

The river Rhine: a global highway for dispersal of aquatic invasive species

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Received: 15 February 2008 / Accepted: 19 February 2009 / Published online: 25 June 2009
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Abstract The river Rhine is heavily influenced by human activities and suffers from a series of environmental constraints which hamper a complete recovery of biodiversity. These constraints comprise intensive navigation and habitat modification by hydraulic engineering. Improving water quality while these constraints remain in place has led to increased colonization by aquatic invasive species. This tendency has been accelerated by the construction of canals connecting river basins. Over the last two centuries, the total surface area of river catchments connected to the river Rhine via inland waterways has been increased by a factor 21.6. Six principal invasion corridors for aquatic species to the river Rhine are discerned. The extensive network of inland waterways has allowed macroinvertebrate species from different bio-geographical regions to mix,

changing communities, affecting the food webs and forming new constraints on the recovery of the native biodiversity. From the eighteenth century onward, in the freshwater sections of the river Rhine, a total of 45 non-indigenous macroinvertebrate species have been recorded. The average number of invasions per decade shows a sharp increase from <1 to 13 species. Currently, the contribution of non-indigenous species to the total species richness of macroinvertebrates in the river Rhine is 11.3%. The Delta Rhine and Upper Rhine exhibit higher numbers of non-indigenous species than other river sections, because the sea ports in the Delta Rhine and the Main-Danube canal function as invasion gateways. Important donor areas are the Ponto-Caspian area and North America (44.4 and 26.7% of the non-indigenous macroinvertebrate species, respectively). Transport via shipping and

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dispersal via man made waterways are the most important dispersal vectors. Intentional and unintentional introductions are highest for the period 1950–1992. The cumulative number of non-indigenous species in time is significantly correlated with the increase in total surface area of other river catchments connected to the river Rhine by means of networks of canals. The species richness of non-indigenous macroinvertebrates is strongly dominated by crustaceans and molluscs. Invasive species often tolerate higher salt content, temperature, organic pollution and current flow than native species. Spatiotemporal analyses of distribution patterns reveal that average and maximum dispersal rates of six invasive species vary between 44–112 and 137–461 km year⁻¹, respectively. Species arriving in upstream sections first show a shorter time lag between colonisation of the Delta and Upper Rhine than species initially arriving in downstream areas. Temporal analyses of macroinvertebrate assemblages in the littoral zones indicate that native species are displaced by non-indigenous species. However, established non-indigenous species are also displaced by more recent mass invaders.

Keywords Dispersal rate · Invasion corridor · Macroinvertebrates · Non-indigenous species · Shipping · Species replacement · Waterways

Introduction

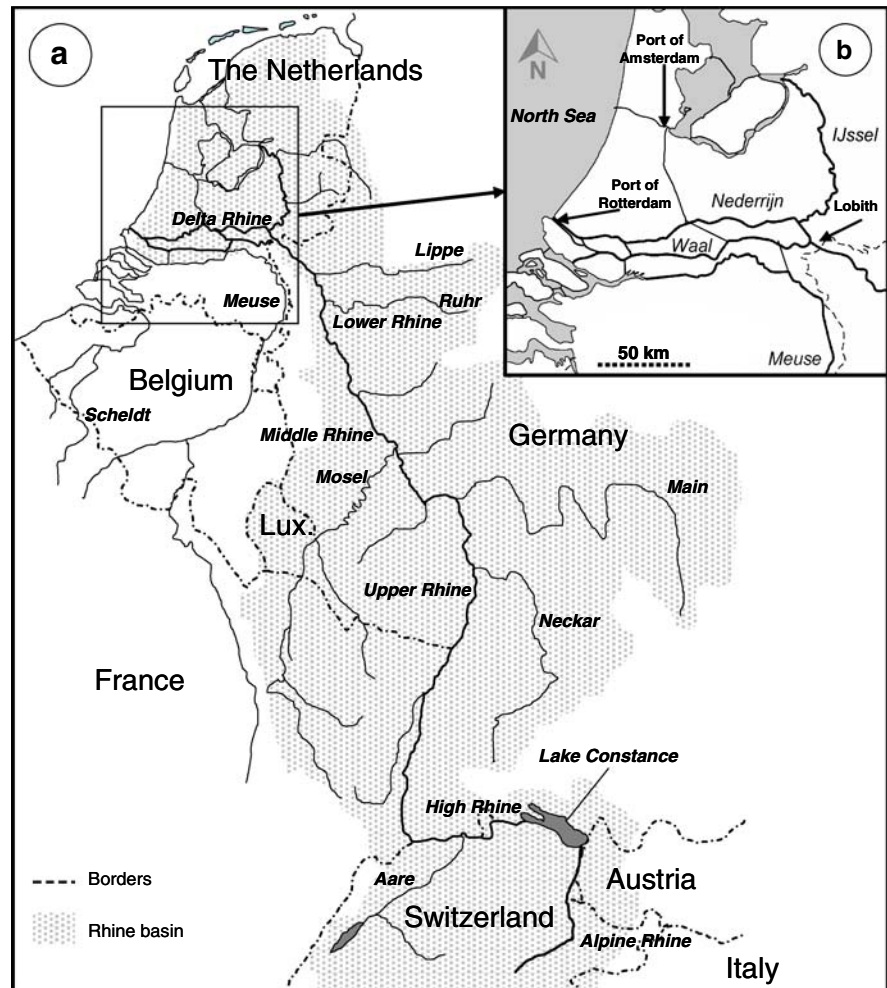
The river Rhine is the primary artery of one of the most important economic regions of Europe. The river has a total length of about 1,250 km, a drainage area of circa 185,260 km² and an average discharge of about 2,300 m³ s⁻¹ (Uehlinger et al. 2009). Nine states are in part or entirely situated within its catchment (Austria, Belgium, France, Germany, Italy, Liechtenstein, Luxemburg, the Netherlands and Switzerland). Six morphologically and ecologically distinct river sections are distinguished (Van der Velde and Van den Brink 1994; IKS 2002; Uehlinger et al. 2009): (1) the Alpine Rhine and its tributaries, i.e., the reach between the source (Lake Toma) and Lake Constance; (2) the High Rhine that flows from lower Lake Constance to Basel, there merging with the river Aare; (3) the Upper Rhine,

flowing through the rift valley of the Rhine Graben that extends from Basel to Bingen with the rivers Neckar and Main as major tributaries; (4) the Middle Rhine, flowing through a narrow valley deeply incised in the Rhenish Slate Mountains and picking up waters of the river Mosel at Koblenz; (5) the Lower Rhine, extending from Bonn to Lobith with the rivers Ruhr, Emscher and Lippe as major tributaries; (6) the Delta Rhine in the Netherlands, where the river divides into three major distributaries called the Waal, Nederrijn, and IJssel (Fig. 1). The river provides services for transportation, power generation, industrial production, urban sanitation, drinking water, agriculture and tourism, and is a classic example of a multipurpose waterway (Van der Velde and Van den Brink 1994; Cioc 2002; Uehlinger et al. 2009). However, its biodiversity and ecological integrity are severely affected by these human activities (Van den Brink et al. 1990; Nienhuis et al. 2002; Bij de Vaate et al. 2006; Leuven et al. 2006; Nienhuis 2008; Uehlinger et al. 2009).

In spite of ambitious and successful rehabilitation programmes aiming at improvement of water quality, restoration of riverine ecosystems and enhancement of habitat connectivity, the river still suffers from a series of environmental constraints which hamper a complete recovery of biodiversity (Leuven and Poudevigne 2002; Nienhuis et al. 2002; Bij de Vaate et al. 2006; Van der Velde et al. 2006a, b; Van der Velde and Bij de Vaate 2008). Examples of these constraints are intensive navigation and irreversible habitat modification by hydraulic engineering (e.g., canalisation and construction of groynes and stony banks). Improving water quality while these constraints remain in place has led to increased colonization of the river Rhine by non-indigenous species that spread their geographic distribution and caused significant changes in composition, structure and ecosystem processes (Den Hartog et al. 1992; Bij de Vaate et al. 2002; Haas et al. 2002; Van der Velde et al. 2006a, b; Bernauer and Jansen 2006; Baur and Schmidlin 2007; Van Riel et al. 2006b; Panov et al. 2009).

The introduction of non-indigenous species in the river Rhine has occurred both intentionally and unintentionally (Van der Velde et al. 2002). In the past, several species have been introduced for aquaculture, fisheries or ornamental purposes. Examples of unintentional introductions are the release of

Fig. 1 Geographical location of various river sections in the Rhine basin (a) and the river distributaries in the Delta Rhine (b)



species via ballast water or via transport on ship hulls (Ricciardi and MacIsaac 2000). The ports in the Rhine delta are important gateways for non-indigenous species (Bij de Vaate et al. 2002). Moreover, the wish to expand navigation routes across river basin boundaries has led to the construction of navigation canals that connect the river Rhine with previously isolated catchments of the Caspian Sea, the southern European seas (Azov, Black and Mediterranean Sea), the northern European seas (Baltic, North and White Sea) and the Atlantic ocean (Galil et al. 2007; Panov et al. 2009). This network of waterways opened long distance dispersal routes for aquatic species from several bio-geographic areas (Bij de Vaate et al. 2002; Van der Velde et al. 2002; Arbačiauskas et al. 2008; Karatayev et al. 2008; Panov et al. 2009).

This paper describes the development of invasion corridors and the distribution of non-indigenous macroinvertebrate species in freshwater sections of the river Rhine. The study is restricted to aquatic macroinvertebrates that live in the main channel or connected bodies of water in its floodplains. The analysis of invasion pathways, vectors, dispersal rates, taxonomic richness and abundances in local communities is undertaken. The following research questions are addressed:

1. Which spatiotemporal developments in the European inland waterways and sea shipping routes lifted barriers for dispersal of non-indigenous species to the river Rhine?
2. Which non-indigenous species have established in various sections of the river and what are

temporal patterns in their arrival, donor areas, pathways and dispersal vectors?

3. What are the long distance dispersal rates of non-indigenous species in the river Rhine and connected inland waterways?
4. Which trends in richness and abundance of non-indigenous species can be discerned in macroinvertebrate communities in littoral zones of the river Rhine?

Biological and environmental factors explaining dispersal and establishment of non-indigenous species in the river Rhine will be discussed.

Materials and methods

Analyses of the network of inland waterways and shipping activities

Data on spatiotemporal developments of the Eurasian network of inland waterways and sea shipping routes connected to the river Rhine were derived from scientific literature and internet sources (Table 1). Data on shipping activity, yearly discharge of ballast water and introduction rate of invasive species in the Port of Rotterdam were obtained from the Maritime and Coastguard Agency (2006).

Construction of database on non-indigenous species

Existing databases on the distribution of non-indigenous species in the Delta Rhine (Den Hartog and Van der Velde 1987; Van den Brink et al. 1990) were updated and extended with data on other river sections, using a distribution atlas on freshwater molluscs (Gittenberger et al. 1998), recent field surveys (Kelleher et al. 1998; Rajagopal et al. 2000; IKSr 2002; Bij de Vaate 2003; Bernauer and Jansen 2006; Bij de Vaate et al. 2006, 2007), monitoring programmes of the Dutch Institute for Inland Water Management and Waste Water Treatment (RIZA), the database of the Dutch Working Group on Ecological Water Management, the Dutch Species Catalogue and several literature reviews (Bij de Vaate et al. 2002; Van der Velde et al. 2002; Gollasch and Nehring 2006; Van der Velde and Bij de Vaate 2008 and references therein). The following data attributes of non-indigenous

species were collected: taxonomic group, species name, donor area, dispersal vector, pathway (invasion corridor), year and river section of initial arrival, and references. Data on initial record, origin, pathways and dispersal vectors of non-indigenous species were derived from scientific literature. Dispersal vectors were divided in six categories: (1) accidental release from aquaculture, escapes from garden ponds or dumping of aquaria or pond contents, (2) migration or drift via man made waterways (canals connecting rivers), (3) deliberate introduction by humans (e.g., for aquaculture, fisheries, weed control and pest management), (4) transported via seagoing ships (e.g., release from ballast water and ship hull fouling), (5) multiple vectors, and (6) vectors unknown.

Data on total species richness in various freshwater section of the river Rhine was derived from IKSr (2002). The abundances of native and non-indigenous species in macroinvertebrate assemblages on artificial substrates (baskets filled with marbles) in the littoral zone of the river Rhine near Lobith (rkm 882; Latitude 51°07'97", Longitude 05°55'26"; see Fig. 1) were obtained from RIZA. Maximum densities of gammaridean species in the littoral zones of the Rhine river distributaries Waal, Nederrijn and IJssel (Fig. 1b) were obtained from monitoring programmes of RIZA and several field surveys (Van den Brink et al. 1991; Van der Velde et al. 2000, 2002; Van Riel 2007; Van Riel et al. 2009). During these field surveys specimens were cautiously brushed from artificial substrate (marbles), riprap and groyne stones, and subsequently preserved in 70% ethanol, sorted by species and counted in the laboratory. The total surface area of the marbles and stones was calculated in order to quantify the densities of macroinvertebrate species per square metre of substratum. The annual taxa richness and relative abundance of macroinvertebrates were based on pooled data (two baskets per sampling date; four to seven sampling dates per year; sampling from spring to autumn).

Assessment of richness and abundance of non-indigenous species

Trends in richness and abundance of non-indigenous species in the macroinvertebrate communities of the littoral zones of the river Rhine were analysed using the Taxonomic Contamination Index (TCI), the Abundance Contamination Index (ACI) and the Site-

Table 1 Connections of European rivers via canals (Fig. 2 visualises the European network of inland waterways)

Canal	Connection between rivers/seas		Year of opening	References
Elbe-Lübeck Canal ⁱ	Elbe	Baltic Sea	1398	www.en.wikipedia.org
Havel-Oder Canal	Elbe	Oder	1640 ^a	Galil et al. (2007)
Canal de Briare	Seine	Loire	1642 ^b	www.beluga-on-tour.de
Friedrich-Wilhelm Canal ^j	Elbe	Oder	1668 ^c	www.de.wikipedia.org
Mariinsk Canal System	Volga	Baltic Sea	1709 ^d	www.en.wikipedia.org
Bydgoszcz Canal	Oder	Vistula	1774	www.britannica.com
Oginsky Canal	Dnieper	Neman	1784 ^e	Karatayev et al. (2008)
Canal de Centre	Loire	Rhône	1792	Galil et al. (2007)
Canal de Bourgogne	Seine	Rhône	1832	www.en.wikipedia.org
Charleroi-Brussels Canal	Meuse	Scheldt	1832	www.en.wikipedia.org
Rhône-Rhine Canal	Rhine	Rhône	1834	Galil et al. (2007)
Ludwig Canal	Rhine	Danube	1846 ^f	Galil et al. (2007)
Dnieper-Bug Canal ^k	Dnieper	Vistula	1848	Karatayev et al. (2008)
Rhine-Marne Canal	Rhine	Seine	1853	Galil et al. (2007)
Canal de la Meuse ^l	Meuse	Rhine/Seine	1884	www.de.wikipedia.org
Hunte-Ems Canal	Ems	Weser	1893	www.de.wikipedia.org
Dortmund-Ems Canal	Rhine	Ems	1899	Galil et al. (2007)
Rhine-Herne Canal	Rhine	Ems	1914	Galil et al. (2007)
Meuse-Waal Canal	Rhine	Meuse	1927	www.nl.wikipedia.org
White Sea-Baltic Sea Canal	White Sea	Baltic Sea	1932	Galil et al. (2007)
Mittelland Canal	Weser	Elbe	1938 ^g	Galil et al. (2007)
Augustow Canal	Vistula	Neman	1938	www.it.mazury.pl
Volga-Don Canal	Volga	Don	1952	Galil et al. (2007)
Scheldt-Rhine Canal	Rhine	Scheldt	1975 ^h	www.rijkswaterstaat.nl
Main-Danube Canal	Rhine	Danube	1992	Galil et al. (2007)

^a In 1746 re-opened after major constructions

^b Galil et al. (2007) give 1842

^c Earlier link between Elbe and Oder via Havel-Oder Canal

^d Date of first connection, Galil et al. (2007) give 1810/1964 as dates of completion of this canal system

^e Probably closed in 1915

^f Closed in 1950

^g This canal connects the rivers Ems and Elbe through the Weser; in 1893 the rivers Ems and Weser were also connected by means of the Hunte-Ems Canal

^h After 1986 free of tidal influence

ⁱ Elbe-Trave Canal or Stecknitz Canal

^j Müllroser Canal

^k Krolevski Canal

^l Links up with Rhine-Marne Canal

specific Biological Contamination Index (SBCI) (Arbačiauskas et al. 2008; Panov et al. 2009). $TCI = R_{nis}/R_t$; where R_{nis} is the total number of non-indigenous species, while R_t is the total number of identified species. ACI is the relative abundance of non-indigenous species in a sample. With ACI and

TCI scores, the SBCI was derived from the reference table of Arbačiauskas et al. (2008) for the classification of sampling sites corresponding to ecological quality classes of the European Union Water Framework Directive (European Community 2000). SBCI ranks from 0 to 4 (0: no biocontamination, “high”

ecological status; 1: low biocontamination, “good” ecological status; 2: moderate biocontamination, “moderate” ecological status; 3: high biocontamination, “poor” ecological status; 4: very high biocontamination, “bad” ecological status).

Dispersal rates

Long-distance dispersal rates of non-indigenous species were estimated using literature records on the spatiotemporal distribution of aquatic invaders in the river Rhine and connected waterways. Due to lack of detailed observations on species distribution patterns and data on exact time of initial arrival, dispersal rates of non-indigenous species were calculated conservatively using year of first recorded sighting and shortest migration route via the network of inland waterways. Data on geographical locations was always transformed to river or canal kilometres for calculations of singular dispersal distance. Dispersal rates could not be corrected for possible lags of time between dates of initial arrival and first observation.

Statistics

Statistical significance of regression models for the cumulative numbers of non-indigenous species

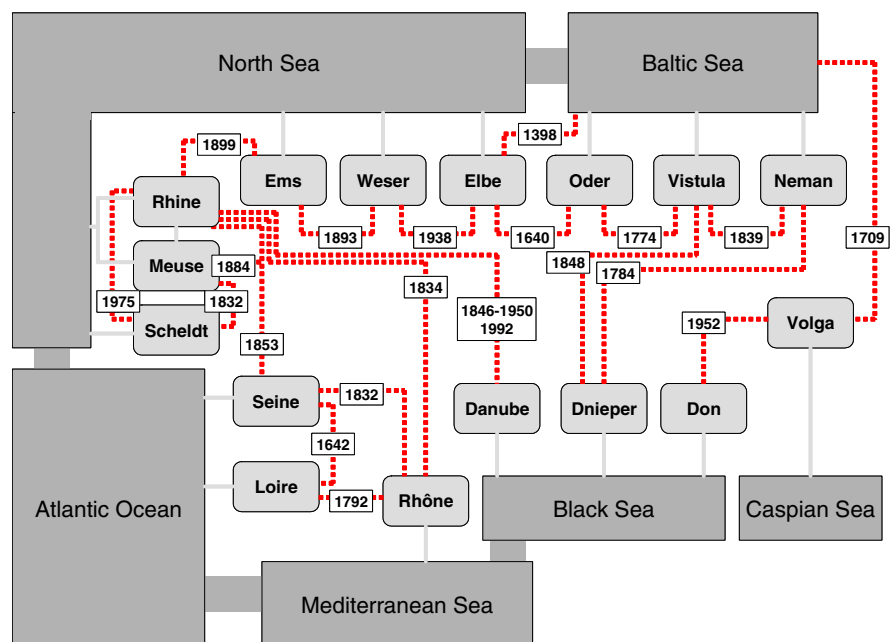
versus the years of arrival and catchment area connected to the river Rhine was analysed using ANOVA. A paired two-sample *t*-test, assuming unequal variances, was performed to determine whether dispersal rates significantly differ for various species. Data on dispersal rate was log-transformed prior to statistical testing. Data was considered statistically significant at $P < 0.05$. All statistical analyses were performed with SPSS 15.0.

Results

Building of water networks resulting in invasion corridors

The wish to expand navigation routes across river basin boundaries has led to the construction of an extensive network of navigation canals that connect the river Rhine with nearly all large rivers in southwestern, southern, central and eastern Europe, and beyond (Fig. 2). Table 1 summarizes the years of opening of the connections between rivers associated with relevant references. Important steps for the connection of the river Rhine to the Eurasian network of inland waterways were: (1) the connection of the river Scheldt with the rivers Meuse and Rhine after opening of the Charleroi-Brussels Canal in 1832; (2)

Fig. 2 Connections between the river Rhine and large rivers in Europe via canals and sea routes (*Light grey boxes: large rivers; dark grey boxes: receiving seas; continuous lines: natural discharge; dotted lines: main artificial canal systems including dates of completion/opening up of canals*)



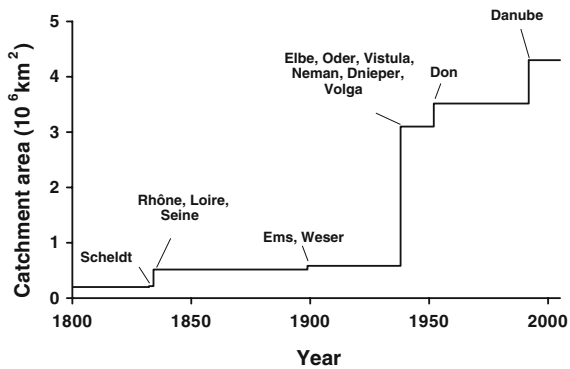


Fig. 3 Punctuated increase in surface area of river catchments connected to the river Rhine due to constructions of canals (Table 1)

the connection of the rivers Rhône, Loire and Seine via the Rhône-Rhine Canal in 1834; (3) the connection of the rivers Ems and Weser after construction of the Dortmund-Ems Canal; (4) the connection with the central and eastern European rivers Elbe, Oder, Vistula, Neman, Dnieper and Volga after the opening of the Mittelland Canal between the rivers Weser and Elbe in 1938; (5) the connection with the river Don in 1952 after construction of the Volga-Don Canal; (6) the connection with the river Danube after the reopening of the Main-Danube Canal in 1992. At present, the network of inland waterways is made up of circa 28,000 km of navigable rivers and canals, connecting 37 countries in Europe and beyond. Figure 3 visualises the spatiotemporal expansion of this network of waterways. The total surface area of river catchments connected to the river Rhine via canals shows a stepwise increase from 0.19×10^6 to 4.30×10^6 km² since the eighteenth century (i.e., an increase with a factor 21.6).

The Eurasian network of inland waterways and sea shipping routes offers nowadays six invasion corridors for aquatic species to the river Rhine (Fig. 4): (1) The Northern corridor, connecting the catchments of the Black, Azov and Caspian seas via the Volga-Don Canal, and the Baltic and White seas via the Volga-Baltic Canal and White Sea-Baltic Sea Canal and the river Rhine via sea shipping; (2) The Central corridor, connecting the Black Sea basin with the Baltic Sea region via the Dnieper and Bug-Prpyat Canal and with the North Sea basin via an extensive network of waterways; (3) The Southern corridor, linking the Black Sea basin with the North Sea basin

via the Danube-Main-Rhine waterway; (4) The South-western corridor, linking the rivers Loire and Seine; (5) The Mediterranean corridor, linking the Mediterranean basin with the North Sea basin via the Rhône and the Rhine-Rhône Canal; (6) The transatlantic and North Sea shipping routes to various sea harbours in the Rhine delta. The sea shipping routes (including the Northern corridor) had already been effective as pathways for dispersal of non-indigenous species to the river Rhine for many centuries. However, in the twentieth century their importance for species dispersal strongly increased due to the expansion of global trade and improvements in shipping technology (e.g., the introduction of ballast water tanks). The South-western and Mediterranean corridors were connected to the river Rhine in 1834. The Central and Southern corridors were completed in 1938 and 1992, respectively.

The Port of Rotterdam is the terminus of Rhine navigation and Europe's largest seaport with circa 30,000 sea going ships and 130,000 inland ships arriving per year. According to the Maritime and Coastguard Agency (2006) the yearly discharge of ballast water is estimated to be 5 billion tons. Most ballast water originates from North Sea (50%), Baltic (11%) and European Atlantic (11%) routes. Of the remaining 28%, most ships originated from the Mediterranean, American, tropical and fresh water routes, although information on shipping routes of ships is often incomplete. The introduction rate of non-indigenous species via ballast water import is estimated to be 1 species every 4 years (Maritime and Coastguard Agency 2006). However, most of these species can only survive in marine and estuarine environments and are not able to establish viable populations in the freshwater sections of the river Rhine.

In the freshwater sections of the river Rhine a total of 45 non-indigenous invertebrate species were recorded from the eighteenth century onward (Table 2). The number of non-indigenous species recorded was highest in the Delta Rhine and Upper Rhine (42 and 37 species, respectively; Fig. 5). The High Rhine exhibited the lowest number of non-indigenous species; the Lower and Middle Rhine held an intermediate position. The contribution of non-indigenous species to total species richness of macroinvertebrates in the Rhine was 11.3%. Relative contribution was highest in the Delta Rhine (48.8%)

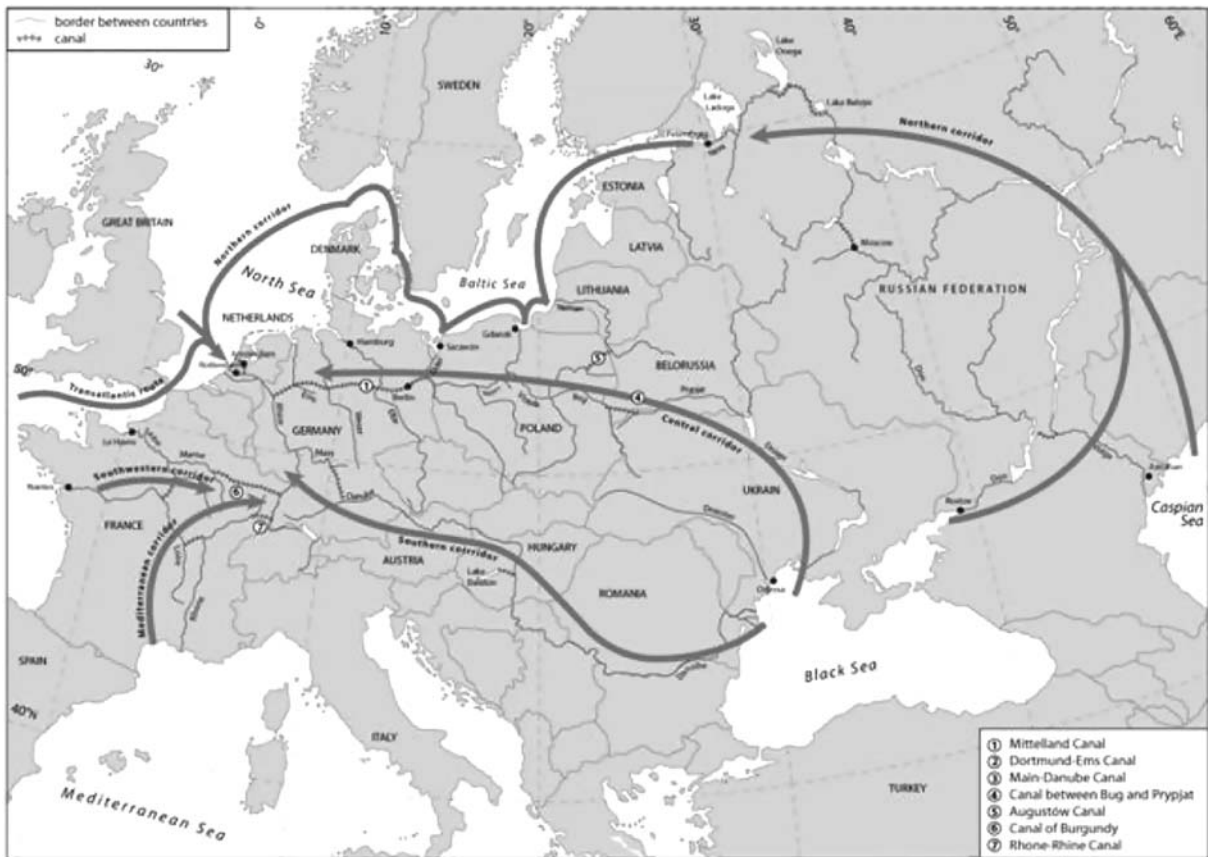


Fig. 4 Principal dispersal corridors for aquatic invasive species to the river Rhine, modified from Bij de Vaate et al. (2002) and Panov et al. (2009)

and lowest in the High Rhine (11.2%). No records of non-indigenous species were available for the Alpine Rhine and its tributaries.

Taxonomic composition of the non-indigenous macroinvertebrate fauna and their origin

Of the non-indigenous macroinvertebrate species, crustacean species were most numerous (51.1%), including nine amphipod, eight decapod, three isopod, two mysid and one cladoceran species (Table 3). Mollusc species contributed to 22.2% of the total number of non-indigenous species. These molluscs were represented by five species of snails and five species of bivalves. Annelid and triclad species contributed to 11.1 and 4.4% of the non-indigenous species, respectively. The occurrence of the remaining taxonomic groups was low (2.2% for mite, bryozoan, hydrozoan, leech and caddis larva species).

Taxonomic contamination (TCI) differed remarkably for various invertebrate groups (1.7–76.7%; in total 23.1% for all discerned taxa). Most non-indigenous species originated from the Ponto-Caspian area and from North America (44.4 and 26.7% of the total number of non-indigenous species, respectively). Southern Europe, Asia, Northern Europe and Oceania contributed to 13.3, 11.1, 2.2 and 2.2% of the non-indigenous species, respectively (in total 28.8%).

Increasing numbers of non-indigenous species

The introductions and invasions of non-indigenous species in the river Rhine strongly increased over the period 1800–2005 (Fig. 6). The cumulative number of non-indigenous species in time shows a punctuated pattern, but the data significantly fit a power function (ANOVA: $P < 0.001$). The average number of records of new non-indigenous species per time period

Table 2 List of non-indigenous species recorded in the freshwater sections of the river Rhine, with origin, invasion corridor, vector, year of first arrival and references

Taxon	Species	Origin	Invasion corridor	Vector	First record river Rhine	References ^s
Coelenterata	<i>Cordylophora caspia</i> (Pallas, 1771)	Ponto-Caspian area	CC, SC	S	1874	Bij de Vaate et al. (2002)
Bryozoa	<i>Pectinatella magnifica</i> (Leidy, 1851)	North America	~	E	1883	Bernaer and Jansen (2006)
Tricladida	<i>Dendrocoelum romanodanubiale</i> (Codreanu, 1949)	Ponto-Caspian area	SC	DW	1997	Bij de Vaate et al. (2002)
Oligochaeta	<i>Dugesia tigrina</i> (Girard, 1850)	North America	AC	I, E	1934	Bernaer and Jansen (2006)
	<i>Branchiura sowerbyi</i> Beddard, 1892	Asia	~	E	1919	IKSR (2002), www.wew.nu/exoten
	<i>Potamothenix vejdoskyi</i> (Hrabe, 1941)	Ponto-Caspian area	SC	DW	1995	www.wew.nu/exoten
	<i>Quistadrilus multisetosus</i> (Smith, 1900)	North America	AR?	S?	1988	Smit (1995)
Polychaeta	<i>Hypania invalida</i> (Grube, 1860)	Ponto-Caspian area	SC	DW	1995	Klink and Bij de Vaate (1996), Bij de Vaate et al. (2002)
Hirudinea	<i>Caspiobdella fadejewi</i> (Epshtein, 1961)	Ponto-Caspian area	SC, CC?	I, DW	1996	Bij de Vaate et al. (2002)
	<i>Barbronia asiuti / weberi</i> complex	Asia, Africa	~	E	1994	IKSR (2002)
Bivalvia	<i>Corbicula fluminalis</i> (O.F. Muller, 1774)	Asia	AC	S	1988	Rajagopal et al. (2000)
	<i>Corbicula fluminea</i> (O.F. Muller, 1774)	Asia	AC	S	1988	Rajagopal et al. (2000)
	<i>Dreissena polymorpha</i> (Pallas, 1771)	Ponto-Caspian area	NC (CC, SC)	I, E	1826	Bij de Vaate et al. (2002)
	<i>Dreissena rostriformis bugensis</i> (Andrusov, 1897)	Ponto-Caspian area	SC	DW	2004	Molloy et al. (2007), Van der Velde and Platvoet (2007)
Gastropoda	<i>Muscilium transversum</i> (Say, 1829)	North America	~	?	1954	Gittenberger et al. (1998)
	<i>Ferrissia wauteri / gracilis</i> ^{ab}	North America	~	E	1961	IKSR (2002)
	<i>Lithoglyphus naticoides</i> (C. Pfeiffer, 1828)	Ponto-Caspian area	CC, NC?, SC?	DW	1874	Bij de Vaate et al. (2002)
	<i>Menetus dilatatus</i> (Gould, 1841)	North America	~	E	1886	Bernaer and Jansen (2006)
	<i>Physella acuta</i> (Draparnaud, 1805) ^c	North America (South-Western Europe)	SWC, MC (AR?)	DW	1870	Gittenberger et al. (1998), Bernaer and Jansen (2006)
	<i>Potamopyrgus antipodarum</i> (Gray, 1843) ^d	New Zealand	AR	S	1913	Bernaer and Jansen (2006)
Crustacea	<i>Astacus leptodactylus</i> (Eschscholtz, 1823)	Ponto-Caspian area	~	I, E	1979	Bij de Vaate et al. (2002)
	<i>Ayaephyra desmarestii</i> (Millet, 1831)	Southern Europe	MC	DW	1915	Van den Brink and Van der Velde (1986), Van der Velde et al. (2000)
	<i>Bythotrephes longimanus</i> Leydig, 1860	Northern Europe	~	?	1987	Ketelaars and Gille (1994)
	<i>Chelcorophium curvispinum</i> (Sars, 1895) ^e	Ponto-Caspian area	CC, SC	S	1987	Van den Brink et al. (1993), Van der Velde et al. (2000), Bij de Vaate et al. (2002)

Table 2 continued

Taxon	Species	Origin	Invasion corridor	Vector	First record river Rhine	References ^s
	<i>Chelicorophium robustum</i> Sars, 1895	Ponto-Caspian area	SC	DW	2003	Bemerth and Stein (2003)
	<i>Crangonyx pseudogracilis</i> (Bousfield, 1958)	North America	~	I?	1979	Van der Velde et al. (2000)
	<i>Dikerogammarus haemobaphes</i> (Eichwald, 1841)	Ponto-Caspian area	CC, SC	DW	1994	Van der Velde et al. (2000), Bij de Vaate et al. (2002)
	<i>Dikerogammarus villosus</i> (Sowinsky, 1894)	Ponto-Caspian area	SC	DW	1995	Van der Velde et al. (2000), Bij de Vaate et al. (2002)
	<i>Echinogammarus berilloni</i> (Catta, 1878)	Southern Europe	MC	DW	2003	Van der Velde et al. (2000), Bernauer and Jansen (2006)
	<i>Echinogammarus ischnus</i> (Stebbing, 1899) ^f	Ponto-Caspian area	CC	DW	1989	Van der Velde et al. (2000), Bij de Vaate et al. (2002)
	<i>Echinogammarus trichiatus</i> (Martynow, 1932)	Ponto-Caspian area	SC	DW	2000	Bij de Vaate et al. (2002)
	<i>Eriocheir sinensis</i> H. Milne Edwards, 1853	Asia	AC	S	1926	Van der Velde et al. (2000)
	<i>Gammarus tigrinus</i> (Sexton, 1939)	North America	AC?	I	1960	Van der Velde et al. (2000)
	<i>Hemimysis anomala</i> (Sars, 1895)	Sout-Eastern Europe, Ponto-Caspian area	CC?, SC?	DW, S?	1997	Van der Velde et al. (2000), Bij de Vaate et al. (2002)
	<i>Jaera istri</i> Veuille, 1979	Ponto-Caspian area	SC	DW, S?	1995	Van der Velde et al. (2000), Bij de Vaate et al. (2002)
	<i>Limnomysis benedeni</i> Czerniavsky, 1882	Ponto-Caspian area	SC	DW, S?	1995	Van der Velde et al. (2000), Bij de Vaate et al. (2002), Bernauer and Jansen (2006), Gergs et al. (2008)
	<i>Orchestia cavimana</i> (Heller, 1865)	Southern Europe, Ponto-Caspian area	MC	DW	1898	Van der Velde et al. (2000), Bernauer and Jansen (2006)
	<i>Oreonectes immunis</i> (Hagen, 1870)	North America	~	I	1999	Bernauer and Jansen (2006)
	<i>Oreonectes limosus</i> (Rafinesque, 1817)	North America	~	I	1932	Van den Brink et al. (1988), Bernauer and Jansen (2006)
	<i>Proasellus coxalis</i> (Herbst, 1956)	Eastern Europe	CC?	DW	1931	Bernauer and Jansen (2006)
	<i>Proasellus meridianus</i> (Racovitza, 1919)	Southern Europe	SWC, MC	DW	1948	Van der Velde et al. (2000)
	<i>Procambarus clarkii</i> (Girard, 1852)	North America	~	I, E	1985	Bernauer and Jansen (2006)
	<i>Rhithropanopeus harristii</i> (Gould, 1841)	North America	AR	S	1874	Van der Velde et al. (2000)

Table 2 continued

Taxon	Species	Origin	Invasion corridor	Vector	First record river Rhine	References ^g
Acarina	<i>Caspihalacarus hyrcanus danubialis</i> Motas, 1943	Ponto-Caspian area	SC	DW	2000	Bij de Vaate et al. (2002), Van der Velde et al. (2002)
Insecta	<i>Hydropsyche bulgaromanorum</i> Malicky, 1977 ^a	Southern Europe	CC, SC	?	1917	Arbaciauskas et al. (2008)

Invasion corridor: AC Atlantic corridor, CC central corridor, NC northern corridor, MC mediterranean corridor, SC southern corridor, SWC south-western corridor; Vector: DW dispersal via waterways, I introduced, E escaped, S shipping (ballast water, ship hulls, etc.)

^a Disputable status as non-indigenous species
^b Synonymous with *Ferrissia clessiniana*
^c Synonymous with *Physa acuta*, *Haitia acuta*, *Physella costatella* and *Physella heterostrophia* (e.g., see Dillon et al. 2002)
^d Synonymous with *Potamopyrgus jenkinsi*
^e Synonymous with *Corophium curvispinum*
^f Synonymous with *Chaetogammarus ischnus*
^g See also references therein

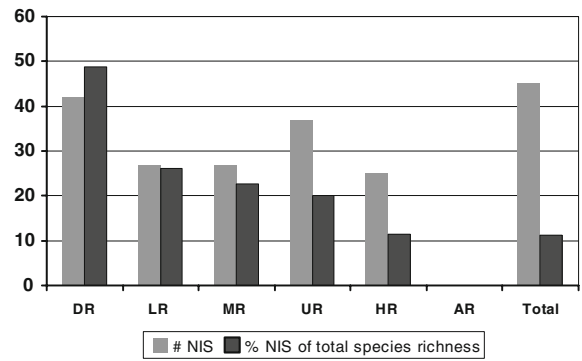


Fig. 5 Total number of non-indigenous species (NIS) and relative contribution to total species richness in various freshwater sections of the river Rhine (DR: Delta Rhine; LR: Lower Rhine; MR: Middle Rhine; UP: Upper Rhine; HR: High Rhine; AR: Alpine Rhine)

increased from <1 to more than 13 species per decade (Fig. 7). The invasion of Ponto-Caspian species in the river Rhine strongly increased after the opening of the Rhine-Main-Danube waterway in 1992. The cumulative number of non-indigenous species is significantly correlated with the total surface area of the river catchments connected to the river Rhine (ANOVA: $P = 0.025$). The logarithmic non-indigenous species—area plot linearly aligns the data (Fig. 8).

Dispersal vectors and time lags

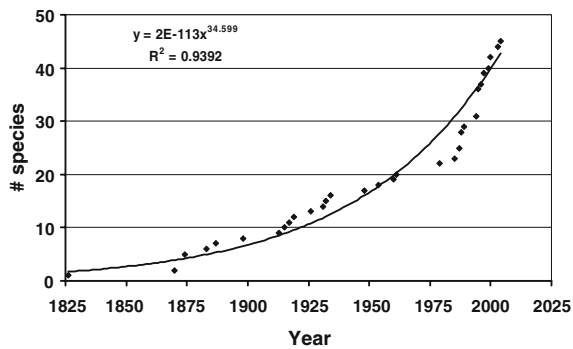
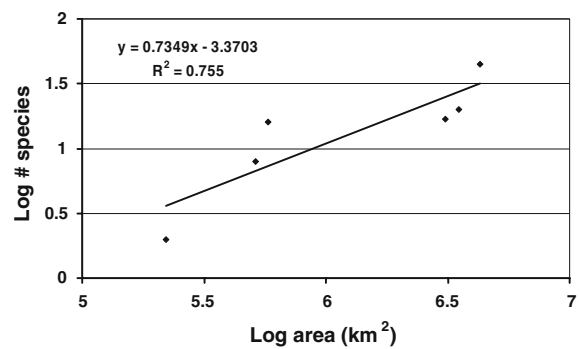
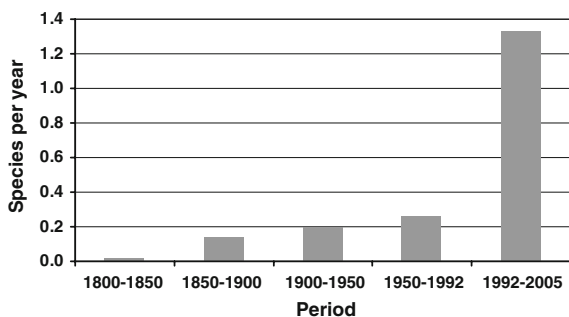
The relative contribution of various dispersal vectors differed remarkably in various time spans (Fig. 9). Deliberate introductions and accidental releases (including escapes and dumping) of non-indigenous species decreased, whereas transport via seagoing ships (ballast water and fouling of ship hulls) and natural migration or drift via man made waterways increased. Until 1992, the sea shipping routes and central corridor were important invasion corridors for the spread of non-indigenous species in the river Rhine (Table 2). After the opening of the Rhine-Main-Danube waterway, the southern corridor became the principal invasion corridor. Up to the present time, the South-western and Mediterranean corridors were only related to the dispersal of a few non-indigenous species to the river Rhine.

Initial arrivals of non-indigenous species in the Upper Rhine show that the time lag from their initial occurrence to their observance in the Delta Rhine is at most 50 years (Fig. 10). Seven species spread from

Table 3 Contribution of non-indigenous species (NIS) to taxa richness of macroinvertebrates in the freshwater sections of the river Rhine

Taxon	Total number of species in 2000 (IKSR 2002) ^a	Number of NIS in 2005	Percent NIS per taxon of total number of NIS	Percent NIS of total number of species per taxon
Acarina	6	1	2.2	16.7
Bryozoa	6	1	2.2	16.7
Hydrozoa	2	1	2.2	50.0
Hirudinea	14	1	2.2	7.1
Trichoptera	58	1	2.2	1.7
Tricladida	6	2	4.4	33.3
Annelida	28	5	11.1	17.9
Mollusca	45	10	22.2	22.2
Crustacea	30	23	51.1	76.7
Total	195	45	100	23.1

^a Updated with data of Table 2

**Fig. 6** Cumulative number of non-indigenous species in the freshwater sections of the river Rhine**Fig. 8** Relation between the total number of non-indigenous species and the cumulative surface area of river catchments connected to the river Rhine**Fig. 7** Yearly average number of new non-indigenous species colonizing the freshwater sections of the river Rhine

the Upper Rhine to the Delta Rhine within 1 year. Upstream dispersal of species showed higher average and maximum time lags.

More detailed records on dispersal of six non-indigenous species in the river Rhine and connected waterways showed average dispersal rates of 44–112 km year⁻¹ (Table 4). The minimum and maximum dispersal rates of species ranged between 14–58 and 137–461 km year⁻¹, respectively. However, the mean log-transformed dispersal rates did not significantly differ (paired two-sample *t*-test; *P* > 0.05).

Contribution of non-indigenous species in macroinvertebrate assemblages

Available data on macroinvertebrate assemblages in the littoral zone of the river Rhine at Lobith allowed the analyses of temporal trends in biocontamination with non-indigenous species over time (Fig. 11). In

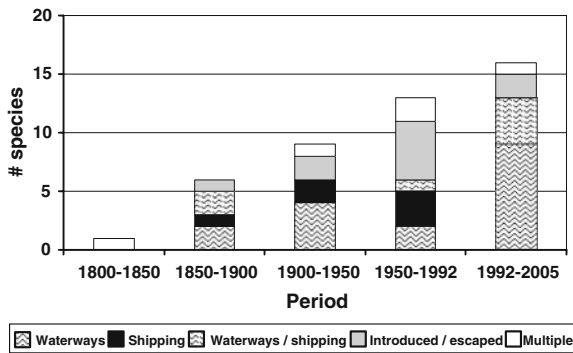


Fig. 9 Dispersal vectors of non-indigenous species in the Rhine river distributaries. Waterways: migration or drift via man made waterways (canals connecting river basins); Shipping: transported via seagoing ships (e.g., release from ballast water and ship hull fouling); Introduced/escaped: deliberate introduction by humans (e.g., for aquaculture, fisheries, weed control and pest management) or accidental release from aquaculture, escapes from garden ponds or dumping of aquaria or pond contents

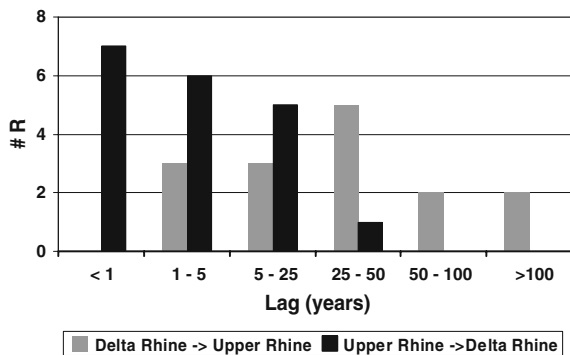


Fig. 10 Lag in first records of non-indigenous species in the Delta Rhine and Upper Rhine

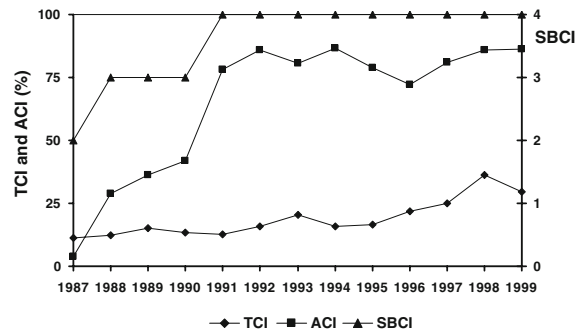


Fig. 11 Temporal changes of abundance contamination index (ACI), taxonomic contamination index (TCI) and site-specific biological contamination index (SBCI) of the river Rhine near Lobith

total, 17 non-indigenous macroinvertebrate species were recorded from 1987 to 1999 in the local macroinvertebrate assemblages on artificial substrates. The taxonomic contamination at species level (TCI) increased from 11.1 to 36.1% over the period 1987–1998 and slightly decreased to 29.5% in 1999. The increase in taxonomic contamination over this time span could be mainly attributed to invasions of Ponto-Caspian species after the opening of the Rhine-Main-Danube waterway in 1992. The abundance contamination steeply increased from 4 to 86.0% over the period 1987–1992, followed by a state of dynamic equilibrium with an average value of 82.2% over the period 1992–1999. High abundance contamination could be mainly attributed to seven invasive species, i.e., the isopod *Jaera istri*, the amphipods *Chelicorophium curvispinum*, *Dikergammarus villosus*, *Echinogammarus ischnus* and *Gammarus tigrinus*, and the bivalve molluscs

Table 4 Dispersal rates of aquatic invasive species in European waterways (km year⁻¹)

Taxon/species	Number of records	Mean dispersal rate	Standard deviation	Minimum dispersal rate	Maximum dispersal rate
Bivalvia					
<i>Corbicula fluminea</i>	6	63	95	27	276
<i>Dreissena polymorpha</i>	3	65	93	14	199
Crustacea					
<i>Chelicorophium curvispinum</i>	6	44	46	14	137
<i>Dikergammarus villosus</i>	4	112	194	40	461
<i>Jaera istri</i>	5	109	68	31	185
<i>Obesogammarus obesus</i>	3	130	203	58	424

Dreissena polymorpha and *Corbicula fluminea*. However, the relative contribution of each species changed remarkably during the sampling period (see also below). The ecological quality of the macroinvertebrate assemblages, as indicated by the site specific biocontamination index (SBCI), decreased from moderate (score 2) to bad (score 4), due to the high species richness and numerical dominance of non-indigenous species.

Species succession

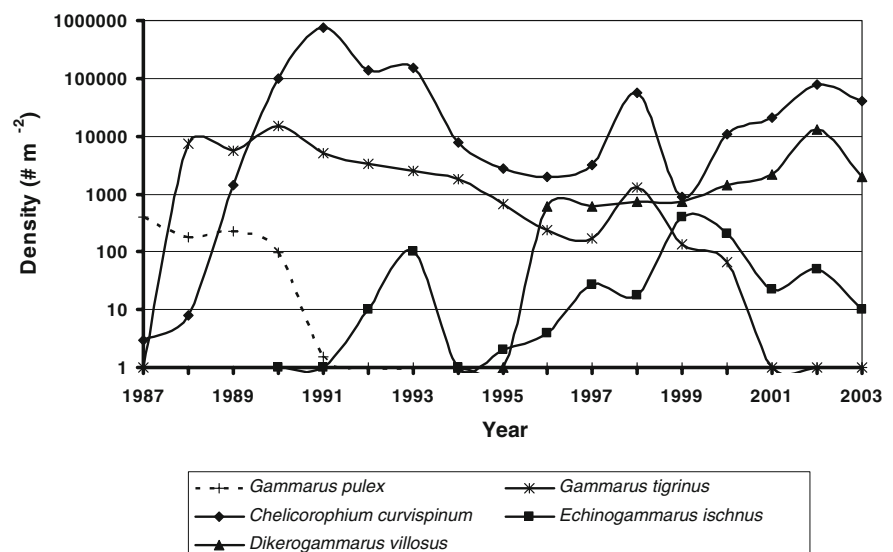
The maximum densities of amphipods in the littoral zones of the Delta Rhine showed sudden changes over the period 1987–2003 (Fig. 12). The populations of the native omnivorous *Gammarus pulex* and North American omnivorous *G. tigrinus* collapsed due to severe emissions of pesticides during the Sandoz disaster in 1986 (Den Hartog et al. 1992). *G. pulex* recovered slightly in 1987 but was subsequently replaced by *G. tigrinus*. Since 1990 *G. pulex* has only occurred in low densities. The Ponto-Caspian *C. curvispinum*, a filter-feeder, arrived in 1987 and reached maximum densities in 1991. This species out-competed the native as well as non-indigenous species by building extensive networks of mud-tubes, forming mud layers of several centimetres thick on firm substrate smothering sessile fauna and preventing settlement of species which need bare substrate (Van den Brink et al. 1993; Van der Velde et al. 1994). In 1990 and 1994 the

omnivorous *E. ischnus* and *D. villosus* arrived from the Ponto-Caspian area, respectively. From that time on the densities of *G. tigrinus* continuously decreased, whereas densities of *D. villosus* strongly increased. Since 2001, numbers of *C. curvispinum* have also declined, but even so it remained the most numerous macroinvertebrate species. Our data describing the maximum densities of amphipods clearly documented the displacement of the native *G. pulex* and the North American invader *G. tigrinus* by the Ponto-Caspian species and the co-existence of the recent Ponto-Caspian invaders *C. curvispinum*, *E. ischnus* and *D. villosus* in the main channel of the Rhine.

Discussion

Economic development and globalisation of trade have resulted in a strong expansion of sea cargo and inland shipping (Karatajev et al. 2007). The construction of canals has resulted in an extensive Eurasian network of inland waterways and a stepwise increase of large rivers connected to the river Rhine. This network of waterways and shipping activities removed physical barriers for dispersal of species between previously biogeographically isolated regions and opened six principal invasion corridors for dispersal of aquatic species to the river Rhine (Bij de Vaate et al. 2002; Arbačiauskas et al. 2008; Karatajev et al. 2008; Panov et al. 2009).

Fig. 12 Temporal changes in maximum density of gammaridean species in the littoral zones of the river Rhine distributaries in the Netherlands



The stepwise development of a Eurasian network of inland waterways and the removal of some critical barriers in potential invasion corridors coincided with the punctuated increase of non-indigenous macroinvertebrate species richness in the river Rhine. The significant correlation between non-indigenous species richness and total surface area of catchments connected to the river Rhine confirms this pattern. Logarithmic species—area plots normally align the data linearly (Rosenzweig 1995). Our study shows that this relation also holds true for the diversity of non-indigenous macroinvertebrate species in networks of formerly biogeographically isolated river catchments.

The relative importance of dispersal vectors for non-indigenous species differs remarkably for various time spans. Deliberate introductions and accidental releases decrease, whereas transport via ships (ballast water and fouling of ship hulls) and natural migration or drift via man made waterways increase. Until the opening of the Main-Danube canal in 1992, the sea shipping routes and central corridor were the dominant pathways for the spread of non-indigenous species in the river Rhine. Currently, the southern corridor is the most important dispersal route. The south-western and Mediterranean corridors only appear to be of minor importance for the dispersal of non-indigenous species to the river Rhine.

Data availability allowed estimation of long distance dispersal rates of six non-indigenous species in the river Rhine and some connected waterways. The mean dispersal rates of these species did not differ significantly due to the low numbers of records and the large variance between dispersal rates estimated for various river sections. Moreover, dispersal rates may be underestimated due to the time lag between dispersal, establishment of populations and the first recorded observation of each non-indigenous species. In spite of underestimation, the calculated dispersal rates of non-indigenous species in the Rhine are rather high in comparison with literature data for other rivers. This even holds true for upstream dispersal of the bivalves such as *Corbicula fluminea* (up to 276 km year⁻¹). Josens et al. (2005) reported upstream dispersal of the amphipod species *C. curvispinum* and *D. villosus* in the river Meuse at rates of 15 and 30–40 km year⁻¹, respectively. High upstream dispersal rates of non-indigenous macroinvertebrates in the river Rhine may be related to

human mediated transport as a result of intensive shipping activities. The exotic bivalve *Limnoperna fortunei* also spread rapidly (around 250 km year⁻¹) in South American river tributaries that have intensive year-round shipping, but the upstream colonization in river tributaries with very restricted river traffic has been almost an order of magnitude slower (Karatayev et al. 2007). However, empirical evidence of shipping mediated upstream dispersal of invasive species is still scarce.

The water quality of the river Rhine has been strongly improved over the last decades (Bij de Vaate et al. 2006). Conventional biological water quality indicators, such as the Biological Monitoring Working Party index (Armitage et al. 1983), suggest a moderate ecological status of the river (Arbačiauskas et al. 2008). However, this indicator system does not yet take into account the effects of invasive species on the structure and functioning of river systems. Our site specific biological contamination scores for macroinvertebrate communities in the littoral zones of the Delta Rhine clearly indicate a decrease of the ecological status from moderate to bad, due to the strong dominance of non-indigenous species in richness and abundance. Currently, the river Rhine is amongst the inland waterways with the highest richness and abundance of non-indigenous species (Arbačiauskas et al. 2008; Panov et al. 2009). Nevertheless, the total number of non-indigenous species and their contribution to species richness of macroinvertebrate communities vary between river sections and sampling sites (IKSR 2002).

At many sampling sites in the river Rhine a relatively small group of mass invaders dominate in abundance by more than 80% (Van den Brink et al. 1993; Van der Velde et al. 1994; Haas et al. 2002; Bernauer and Jansen 2006; Bij de Vaate et al. 2006; Van Riel et al. 2006a; Baur and Schmidlin 2007). The analysis of temporal changes in species composition and abundance of amphipods in the littoral zone of the Delta Rhine clearly shows a replacement of native species by non-indigenous ones and changes in the dominance from established non-indigenous species to recent invaders. Similar replacements of native and non-indigenous species by new mass invaders are also observed in the Middle and Upper Rhine (Haas et al. 2002; Bernauer and Jansen 2006), in other large rivers in Europe (Dick and Platvoet 2000; MacNeil et al. 2004; Jazdzewski et al. 2004; Grabowski et al.

2007; Arbačiauskas et al. 2008) and in North America (Palmer and Ricciardi 2004; Haynes et al. 2005; Kestrup and Ricciardi 2009).

A variety of mutually non-exclusive hypotheses have been suggested to explain the success of invaders in the river Rhine (Van der Velde et al. 2002, 2006a, b; Baur and Schmidlin 2007): (1) specific biological traits to facilitate dispersal, colonisation and population establishment, (2) high competitive ability with native species and released from enemies, (3) habitat alterations and environmental disturbances preventing strong interspecific competition by native species, (4) availability of vacant niches, (5) ecosystem instability (invasional meltdown), and (6) groups of co-adapted invaders.

Biological trait analyses show that aquatic invaders in North America and Europe are not a random selection of species (Karatayev et al. 2009). Invaders are over-represented by molluscs and crustaceans (mainly collector-filterers) and tolerate at least moderate amounts of organic pollution. Compared to native macroinvertebrates, invasive species and genera tend to reproduce more frequently and to have a higher abundance (higher propagule pressure), significantly more reproduction strategies enabling colonization by a single individual that releases viable offspring, larger size and longer life (providing resistance against mortality), food and feeding habits that allow the exploitation of food resources in streams more effectively, and are more dominant in their communities (Grabowski et al. 2007; Statzner et al. 2007). These traits may favour the establishment and population growth of invaders in disturbed systems, such as the river Rhine.

Dominance of macroinvertebrate communities in the littoral zones of the river Rhine is also determined by the high competitive ability of invaders (Van den Brink et al. 1991, 1993; Van Riel et al. 2006b; Van Riel 2007; Van der Velde et al. 2009) and the lack of enemies (enemy release hypothesis; Van der Velde et al. 2006b). Experimental studies show that interference competition can explain the replacement of the native *G. pulex* and the North American invader *G. tigrinus* by the Ponto-Caspian *D. villosus* and the co-existence of the Ponto-Caspian invaders *C. curvispinum*, *E. ischnus* and *D. villosus* in the river Rhine (Van Riel et al. 2007, 2009). Differences in predator avoidance behaviour between invasive and native species may also lead to increased predation on native

species (Pennuto and Keppler 2008). In addition, human disturbances may prevent strong interspecific competition by native species. Competitive stress between native and invasive species is strongly influenced by local environmental circumstances, such as type of substratum, water temperature, salinity, current velocity and habitat heterogeneity (MacNeil et al. 2001, 2003, 2004; Wijnhoven et al. 2003; Palmer and Ricciardi 2004; MacNeil and Platvoet 2005; Van der Velde et al. 2009; Kestrup and Ricciardi 2009; Van Riel et al. 2009). The ongoing rise in water temperature in the river Rhine due to thermal pollution and global warming will also affect the establishment success of non-indigenous species and interspecific competition (Leuven et al. 2007). Extremely low summer discharges are generally accompanied by an increase in the ionic content and temperature of the river water. Experimental studies indicate a wider tolerance range and thus a higher competitive ability of non-indigenous species to water temperature and salt content in comparison with native species (Wijnhoven et al. 2003).

Recently, it has been hypothesized that high invasiveness of the river Rhine may also be related to the presence of vacant niches. The native fauna diversity of the river is rather low in comparison with rivers in south-eastern biogeographic regions, and this particularly holds for gammarids (Devin and Beisel 2008; Uehlinger et al. 2009). The Alps formed a barrier that reduced the accessibility of southern refuges during Pleistocene glaciations. This enhanced species extinction and impeded or delayed re-colonization from these refuges after the last glacial period (Uehlinger et al. 2009). Moreover, vacant niches were also created by human interventions such as large scale hydraulic engineering and severe water pollution, including accidental spills of toxic substances (e.g., the Sandoz disaster in 1986). The rapid spread of Ponto-Caspian species in the river Rhine coincides with the opening of invasion corridors and the improvement of river water quality (Van der Velde et al. 2000, 2002; Bij de Vaate et al. 2002, 2006).

Finally, a mass invader such as *D. villosus* also appear to impact on freshwater ecosystems through its exceptional predatory capabilities and is expected to have serious direct and indirect effects on ecosystem stability, with its invasion causing a larger “invasional meltdown” (Dick et al. 2002; Van der Velde et al. 2006a, b; Van Riel et al. 2006b). These

processes may be facilitated by colonization of groups of co-adapted invaders. Karatayev et al. (2009) conclude that the ongoing spread of non-indigenous species not only affects biodiversity but also strongly shifts communities toward greater tolerance of organic pollution and increases the numbers of suspension feeders, thereby enhancing benthic pelagic coupling in aquatic ecosystems with high densities of invaders.

Several European countries have plans to develop or to improve waterways in order to increase inland shipping and to accommodate larger vessels (Panov et al. 2009). The current invasion corridors and future developments of the Eurasian network of inland waterways may highly facilitate the active and passive dispersal of invasive species across Eurasian inland waters and coastal ecosystems. Appropriate risk assessment tools are required to address ecological and socio-economic risks posed by human-mediated introductions of non-indigenous species and to formulate sound preventive measures and management options (Arbačiauskas et al. 2008; Panov et al. 2009). Novel risk assessment tools should not only account for negative effects of invaders on biodiversity, but must also weigh their effects on ecosystem functioning. In addition to negative impacts attention should also be paid to the potential positive effects of invaders, such as the application of filter-feeders to fight eutrophication of lakes or their significance as staple food for endangered fish species or waterfowl (MacNeil et al. 1999; Nienhuis 2008).

Conclusions

The number of non-indigenous macroinvertebrate species in the river Rhine exhibits a strong increase over the period from 1800 to 2005, from <1 to more than 13 species per decade. The rapid range extension of non-indigenous species is strongly facilitated by shipping activities and the interconnection of river basins by canals. The sea harbours in the Delta Rhine (Atlantic and Northern invasion routes) and the recent Rhine-Main-Danube waterway (southern invasion corridor) are regarded as the most important gateways for the dispersal of non-indigenous species. A few non-indigenous species strongly dominate the littoral macroinvertebrate communities and cause harmful

effects on the biological integrity of the river Rhine (such as displacements of native species). Mass invaders in the river Rhine are the isopod *J. istri*, the amphipods *C. curvispinum*, *D. villosus*, *E. ischnus* and *G. tigrinus*, and the bivalves *D. polymorpha* and *C. fluminea*. Currently *D. rostriformis bugensis* is also regarded as a mass invader in the Delta Rhine (Personal observation). A variety of mutually non-exclusive hypotheses have been suggested to explain the success of invaders in the river Rhine. Appropriate risk assessment tools are required to balance both negative and positive ecological impacts and to derive scientifically sound and feasible management options of invasive species in the river Rhine.

Acknowledgments This paper was presented as keynote lecture at the 15th international conference on aquatic invasive species organised September 23–27, 2007 in Nijmegen, the Netherlands. The authors thank Jon Matthews for critical comments on an earlier draft of this paper.

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