikerogammarus haemobaphes</i>	Schleuter et al. 1994
	<i>Dikerogammarus villosus</i>	Bij de Vaate and Klink 1995
	<i>Echinogammarus ischnus</i>	Schöll 1990
	<i>Echinogammarus trichiatus</i>	Podraza et al. 2001
	<i>Jaera istri</i>	Schleuter and Schleuter 1995

Using one of the three corridors, Ponto-Caspian species have been able to reach important trade harbours outside their native ranges (Fig. 1). Subsequently, transport in ballast water has been an important vector for their further dispersal (secondary introduction). *Dreissena polymorpha* and *C. curvispinum* are two clear examples of species that have made use of this dispersal mechanism.

### Invasive Ponto-Caspian species

Ricciardi and Rasmussen (1998) identified some Ponto-Caspian euryhaline macroinvertebrate species with recent invasion histories that have likely been transported in ballast water. As a result, these species have been classified as high invasion risk species: the amphipods *C. curvispinum*, *Chelicorophium sowinskyi*, *D. haemobaphes*, *D. villosus*, *Obesogammarus obesus*, *O. crassus*, and *Pontogammarus robustoides*, the mysids *Hemimysis anomala*, *L. benedeni*, *Paramysis intermedia*, *Paramysis lacustris*, and *Paramysis ullskyi*, the freshwater polychaete *H. invalida*, and the bi-

valve *Monodacna colorata*. Most of these species have already been found either in the brackish areas of the Baltic Sea (Table 2) or in the Rhine basin (Table 3).

### *Cordylophora caspia*

The hydroid *Cordylophora caspia* originates from the Black and Caspian seas, where it lives in brackish as well as fresh water. In general, it commonly occurs in estuaries, lagoons, and coastal lakes (Arndt 1989), rarely in oligohaline freshwater. Colonies of *C. caspia* develop well at 2–12‰ salinity with relatively constant environmental conditions, and at 2–6‰ with considerable tidal influence (Arndt 1989). The occurrence of *C. caspia* has also been reported from upper reaches of rivers at favourable conditions such as fast flow, high oxygen availability, and positive ion anomalies ( $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{Na}^{+}$ ) (Arndt 1989).

*Cordylophora caspia* has been dispersed via canals and rivers attached to ships' hulls, floating reed, water lily stems, and other macrophytes (Roos 1979), and in ballast water for overseas transportation. Most likely the northern but certainly

the southern corridor (Fig. 1) (Kinzelbach 1995) was used for range expansion. According to Tittizer (1996), the species occurs in all rivers and canals in the Rhine, Weser, Oder, and Danube basins. *Cordylophora caspia* was recorded in 1874 in The Netherlands (Vervoort 1946). In 1924 the species already had a worldwide distribution, from the cold boreal and anti-boreal to the subtropical regions (Roch 1924; Arndt 1989). However, its distribution was discontinuous owing to its dispersal via ballast water into estuaries, from where it then migrated upstream.

*Cordylophora* colonies are very plastic, and numerous growth forms are described relative to the environmental conditions (e.g., salinity, light, temperature). The species has no medusal stage, its sexual stage is at the polyp, and planula larvae released settle after a short planktonic life. Asexual dispersal mechanisms, e.g., body fragments (hydro-rhiza) and menonts, which survive in wintertime, contribute to its colonization success. In its menont stage *C. caspia* can easily be transported over large distances, because in this stage the species is temperature and drought resistant. Menonts survive in sea water and can even develop into polyps at maximum salinity of 40‰ (minimum: 0.08‰) (Vervoort 1946). The polyp prefers solid substrates (stones, wooden piles, bivalve shells (e.g., *Dreissena*), crabs, macrophytes). It is carnivorous (eating small crustaceans, worms, insect larvae, watermites) and profits from eutrophication.

#### *Dendrocoelum romanodanubiale*

According to Weinzierl and Seitz (1994) the Ponto-Caspian triclad *D. romanodanubiale* was first recorded in the upper Danube (Germany) in 1994, indicating that the southern corridor (Fig. 1) was used for western range expansion. In August 1997 and July 1998 the species was observed in the Rhine River (Schöll and Behring 1998) and first recorded in the Rhine delta in September 1999 (Bij de Vaate and Swarte 2001).

#### *Hypania invalida*

Migration pattern of the polychaete *H. invalida* has been similar to that of the isopod *J. istri*. Its range expansion to the west was only observed through the southern corridor (Fig. 1). In 1967, the species was first observed in the upper section of the Danube River (Germany) (Kothé 1968). Although the colonization of the Main River was reported in 1996, *H. invalida* was already observed in the lower Rhine River in 1995 (Klink and Bij de Vaate 1996).

#### *Caspiobdella fadejewi*

Outside its native distribution area, mainly in rivers emptying into the Black Sea (Geissen and Schöll 1998), the Ponto-Caspian leech *Caspiobdella fadejewi* is known from two Vistula River affluents, the San and Biebrza rivers, in Poland (Bielecki 1990), and from the Rhine River. In the Biebrza River it was observed in 1989 on the heads and gill opercula of several common fish species (Bielecki 1990), in 1998 in the lower Rhine River on solid substrates (Geissen and Schöll 1998), and in 2000 in bottom samples from a river restoration area in the forelands along the Waal River, the main tributary in the Rhine delta (A. Bij de Vaate, unpublished data). *Caspiobdella fadejewi* is the dominant species of the Piscicolidae in the Austrian part of the Danube River

and was recently observed upstream in the German part of that river (Geissen and Schöll 1998). To reach the Rhine delta, it is thought that the southern corridor must be traversed; however, unintentional introductions as a result of the living fish trade remains a possible vector for the spread of this fish parasite.

#### *Lithoglyphus naticoides*

The gastropod *Lithoglyphus naticoides* originates from the western Black Sea, and it is considered to be a species of slowly flowing waters like those in the downstream parts of rivers, canals, and lakes (Gittenberger et al. 1998). In the second part of the 19th century, it was discovered in The Netherlands (Schepman 1874). The dispersal of this species was thought to be a consequence of canal construction in the previous centuries. The northern and the central corridor (Fig. 1) could have been the main route for western migration. Records of the species in Poland (Piechocki 1979) and in the vicinity of Berlin (Sukopp and Brande 1984) support this hypothesis. However, Gittenberger et al. (1998) considered the southern corridor (Fig. 1) to be the most probable migration route to The Netherlands. *Lithoglyphus naticoides* was suspected to have dispersed via the Ludwig Canal, which was the first connection between the Rhine and Danube basins. In Poland, the species generally shows a similar distribution pattern to *D. polymorpha*, occurring in large- and medium-sized lowland rivers, in the Szczecin and Vistula lagoons, and in lakes of the Mazurian Lake district (Piechocki 1979). In The Netherlands, *L. naticoides* has been found in the Rhine delta and in Lake IJsselmeer (Gittenberger et al. 1998).

#### *Dreissena polymorpha*

Distribution of the zebra mussel in Europe was reviewed by Strayer and Smith (1993). It represents the first mass invasion of a Ponto-Caspian species in the area, and therefore provides a good example of how and in which directions a Ponto-Caspian invader is able to extend its range. The construction of canals in the 18th century, connecting the Dnieper, Neman, and Vistula rivers was the beginning of its westward expansion (Decksbach 1935; Kinzelbach 1992). In general, expansion took place through the northern and central corridor (Fig. 1), (i) attached to rafts by which timber was transported through canals and rivers to harbours along the Baltic Sea, and from there overseas by ships, (ii) attached to ship's hulls, and (iii) by planktonic larvae using canals that connect rivers and lakes (Sukopp and Brande 1984). In the case of expansion by timber transport aboard ships, *D. polymorpha* was able to reach Great Britain in 1824 and The Netherlands in 1826 (Kinzelbach 1992). Its recent invasion of Ireland in 1997 is most likely a result of the transportation of yachts, aboard ships from Great Britain or The Netherlands (Minchin and Moriarty 1998). The species can also be transported across land while attached to boats on trailers because it is able to withstand exposure to air for several weeks (Ricciardi et al. 1995). In Western Europe, the zebra mussel crossed the Alps between 1960 and 1970, and established in Italy (Giusti and Oppi 1972). Transportation of yachts from one lake to another was considered to be the vector for their spread (Kinzelbach 1992). Recently the Pyrenees Mountains were probably crossed in the same way; first observation of

the species was made in Spain in the lower part of the Ebro River in 2001 (Dr. Rafael Araujo, Museo Nacional de Ciencias Naturales, José Gutiérrez Abascal 2, 28006 Madrid, Spain, personal communication). Its range extension further north seems to be limited by climatic conditions, largely because it requires a water temperature above ca. 12°C for spawning (Borcherding 1991).

*Dreissena bugensis*, which is sympatric with *D. polymorpha* in the Ponto-Caspian area, did not disperse into western Europe despite its further range of expansion in Russia (Pligin 1979) and its successful immigration to the North American Great Lakes between 1985 and 1989 (Mackie 1999).

### *Caspihalacarus hyrcanus*

According to Bartsch (1998), the distribution area of the freshwater mite *Caspihalacarus hyrcanus* covers the Caspian and Black seas, including the rivers emptying into these basins. In the Danube River it was found upstream as far as Bratislava (Slovakia). It has been recorded in fresh and brackish waters up to a salinity of 12.5‰. In 2000, the species was found in the same area in the Rhine delta where *Caspiobdella fadejewi* was found. *C. hyrcanus* had colonized woody debris in a newly constructed secondary channel (A. Bij de Vaate, unpublished data). Lack of data from other regions in western Europe hampers the reconstruction of their spreading history to the Rhine delta. However, the southern corridor (Fig. 1) forms the shortest connection between the Rhine delta and the nearest by known population in the Danube River. It should be noticed that *C. hyrcanus* easily could be overlooked during sampling because of its size ( $\pm 500 \mu\text{m}$ ) if unsuitable ( $>500 \mu\text{m}$  mesh) handnets are used for sampling and if small-meshed sieves are used for rinsing the samples.

### *Astacus leptodactylus*

According to Ingle (1997), the crayfish *Astacus leptodactylus* is endemic to rivers discharging into the Black and Caspian seas. Intentional introductions and subsequent escapes from aquaculture facilities appear to have been the major vector for its range extension in western Europe during the 19th century. Today, *A. leptodactylus* has been dispersed all over western Europe and can be found in different water types such as rivers, canals, and lakes.

### *Hemimysis anomala*

The euryhaline mysid *H. anomala* occurs in a wide range of salinities in the Ponto-Caspian area, from fresh water to 19‰ salinity (Bacescu 1954; Mordukhai-Boltovskoi 1979; Komarova 1991). Preferring lentic conditions, it has been observed in the coastal regions of the Caspian, Black, and Azov seas, in adjacent lagoons, and up to 50 km upstream in the Don, Dniester, Dnieper, Pruth, and Danube rivers (Bacescu 1954; Komarova 1991). In the 1950s and 1960s, *H. anomala* was intentionally introduced into several impoundments in the Dnieper River, water reservoirs near Chernorechensk and Simferopol on the Crimean peninsula, and the Dubossary reservoir in Moldavia (Komarova 1991). In the 1960s, *H. anomala* was successfully transferred from the Dnieper hydropower reservoir into reservoirs in Lithuania; for example, the Kaunas reservoir in the Neman River (Gasjunas 1968b; Mordukhai-Boltovskoi 1979). From there it dispersed into the Baltic Sea, where it was first recorded

in 1992 in the Gulf of Finland (Salemaa and Hietalahti 1993). The first observation in the Rhine basin (Neckar River) is from 1997 (Schleuter et al. 1998). In July 1998 *H. anomala* was recorded in the Main River, another tributary of the Rhine River (Schleuter and Schleuter 1998). Kelleher et al. (1999) found *H. anomala* in stomachs of young percids caught in the Rhine delta near Nijmegen in September 1997, being its first record in The Netherlands. All of these observations, including that in the upper Danube (Wittmann et al. 1999), indicate that the southern corridor (Fig. 1) was used for range extension. However, *H. anomala* has been observed in the same period at several locations in the western part of The Netherlands: (i) in June 1997 and November 1998 in the littoral zone of the brackish Lake Noorder-IJ close to, but isolated from, the North Sea Canal and the port of Amsterdam, The Netherlands; (ii) in 1998 in the Andijk reservoir; and (c) from 1997 onwards in the Biesbosch reservoirs (Ketelaars et al. 1999). In 1999 the species was also found in Belgium in the Broechem reservoir, close to the port of Antwerp (H.A.M. Ketelaars, unpublished data). Since all these observations were made in the vicinity of the international ports, *H. anomala* was likely introduced as a result of ballast water transfer as well. Its recent observation in the Salzgitter Canal in northern Germany (Eggers et al. 1999) is an indication that the central corridor also has been used for range expansion.

From the above-mentioned observations it can be concluded that the present distribution of *H. anomala* in western Europe is very scattered, and raises suspicions that it might not have been found in monitoring studies because of its nocturnal activity. Emphasis should therefore be placed on more appropriate sampling in monitoring programs (e.g., Ketelaars et al. 1999).

### *Limnomysis benedeni*

The mysid *L. benedeni* is a euryhaline species; 6.5‰ salinity is tolerated (Wittmann 1995). Lentic environments with aquatic vegetation are its preferred habitat. It is 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 (Bacescu 1954). The species was intentionally introduced into several habitats along the Baltic coast of the former Soviet Union (Leppäkoski 1984) and in Lake Balaton (Hungary) for the enhancement of fish production (Woynarovich 1955).

In 1947, *L. benedeni* was found in the Danube River in the vicinity of Budapest (Dudich 1947). Further range extension upstream has been well documented from 1973 to present. The upper Danube (in Germany) was reached in 1993 (Wittmann 1995), and in 1998 the species was found in the Main–Danube Canal (Reinhold and Tittizer 1998). However, by 1998, the species had already reached the middle Rhine River and the Rhine delta (Kelleher et al. 1999; Ketelaars et al. 1999). The successive records of *L. benedeni* in the Danube River, the Main–Danube Canal, and the Rhine basin clearly indicate that the southern corridor was the migration route for westward range extension (Figs. 1 and 2).

### *Chelicorophium curvispinum*

The amphipod *C. curvispinum* originates from large rivers discharging into the Black Sea and the Caspian Sea (Volga,

--- border between countries  
 +++ canal  
 → migration direction  
 19xx year of first observation of *Limnodynastes benedeni*  
 19xx year of first observation of *Jaera istri*

The map shows the distribution and migration of two species across Europe. Key locations and years of first observation include:
 

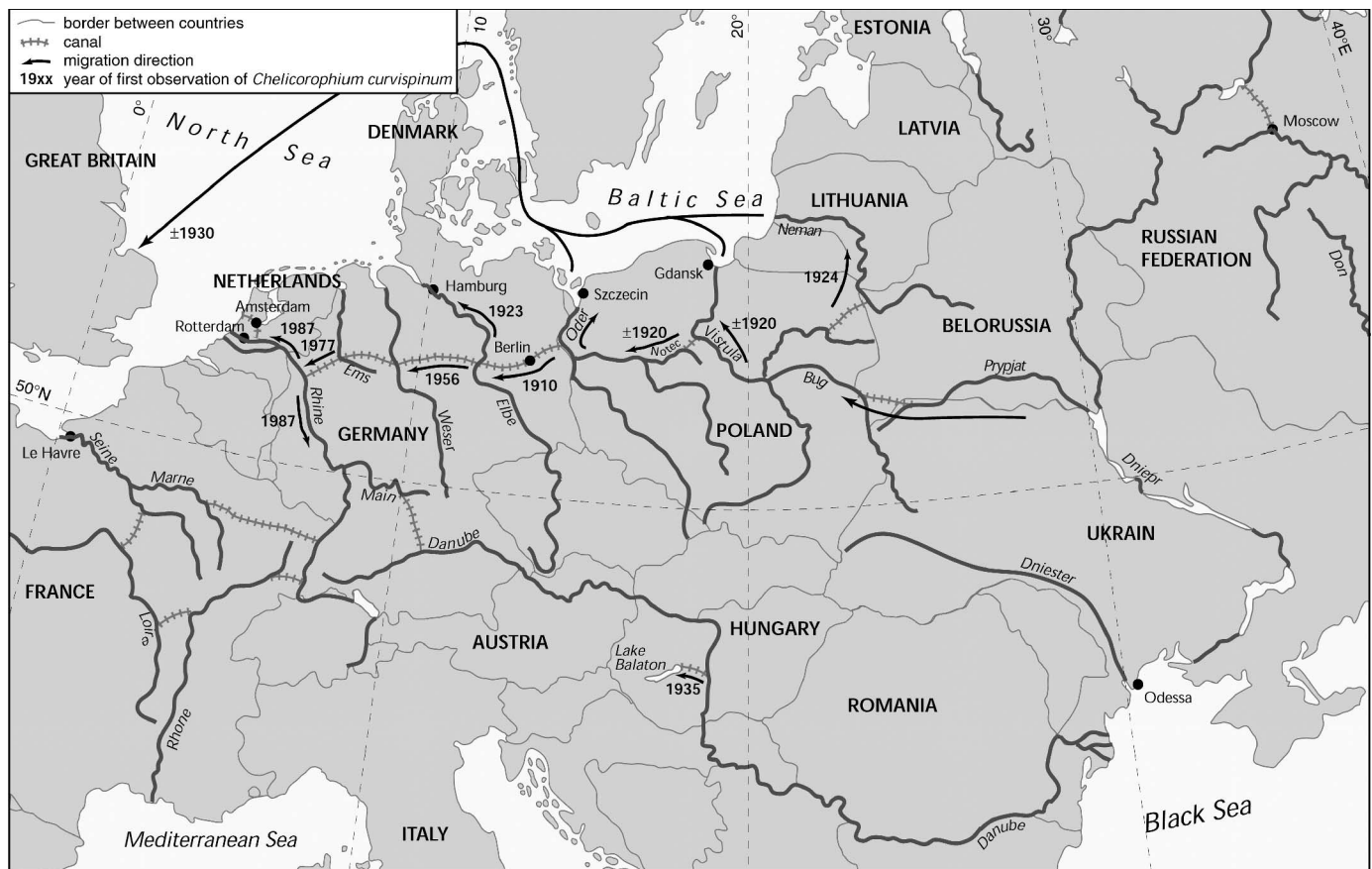
- Le Havre (1997)
- Paris (1997)
- Amsterdam (1998)
- Rotterdam (1997)
- Hamburg (1999)
- Szczecin (1999)
- Gdansk (1999)
- Odessa (1950)

 Major rivers shown include the Rhine, Ems, Weser, Elbe, Oder, Vistula, Bug, Prypjat, Dniester, Danube, Dniepr, Rhone, and Don. The map also shows the North Sea, Baltic Sea, and Mediterranean Sea.

river. Monitoring data from artificial substrate samplings and other field observations have shown that the macroinvertebrate species richness was reduced with high densities of *C. curvispinum* (Van den Brink et al. 1991; Van der Velde et al. 1998). The animals collect suspended particles from the water column for the construction of tubes on solid substrates in which they live. In such densities as found in the Rhine River, the species was able to cover large parts of the substrates with these tubes, altering the environment for lithophilic communities. According to Kinzelbach (1997), *C. curvispinum* also outcompeted the freshwater isopod *Asellus aquaticus* and several species of chironomid larvae. The high densities of *C. curvispinum* observed in the Rhine River strongly impacted another Ponto-Caspian invader negatively, the zebra mussel (*D. polymorpha*) (Van der Velde et al. 1998), which was a dominant species in the Rhine delta around 1990 (Bij de Vaate et al. 1992). In contrast, in Lake Balaton (Hungary), both *D. polymorpha* and *C. curvispinum* arrived at about the same time after their expansion from the Ponto-Caspian region (1932 and 1935, respectively), but seemed to be associated with each other (Sebestyen 1938). Similar observations were made in the lower Vistula, where *D. polymorpha* was always accompanied by *C. curvispinum*.

Migration patterns of *C. sowinskyi* are unclear because of the difficulty of distinguishing it from *C. curvispinum* (Jazdzewski 1980; Jazdzewski and Konopacka 1996). The species originates from the Danube, Dnieper, Volga, Don, and



**Fig. 3.** Migration patterns of *Chelicorophium curvispinum*.

Dniester rivers (Mordukhai-Boltovskoi 1979; Jazdzewski and Konopacka 1996). Records of this species in the Danube River in the Czech Republic indicate that the southern corridor (Fig. 1) could become the most obvious route for its range extension.

#### *Dikerogammarus bispinosus*

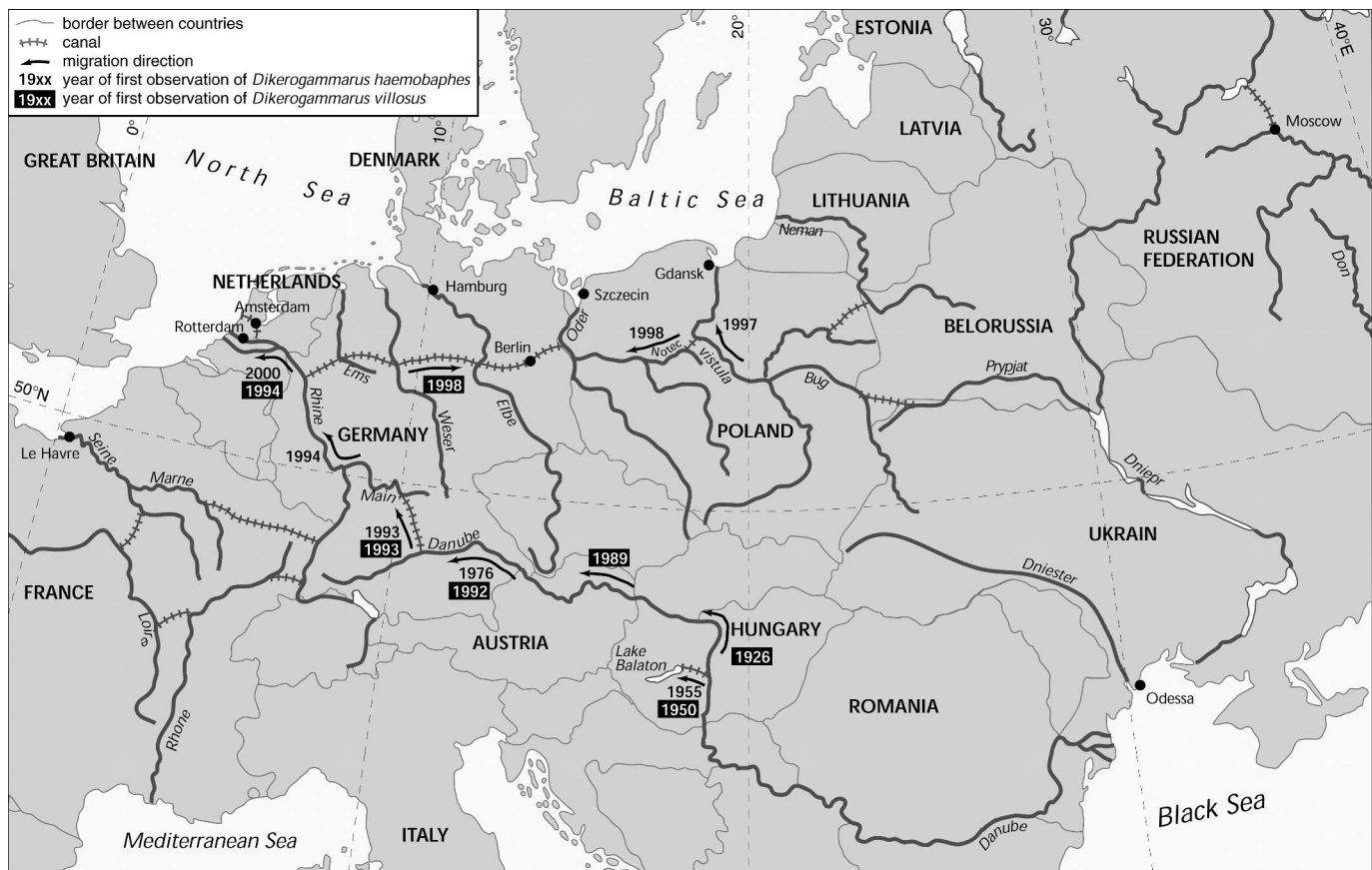
Although *D. villosus* and *Dikerogammarus bispinosus* are clearly different species (Müller and Schramm 2001), *D. bispinosus* is often considered and mentioned as a sub-species of *D. villosus*. In the Dniester River, the relative abundance of *D. bispinosus* decreased in the downstream direction. *Dikerogammarus bispinosus* penetrates farthest upstream in Ponto-Caspian rivers (Jazdzewski and Konopacka 1988). *Dikerogammarus bispinosus* and *D. haemobaphes* invaded Lake Balaton in Hungary in the early 1950s, where they outcompeted *Gammarus roeselii*. It is interesting that the latter species had replaced the indigenous *Gammarus pulex* between 1930 and 1950 (Muskó 1994). Recent observations of *D. bispinosus* in Austria and Germany make clear that the southern corridor (Fig. 1) is traversed for westward range extension (Müller and Schramm 2001).

#### *Dikerogammarus haemobaphes*

The gammarid *D. haemobaphes* is a euryoecious species preferring solid substrates, macrophytes, and filamentous algae in large rivers and lakes (Kititsyna 1980; Muskó 1994). It tolerates salinities from fresh water up to 8‰ (Ponomareva 1976), and is able to tolerate a wide temperature

range (6–30°C) (Kititsyna 1980). It generally reproduces from April to October, but year round in thermal polluted waters, like cooling water discharges of electric power plants (Kititsyna 1980). In Lake Balaton, this species reproduces from May to the end of August on submerged macrophytes (Muskó 1994).

In the 1960s, Mordukhai-Boltovskoi (1964) predicted that *D. haemobaphes* soon would penetrate into another sea basin beyond the Ponto-Caspian system. It migrated up the Danube River using the southern corridor (Figs. 1 and 4) (Nesemann et al. 1995). The first record of the species in the upper Danube (the German section of the river) is from 1976 (Tittizer 1996), followed by observations in the Main–Danube Canal in 1993 (Schleuter et al. 1994), through which the North Sea basin was reached via the Rhine River (Schöll et al. 1995). In 1997, Konopacka (1998) found that *D. haemobaphes* had immigrated to Poland. Studies along the lower and middle Vistula in 1998 and 1999 revealed that the species was already a dominant gammarid in this river. In the lower sections, it co-occurred with two other Ponto-Caspian immigrants: the less numerous *Pontogammarus robustoides* and the scarce *E. ischnus*. In the middle section (at least as far as upstream to Sandomierz), it was the only gammarid species present. *Dikerogammarus haemobaphes* was also found in the Notec and Bug rivers, tributaries of the Oder and Vistula rivers, respectively, clearly indicating that the central corridor (to the Baltic Sea basin) has been used for range extension as well. In the Notec River, *D. haemobaphes* co-occurs with *G. roeselii* and *Gammarus*

**Fig. 4.** Migration patterns of *Dikerogammarus haemobaphes* and *Dikerogammarus villosus*.

*varsoviensis* (Jazdzewski and Konopacka 2000). Recent observations of *D. haemobaphes* in the central and southern corridors as well as in the upper Volga basin (L'vova et al. 1996) clearly indicate that the species is still dispersing.

#### *Dikerogammarus villosus*

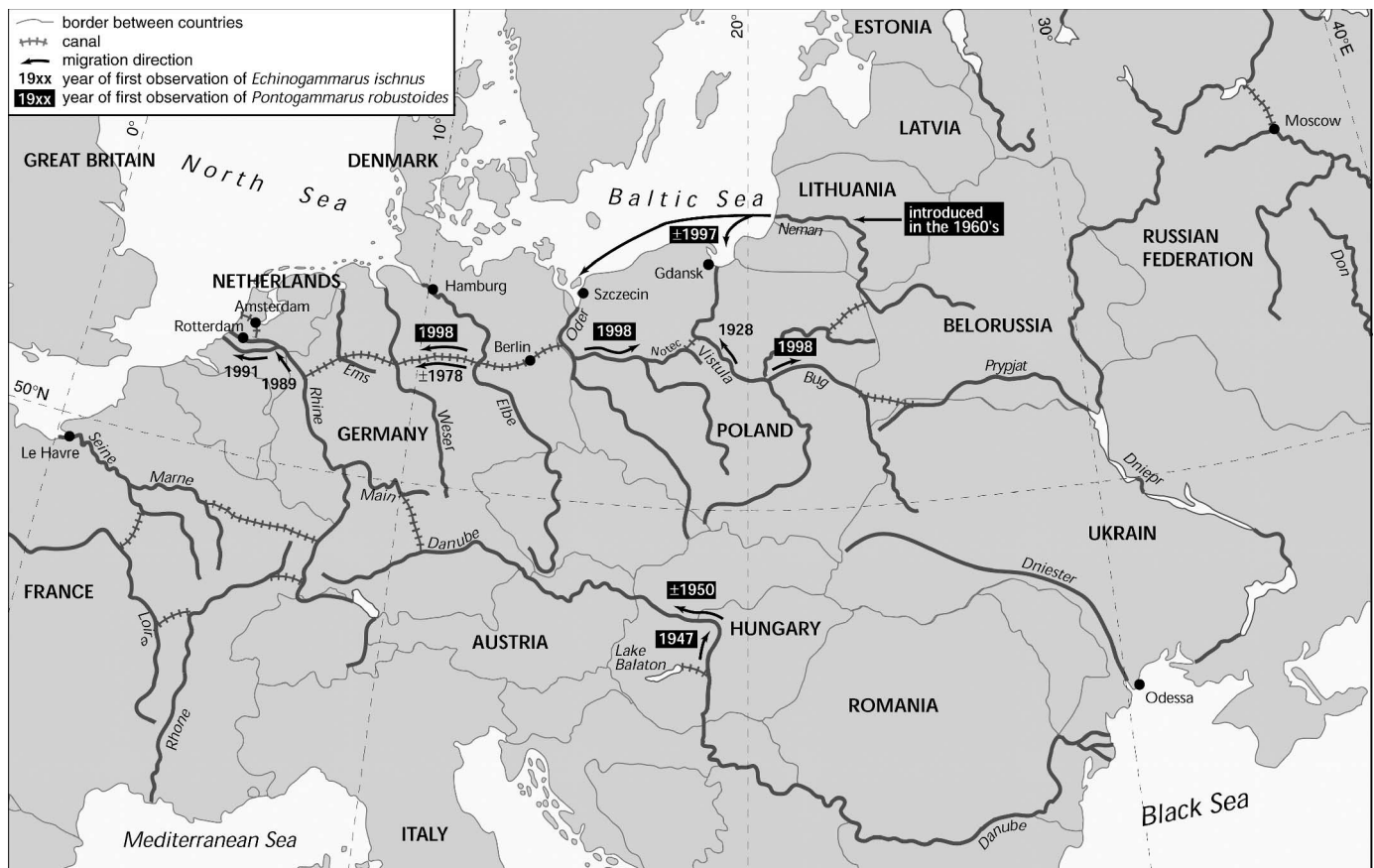
The gammarid *D. villosus* evidently used the southern corridor (Figs. 1 and 4) for range extension. After invading the lower and middle reaches of the Danube River the species was found for the first time in the upper reaches of that river in 1992 (Nesemann et al. 1995), where it had outcompeted *D. haemobaphes* (Weinzierl et al. 1996). Two years later *D. villosus* was discovered in the lower reaches of the Rhine River (Bij de Vaate and Klink 1995) and is currently developing relatively dense populations in that river (A. Bij de Vaate, unpublished data).

The species is suspected to be more predatory than other gammarids. Isotope analyses ( $\delta^{15}\text{N}$ ) indicated that they are active at the same trophic level as fish species (Marguillier et al. 1998). Dick (1996) mentioned that differences in predatory and survival abilities of gammarid species are influenced by body size. Larger specimens prey upon the smaller ones. Therefore, *D. villosus* may have considerable impact on populations of the North American invader *Gammarus tigrinus*, the dominant gammarid in the Rhine River before the introduction of *D. villosus*. Recently, *D. villosus* started to dominate the rheolithophilic gammarid communities in that river, while *G. tigrinus* dominates the gammarids in lentic psammophilic communities (Kelleher et al. 2000a). In

The Netherlands, *D. villosus* also immigrated into canals and lakes (e.g., Lake IJsselmeer), reducing populations of the indigenous *Gammarus duebeni* and the nonindigenous *G. tigrinus* (Dick and Platvoet 2000).

#### *Echinogammarus ischnus*

The earliest record of *E. ischnus* outside the drainage systems of the Black and Caspian seas is from 1928 (Jarocki and Demianowicz 1931). In that year, the species was found in the middle and lower sections of the Vistula River below Warsaw (Jarocki and Demianowicz 1931). The presence of this species in the Vistula estuary was confirmed by Jazdzewski (1975). Samples taken in the summer of 1998 in the middle and lower Vistula and in its tributary the Bug River showed that *E. ischnus* still occurs in these rivers but not as abundantly as *D. haemobaphes*. Nevertheless, *E. ischnus* is evidently an invasive species, exploiting the central corridor (Figs. 1 and 5). In the late 1970s it was recorded in the North Sea drainage basin, in the canals joining the Elbe, Weser, and Ems rivers, and at the end of the 1980s in the Rhine–Herne Canal and Weser–Datteln Canal (Schöll 1990). At about the same time, *E. ischnus* was also found in some Mecklenburgian and Pommeranian lakes (Jazdzewski and Konopacka 1990; Köhn and Waterstraat 1990), being an indication that in western Europe, habitats are being colonized that are comparable to its natural Ponto-Caspian distribution area, where it occurs in several inshore Black Sea lakes (Jazdzewski 1980). The species arrived in the lower Rhine in 1989 (Schöll 1990) and in 1991 in the Rhine delta

**Fig. 5.** Migration patterns of *Echinogammarus ischnus* and *Pontogammarus robustoides*.

(Van den Brink et al. 1993). However, *E. ischnus* did not develop dense populations in that river. It may have been hindered by *G. tigrinus* as well as by the mass abundance of *C. curvispinum*. The latter species probably reduced the colonization success of *E. ischnus*, being a lithophilic dweller, by covering the solid substrates in the river with mud tubes. When densities of *C. curvispinum* decreased, the subsequent invasion of *D. villosus* may have prevented *E. ischnus* from increasing its density.

Köhn and Waterstraat (1990) suggested that *E. ischnus* is closely associated with *Dreissena* clumps in Lake Kummerow (Germany). In the Great Lakes in North America it forms relatively high densities in *Dreissena*-dominated habitats, despite its somewhat lower fecundity and shorter life span in comparison to the indigenous *Gammarus fasciatus*. The physical structure of *Dreissena* clumps favours *E. ischnus*. However, in dense submerged vegetation or turbid water, *E. ischnus* shows lower densities than *G. fasciatus*, which is well equipped to cling to vegetation. *Cladophora* growing on rocks supports *G. fasciatus* as well (Dermott et al. 1998). The association between *Dreissena* and *E. ischnus* provides a good example of a habitat being conditioned for *E. ischnus* by an earlier Ponto-Caspian invader, *D. polymorpha*.

#### *Echinogammarus trichiatus*

First observations of *E. trichiatus* in western Europe were made by Weinzierl et al. (1997) in the German part of the Danube River in 1996. Podraza et al. (2001) found the species in the middle and lower Rhine River in 2000 and 2001,

respectively. It was also found in the Rhine delta in 2001 (A. Bij de Vaate, unpublished data). Although the number of observations is relatively low, they clearly demonstrate that the southern corridor (Fig. 1) was traversed to the west, if the absence of information from potential migration routes is taken into account.

#### *Echinogammarus warpachowskyi*

*Echinogammarus warpachowskyi* originates from the brackish parts of the Caspian Sea and the deltas and estuaries of many large Ponto-Caspian rivers. The species has been used in the former Soviet Union for intentional introductions. It was introduced into reservoirs and lakes in the Ukraine, and in Lithuania in the Neman River drainage area. *Echinogammarus warpachowskyi* penetrated into artificial reservoirs in the Dnieper River (Jazdzewski 1980) and into the Kuronian Lagoon (Olenin and Leppäkoski 1999).

#### *Obesogammarus crassus*

This species 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 (Jazdzewski 1980; Leppäkoski 1984). From the Neman River, the species colonized the Kuronian Lagoon. Recently *O. crassus* was observed in the Vistula Lagoon (A. Konopacka and K. Jazdzewski, unpublished data). Westward dispersal has been the result of offshore transportation (in ballast water) via the Baltic Sea; however, part of

**Table 4.** Summary of migration routes of some Ponto-Caspian macroinvertebrate species that successfully colonized Europe.

Species	Corridor used			Via ballast water
	northern	central	southern	
<i>Cordylophora caspia</i>		+	+	+
<i>Dendrocoelum romanodanubiale</i>			+	
<i>Hypania invalida</i>			+	
<i>Caspiobdella fadejewi</i>			+	
<i>Lithoglyphus naticoides</i>	+	±	+	+
<i>Dreissena polymorpha</i>	+	+		+
<i>Caspihalacarus hyrcanus</i>			+	
<i>Astacus leptodactylus</i>	Intentional introductions			
<i>Hemimysis anomala</i>		+	+	+
<i>Limnomysis benedeni</i>			+	
<i>Chelicorophium curvispinum</i>		+	+	+
<i>Chelicorophium sowinskyi</i>			+	
<i>Dikerogammarus bispinosus</i>			+	
<i>Dikerogammarus haemobaphes</i>		+	+	
<i>Dikerogammarus villosus</i>			+	
<i>Echinogammarus ischnus</i>		+		
<i>Echinogammarus trichiatus</i>			+	
<i>Echinogammarus warpachowskyi</i>	Intentional introductions			
<i>Obesogammarus crassus</i>	Intentional introductions			
<i>Obesogammarus obesus</i>			±	
<i>Pontogammarus robustoides</i>		+		+
<i>Jaera istri</i>			+	

Note: ±, partly used; ?, migration route not clear.

the central corridor (Fig. 1) is considered to be a potential second dispersal route.

#### *Obesogammarus obesus*

Although Nesemann et al. (1995) concluded that this species belongs to macroinvertebrate communities in the middle and lower parts of the Danube River, Weinzierl et al. (1996) found *O. obesus* for the first time in the upper part of that river in 1995. Like other Ponto-Caspian gammarids, it is unclear why the species began to move upstream. Because of its mobility, *O. obesus* is expected to invade the Main–Danube Canal in the near future using the southern corridor (Fig. 1) for further dispersion into western Europe.

#### *Pontogammarus robustoides*

*Pontogammarus robustoides* originates from the lower sections of large Ponto-Caspian rivers (Volga, Don, Dnieper, Dniester, and Danube rivers) as well as from some inland brackish and freshwater lakes around the Black Sea (Jazdzewski 1980). In the 1960s, this species was successfully introduced into many Ukrainian, Caucasian, and Lithuanian artificial lakes. In Lithuania, the species “naturalized” in the Neman drainage system, including the Kuronian Lagoon of the Baltic Sea (Gasjunas 1968a; Jazdzewski 1980). *Pontogammarus robustoides* was recently found in Poland in the Vistula River (including the Vistula Lagoon) (Konopacka 1998; Jazdzewski and Konopacka 2000) and in the mouth of the Oder River (including the Szczecin Lagoon) (Gruszka 1999), whereas in Germany, records exist from Mecklenburgian waters and the Mittelland Canal (Martens et al. 1999). There are two possible routes for the range extension of this species from the Dnieper basin: (i) westward through

the Neman River and the Kuronian Lagoon, and (or) (ii) via the central corridor (Figs. 1 and 5).

#### *Jaera istri*

The lithophilous isopod *J. istri* inhabits the littoral zones of the lower reaches and estuaries of large rivers discharging into the Black and Caspian seas (Tittizer 1997). Range expansion to the west was only observed through the southern corridor (Fig. 1). The first observation outside its native range was made in 1967 in the upper section of the Danube River (in Germany) (Kothé 1968). In 1993, *J. istri* was observed in the Main–Danube Canal (Tittizer 1997), in 1994 in the Main River (Schleuter and Schleuter 1995), and in 1996 in the middle section of the Rhine River (Schöll and Banning 1996). The Rhine delta was colonized in 1997 (Kelleher et al. 2000b), where it inhabits solid substrates. In 1999, the species was found in the Elbe River using the central corridor (Figs. 1 and 3) for further range extension into the north-eastern part of Europe (Schöll and Hardt 2000).

## Discussion

The Ponto-Caspian macroinvertebrates that have expanded their range in Europe are euryhaline with an oligohaline preference. As a relict fauna of the Sarmatian or Pontian Age, these species are endemic for areas of the Black and Caspian seas with relatively low salinity (0.5–5‰), such as estuaries and lagoons. The colonization success of the Ponto-Caspian macroinvertebrates that have invaded regions of Europe beyond their native range can be attributed to several biological features. The most important are euryhaline and euryoecious characters, their nonspecific food prefer-

ence, and the protection of juveniles (crustaceans). Most successful in extending their territory in westward direction were the Crustacea. Their expansion is considered to be attributable to shipping and their ease of mobility. Because of this, they easily can colonize a ship's hull to use it as a transport facility. This is mechanism of spread is considered to be important in rivers for upstream migration and explains the successful passage of the southern corridor. Once having arrived in a new area, their mobility enables them to spread quickly.

Observations of Ponto-Caspian species outside their native range in European continental waters make clear that there are at least three main vectors for their spread westward. (i) Construction of canals connecting river basins, (ii) water management in some of those canals (e.g., the Main–Danube Canal), and (iii) transportation attached to a vessel's hull in ballast water. These vectors are also important in the case of secondary introductions, for those species (e.g., gammarids, mysids) that were intentionally introduced elsewhere.

Canal construction, mainly for navigation, had already started in the 17th century (Snyder et al. 1992). Lack of detailed information from this time period makes it difficult to reconstruct migration patterns for range extension for some species (Table 4) and to determine the main vector for their range expansion. In addition, intentional introductions in regions, particularly along the northern and central corridor, make natural migration patterns unclear.

More recently, the construction of irrigation canals and canals for drinking water supply in the former U.S.S.R. can facilitate the range extension of Ponto-Caspian macroinvertebrates. These canals were mainly constructed in the second part of the last century and also serve as river basin interconnections (e.g., Muraschko and Kuksin 1984). However, their importance in the range expansion of macroinvertebrates is unknown. Another difficulty in understanding migration routes in Europe is the possibility for Ponto-Caspian species to travel in ballast water of seagoing vessels using the route between the Black Sea via the Mediterranean to the coastal waters of western Europe, and from the Baltic Sea to harbours elsewhere.

The geographical invasion patterns described above were based on the years of first records combined with knowledge on years of the connection between river basins. Perhaps, the immigration routes are more complicated than is described above. Other techniques must be applied to check possible migration routes. Genetic analyses offer good possibilities for this purpose.

After the opening of a new Main–Danube Canal in 1992, connecting the Rhine and Danube basins, the southern corridor is today the most important link between the Ponto-Caspian area and western Europe for Ponto-Caspian species to immigrate into western Europe. This led to dramatic changes in macroinvertebrate communities in the Rhine River. In 1990 it was estimated that >95% of the macroinvertebrate density in the main distributaries of the Rhine delta consisted of nonindigenous species of which the major part originated from the Ponto-Caspian area (A. Bij de Vaate, unpublished data). In 1995, the most abundant species were *C. curvispinum*, *D. villosus*, and *D. polymorpha* (Van der Velde et al. 2000). Other mobile species are expected to

migrate into the Rhine River via the Main–Danube Canal, especially those species that have already been observed in the upper and middle Danube, like the amphipods *O. obesus*, *D. bispinosus*, and *C. sowinskyi* (Jazdzewski and Konopacka 1996; Weinzierl et al. 1996; Müller and Schramm 2001). However, other transport mechanisms, like shipping, are also expected to contribute to the Ponto-Caspian species dispersal through that canal in the near future.

Knowing that each introduced species potentially can have an ecological or (and) economic impact, preventative measures against the introduction of alien species should be given high priority. For future canal constructions, the installation of migration barriers of species (e.g., deterrent electrical systems) should be considered to reduce natural migration of species. Additionally, ballast water guidelines and measures to reduce the hull fouling of ships in inland services should be prepared and implemented in the near future with the aim to reduce the uncontrolled number of unintentionally transported organisms.

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