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Research article

Recent invasions of alien macroinvertebrates and loss of native species in the upper Rhine River, Germany

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Abstract

In the summers of 2003-2005 we sampled the macroinvertebrate community of the upper Rhine River at 28 locations between kilometer 351.9 and 399.5 with a dredge and a hydraulic grab from a ship, or by hand sampling. Additionally, 16 samples were obtained from the cooling water intake screens of a thermal power plant in 2003. A total of 133 species and higher taxa were identified from approximately 140,000 organisms. A total of 33 neozoa (alien) species were identified, including the first record of *Chelicorophium robustum* in the Rhine River. Neozoa contributed approximately 74% to the total number of organisms collected from the ship-based samples and 85% to those from the power plant cooling water. Almost 64% of all individuals from the cooling water intake belonged to the Ponto-Caspian amphipod *Dikerogammarus villosus*. Similarly, only 13 taxa, four native and nine alien species, numerically dominated in the ship-based samples, representing 95% and 98% of all organisms in 2003 and 2004, respectively. The nine alien species contributed 74.7% and 72.1%, respectively, to the number of organisms. Only six species occurred abundantly in the main channel of the Rhine River, five of which were neozoa: *Jaera istri, Dikerogammarus villosus, Dreissena polymorpha, Chelicorophium curvispinum*, and *Hypania invalida*. The six abundant species colonized near-shore substrates, whereas only few species were retrieved at low densities from the bottom gravel of the central shipping lane. Species diversity was generally higher and relative abundance of neozoa was lower in backwater areas than in the main river channel. Some pronounced changes in the abundance of three numerically dominant species, including the neozoa *D. polymorpha* and *C. curvispinum,* occurred between 2003 and 2004, which likely correlated with differences in water levels and temperatures. Overall, our results demonstrate that the macroinvertebrate community of the upper Rhine River has been severely altered by the invasion of several highly successful alien species and the disappearance or population decline of native species, and that these processes are still ongoing. Changes in species composition and relative numerical abundance indicate both a displacement of native species by invasive species, and a relative rapid succession in the numerical dominance of "old" neozoa and "new" neozoa.

Key words: Upper Rhine River, macroinvertebrates, invasions, succession, abundance, habitat use, cooling waters

Introduction

Macroinvertebrate species richness of the Rhine River has been substantially reduced during the last century, mainly because of anthropogenic impacts, such as declining water quality and alterations to river morphometry and hydrology (Kinzelbach 1982, 1983). By the early 1970s, less than one fourth of the more than 160 species identified prior to 1920 could still be found in the river (Titizer et al. 1991). The water quality of the Rhine River has substantially improved over the last 30 years, and while macroinvertebrate species richness has largely recovered to former numbers, community composition has been substantially altered primarily by invasive species (IKSR 2002). With the opening of the Main-Danube canal in 1992, one further route for the exchange of biota between the Rhine

River and other biogeographical regions was established.

Within a year, the first macroinvertebrate species of Ponto-Caspian origin were documented near the mouth of the Main River tributary (IKSR 2002). The aim of this study was to document the current species composition and abundance of macroinvertebrates over a 48 km section of the Upper Rhine River, including the mouths of some tributaries and backwaters. Particular focus was given to a complete inventory of neozoa and the dominace relationship between native and invasive species.

Material and Methods

During April, July, and November of 2003 and April, August, and November of 2004 we took 43 and 55, respectively, macroinvertebrate samples from aboard the research vessel „Max Honsell“ (LfU Baden-Württemberg) from 29 sites between Rhine-kilometer 351.9 and 399.5 (Figure 1). Ship samples were taken using three different methods: with a dredge, a grab, and by hand sampling. Invertebrate samples were obtained using one, two, or all three methods depending on the available substrates at

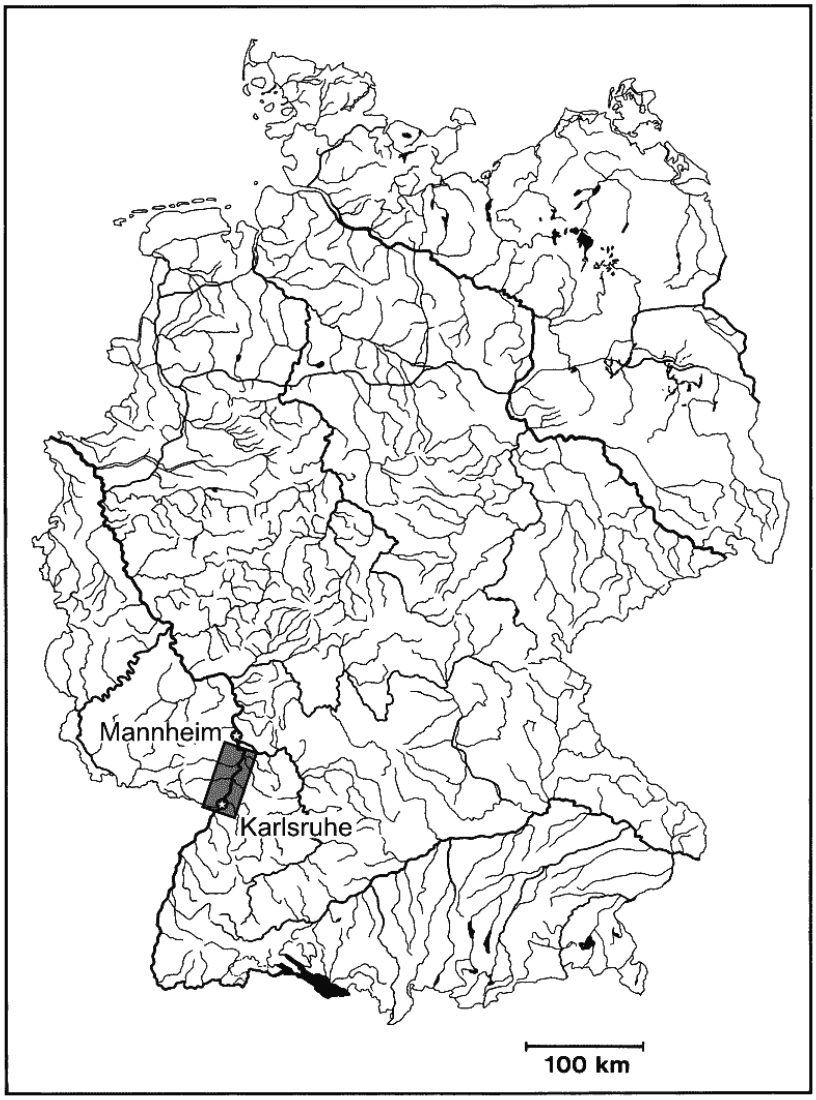

Figure 1. Map of Germany with river systems. The sampling area on the upper Rhine River is indicated by a rectangle

a sampling site (Annex 1). The dredge consisted of a 100 cm long, 60 cm wide, and 25 cm high steel frame with a removable inside nylon mesh (1000 µm) bag. It was pulled behind the ship in areas of >1.6 m water depth over the bottom substrate for approximately 100 m at a speed of 3-5 $km \cdot h^{-1}$. The drege content was sorted on deck through a set of 10, 5, and 1 mm sieves and washed. The grab was mounted on a hydraulically operated arm with a 7 m reach from the ship deck and sampled an area of approximately 0.8 m^2.

Larger pieces of wood, stones and boulders were separated from fines, sand, and gravel on deck and were hand-brushed inside of large water filled tubs. The water and a 20-30 L sub-sample of the smaller substrate fractions were treated similarly to the dredge material. Because of the fast current speeds (1.5-2 $m \cdot s^{-1}$) of the main river channel, grab samples could only be taken in sheltered areas or when the ship was fastened on shore. Hand sampling was performed in near-shore areas inaccessible to the ship or on substrates unsuitable to sampling by the other two methods. Areas of 0.5–1.0 m^2 were sampled by kick-netting (0.3 x 0.3 m net opening, 200 µm mesh) and/or by picking organisms from large pieces of substrate with forecepts.

In addition, 16 macroinvertebrate samples were taken from the water intake screens of the thermal power plant in Karlsruhe (RDK) at Rhine-kilometer 359.3 in May 2003. Invertebrates and debris washed from stainless steel rotating screens with 1 mm^2 openings were sampled with small dip nets (200 µm mesh) for 2-9 minutes, depending on the total amount of debris collected on the screens. The screens filter 17 $m^3 \cdot s^{-1}$ of cooling water under normal operating conditions of the power plant.

On 21 July, 2005, the site at Rhine-kilometer 375.4 was re-sampled as part of a university field trip. This site is located within a section of old river bed and has been used for gravel extraction in the 1960s and 1970s. Five samples of invertebrates were taken at this site with dip-nets and by hand sampling.

All samples were preserved in 75% ethanol and identified and enumerated in the laboratory using dissecting and compound microscopes. Organisms were identified to species or (in a few instances) to genus, except for most Dipera and Tubificidae, which were identified to family. Numbers of juveniles that could not be identified to species (e.g., Gammaridae) were estimated according to the relative abundance of adults in the same sample. In this study, we synonymously refer to those species that historically have not been documented from the Rhine River basin as neozoa (Kinzelbach 1972, Arbeitsgruppe Neozoa 1996), or alien species.

Results and Discussion

We collected approximately 4,800 individuals (Table 2), belonging to 68 species or higher taxa from the cooling water intakes of the thermal power plant at Karlsruhe. Neozoa were represented with 17 species and comprised approximately 85% of all organisms identified (Table 1). The three most abundant species in the power plant samples were also highly abundant in the ship-based samples (see below).

Table 1. Number of individuals of the three most abundant species, of all neozoa, and of all taxa collected from the cooling water of the thermal power plant at Karlsruhe in May 2003

Taxon	n	%
Dikerogammarus villosus	3081	63.6
Chelicorophium curvispinum	318	6.6
Jaera istri	222	4.6
Total neozoa	4114	84.9
Total organisms	4843	100.0

More than 130,000 organisms were identified from the ship based samples. Approximately 45,800 organisms from 116 species/taxa were collected in 2003. Of these, 27 species of neozoa (Table 2) with approximately 34,700 individual were identified, including all invasive species found in the power plant samples. In 2004, approximately 88,800 organisms from 114 species/taxa were collected, of which approximately 64,000 organisms belonged to 27 alien species (Table 2). A total of 133 taxa were identified in both years. Five species of neozoa (*Cordylophora caspia, Physella heterostropha, Echinogammarus berilloni, Procambarus clarkii*, and *Proasellus coxalis*), that were identified with few individuals in 2003, were not collected in 2004 (Table 2). Conversely, five neozoa (*Pectinatella magnifica, Caspiobdella fadejewi, Chelicorophium robustum, Gammarus tigrinus and Hemimysis anomala*) were found with low abundance only in the 2004 samples. Thirteen invasive species were identified from the single shore-based hand sample taken in 2005, including one species (*Orconectes immunis*) that had not been captured in the previous two years (Table 2).

Thus, a total of 33 alien macroinvertebrate species were identified in this study (Annex 2). This includes the first record of *C. robustum* from the Rhine River. This species originates from the Ponto-Caspian region. Similar to several other crustacea (Bij de Vaate et al. 2002), *C. robustum* likely entered the Rhine River drainage basin facilitated by ship traffic through the recently opened Main-Danube canal and was first reported in 2002 from the Main River at Frankfurt harbor (Bernerth and Stein 2003). The 52 specimen of *C. robustum* that we identified in November of 2004 all came from the harbor at Karlsruhe. Two months later, *C. robustum* was collected approximately 55 km downstream at Mannheim harbor (Peter Roos, Büro für Gewässerökologie, Karlsruhe, pers. commun.). These capture locations further suggest ship transport as a major mode of dispersal for *C. robustum*.

The relative abundance (approximately 74%)

Table 2. List of neozoa species identified from 2003-2005, with year of first detection in the Rhine River (Dehus et al. 1999, Tittizer et al. 2000, Gleiter et al. 2002, IKSR 2002) and geographical area of origin. If the location was not the Rhine River, the name of the tributary stream is given in brackets. Two individuals of the species complex *Polycelis nigra/tenuis* that were found in 2003 are not listed as neozoa

Higher taxon	Species	2003	2004	2005	Year	Origin
Coelenterata	*Cordylophora caspia*	x			1934 (Ruhr)	Ponto-Caspian
Bryozoa	*Pectinatella magnifica*		x	x	1883	North America
Turbellaria	*Dendrocoelum romanodanubiale*	x	x		1997	Ponto-Caspian
	Dugesia tigrina	x	x		1934	North America
Oligochaeta	*Branchiura sowerbyi*	x	x	x	1961	Southern Asia
Polychaeta	*Hypania invalida*	x	x	x	~1996	Ponto-Caspian
Hirudinea	*Caspiobdella fadejewi*		x		1998	Ponto-Caspian
Bivalvia	*Corbicula fluminea*	x	x	x	~1990	Asia (via North America)
	Corbicula fluminalis	x	x		~1991	Asia (via North America)
	Dreissena polymorpha	x	x	x	1826	Ponto-Caspian
Gastropoda	*Lithoglyphus naticoides*	x	x		~1950	Russia
	Menetus dilatatus	x	x		~2000	North America
	Physella acuta	x	x	x	1904	South-western Europe
	Physella heterostropha	x			~1983	North America
	Potamopyrgus antipodarum	x	x	x	~1962	New Zealand
	Viviparus viviparus	x	x		~1987	Eastern Europe
Crustacea	*Atyaephyra desmaresti*	x	x	x	1932	Southern Europe
	Chelicorophium robustum		x		First record	Ponto-Caspian
	Chelicorophium curvispinum	x	x	x	1982	Ponto-Caspian
	Crangonyx pseudogracilis	x	x		1992	North America
	Dikerogammarus villosus	x	x	x	1995	Ponto-Caspian
	Echinogammarus ischnus	x	x		1989	Ponto-Caspian
	Echinogammarus trichiatus	x	x		2001	Ponto-Caspian
	Echinogammarus berilloni	x			1924 (Lippe)	Mediterranean
	Gammarus tigrinus		x		1986	North America
	Hemimysis anomala		x		1997	Ponto-Caspian
	Jaera istri	x	x		1995	Ponto-Caspian
	Limnomysis benedeni	x	x	x	1997	Ponto-Caspian
	Orconectes immunis			x	1999	North America
	Orconectes limosus	x	x	x	1932	North America
	Orchestia cavimana	x	x		1937	Mediterranean
	Procambarus clarki	x			1988	North America
	Proasellus coxalis	x			1931	Southern Europe

and relative proportion of species/taxa (approximately 22%) of neozoa captured in the ship-based samples remained almost identical between 2003 and 2004. For the proportion of species, this calculation assumes that the number of (unidentified) species of Tubificidae and Chironomidae did not change between the two years.

The macroinvertebrate community of the Rhine River was numerically dominated by nine alien species and four native taxa (Figure 2). These thirteen abundant species/taxa (found with >500 individuals in one of the two sampling years) contributed 94.5% and 98.4% to the total number of invertebrates collected in 2003 and 2004, respectively. The nine alien species contributed 74.7% and 72.1%, respectively.

Three of the native taxa, Chironomidae, Tubificidae, and the heteropteran *Micronecta* sp. were captured almost exclusively in (slow flowing) backwater areas, where they sometimes reached high densities. These results are in line with findings that the relative abundance of Chironomidae and Oligochaeta in the main (shippable) channel of the upper Rhine River has substantially decreased between 1990 and 2000, and that these two taxa (for which no species identification is done during routine monitoring) no longer numerically dominate the invertebrate community (IKSR 2002). In the backwater areas, species diversity was generally higher and relative abundance of neozoa was lower compared to the main channel. Particularly in the most downstream sections of tributaries, native mayfly species typical of large rivers, such *Ephemera vulgata* and *Ephemera glaucops* were still found regularly and often in association with the neozoa *Limnomysis benedeni* and *Echinogammarus ischnus*.

Ancylus fluviatilis was the only native species that occurred abundantly in the main channel of the Rhine River. This gastropod colonized mainly shoreline rip-rap up to the maximum extent of wave action from ship traffic. The other five species that were consistently found in the main channel at very high abundances were all neozoa: *Jaera istri, Dikerogammarus villosus, Dreissena polymorpha, Chelicorophium curvispinum*, and *Hypania invalida*. The large increase in the relative abundance of *J. istri* between 2003 and 2004 was due mainly to the fact that this species occurred at high densities (up to 17,000 individuals·m^{-2}) at most sampling sites in 2004, whereas in 2003 its abundance was (still) relatively low at many locations.

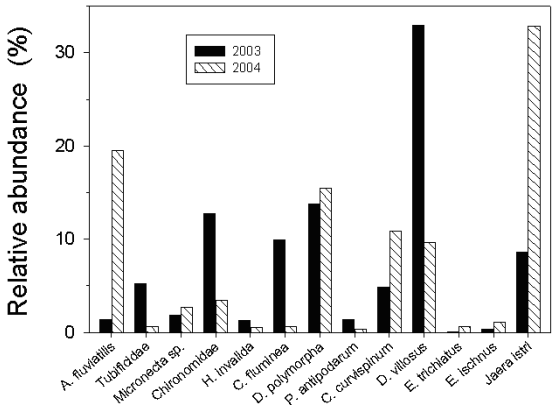

Figure 2. Relative numerical abundance of the 13 most abundant taxa collected from the ship-based samples in 2003 and 2004. The last nine species are all neozoa. For full species names see Table 2

Only a few species were collected between the wing dams or in the central shipping lane of the river where the bottom substrate consists mainly of relatively unstable gravel: the neozoa *Dendrocoelum romanodanubiale, Potamopyrgus antipodarum,* and *Echinogammarus trichiatus,* and the native trichoptera *Hydropsyche bulgaromanorum* and *Psychomyia pusilla,* which both occured at relatively low abundance. IKSR (2002) and Haas et al. (2002) reported that the relative abundance and density of *P. pusilla* in the upper Rhine has increased from 1990-2000, and 1993-2001, respectively. Overall, with a total of 21 species the macroinvertebrate diversity of the main channel (including shoreline areas) of the Rhine River between Speyer and Karlsruhe was very low. Compared to results from similar sampling in 1993 (Bernauer 1995), the abundance of erbobdellid leeches and of the native mayfly *Heptagenia sulphurea* has noticably decreased, and the formerly abundant native (*Aphelocheirus aestivalis*, *Hydropsyche contubernalis*) and invasive (*Gammarus tigrinus*, *Dugesia tigrina*) species have largely disappeared.

Similar changes in community composition, particularly the increase in density and relative abundance of *D. villosus* and *Jaera* sp. and the concomitant decreases of *C. curvispinum* and *G. tigrinus* in the upper Rhine River since the early 1990s have been observed in other studies (IKSR 2002, Haas et al. 2002). The reasons for the sometimes dramatic changes in community composition are not well understood. In addition to competition and predation effects (IKSR 2002,

Haas et al. 2002), these changes may be due to between-year climatic variability, particularly in water temperature/levels. This notion is supported by the strong increase in the abundance of *A. fluviatilis, D. polymorpha,* and *C. curvispinum* between 2003 and 2004, which, at least for the first two species, was largely due to juvenile individuals. These three species were apparently negatively affected by the low water levels and high temperatures in 2003, when large numbers of dead *C. curvispinum* were often seen, and apparently recovered rapidly under the more favorable weather conditions of 2004.

Overall, our results demonstrate, that, likely mediated by changes in the physical and chemical conditions of the river, the macroinvertebrate community of the upper Rhine River has been severely altered by the invasion of several highly successful neozoa and the disappearance or population decline of native species. Although data were mainly collected during only two years, they further show that these changes are still ongoing. The documented changes in species composition and relative numerical abundance indicate both a displacement of native species by alien species, and also a rapid succession in the numerical dominance of ”old“ neozoa (mainly from North America, e.g. *G. tigrinus*) and “new“ neozoa (mainly from the Ponto-Caspian area via the Main-Danube canal, e.g. *J. istri*).

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Annex 1

List of ship-based sampling sites with river kilometer (R-km), waterbody (Rhine River mainstem or backwaters, including the mouth of tributary streams and the old river channel), and location (left or right bank in downstream direction). The substrate(s) sampled and the method(s) of sampling are given

R-km	Waterbody	Location description	Location coordinates		Substrate	Method
			Latitude, N	Longitude, E		
351.9	Backwater	Old river channel, Rastatt	49°57′48′′	8°13′52′′	Deadwood, sand/silt, mud, stones	Dip net
354.7	Rhine River	Wing dam, right	49°58′53′′	8°15′49′′	Stones	Grab
355.8	Rhine River	Wing dam, right	49°59′15′′	8°16′30′′	Stones	Dip net, grab
358.5	Rhine River	Wing dam, right	49°00′24′′	8°17′43′′	Stones, gravel	Dredge
359.0	Rhine River	Wing dam, right	49°00′41′′	8°17′43′′	Stones, gravel	Grab, dredge, dip net
359.6	Backwater	Harbour, Karlsruhe	49°00′54′′	8°18′04′′	Stones, mud	Dredge, grab
359.6	Rhine River	Wing dam, right	49°00′54′′	8°18′04′′	Stones, gravel	Dip net, grab, dredge
359.9	Rhine River	Wing dam, left	49°01′28′′	8°18′06′′	Stones	Grab
360.3	Backwater	Old river channel, Hagenbach	49°01′23′′	8°18′11′′	Mud	Dredge, grab
362.6	Backwater	Harbour, Maxau	49°02′33′′	8°18′27′′	Stones, mud	Grab
363.5	Rhine River	Wing dam, right	49°03′01′′	8°18′41′′	Stones	Dip net
364.9	Backwater	Harbour, Wörth	49°03′43′′	8°18′38′′	Sand, gravel, mud	Dip net, grab
364.0	Rhine River	Wing dam, right	49°03′15′′	8°18′50′′	Stones, gravel	Dredge, dip net
365.3	Rhine River	Wing dam, left	49°04′05′′	8°18′38′′	Stones	Grab
366.0	Rhine River	Wing dam, right	49°03′45′′	8°19′03′′	Gravel	Dredge
367.4	Rhine River	Wing dam, right	49°04′45′′	8°20′28′′	Stones	Grab
368.5	Rhine River	Wing dam, right	49°05′13′′	8°21′01′′	Gravel	Dredge
370.1	Rhine River	Shoreline, right	49°06′02′′	8°21′41′′	Stones	Dip net
374.0	Rhine River	Wing dam, right	49°08′04′′	8°22′04′′	Stones, gravel	Dredge, grab
375.7	Backwater	Gravel pit, Rott	49°08′46′′	8°22′48′′	Deadwood, sand/silt, mud, stones	Dip net, grab
376.4	Backwater	Old river channel, Rott	49°09′15′′	8°22′56′′	Deadwood, mud, silt, sand	Dip net, grab
380.8	Backwater	Old river channel, Rußheim	49°11′27′′	8°23′13′′	Gravel, sand	Grab
385.0	Rhine River	Wing dam, left	49°13′47′′	8°23′20′′	Stones	Dredge, grab
390.0	Rhine River	Wing dam, right	49°15′35′′	8°26′14′′	Stones	Dredge, grab
391.3	Rhine River	Wing dam, left	49°16′16′′	8°27′06′′	Stones	Dredge, grab
392.5	Rhine River	Wing dam, right	49°16′41′′	8°27′29′′	Stones	dip net, grab,
393.5	Backwater	Old river channel, Berghausen	49°17′08′′	8°28′05′′	Mud, stones, silt, gravel	Grab, dredge, dip net
394.3	Rhine River	Wing dam, right	49°17′09′′	8°28′52′′	Stones	Grab
399.5	Backwater	Old river channel, exit	49°19′01′′	8°27′23′′	Silt, detritus, gravel, deadwood	Grab

Annex 2

Records of alien species in the Upper Rhine River, Germany, 2003-2005*

Species	Location** (Rhine River km)	Record date	Species abundance (ind./m^2)	Collector
Atyaephyra desmaresti (Millet, 1831)	364.9	29.11.2004	6	D. Bernauer
	375.7	24.07.2003	81	D. Bernauer
	376.0	23.04.2003	7	D. Bernauer
	376.0	30.04.2004	1	D. Bernauer
	376.5	25.11.2003	2	D. Bernauer
	380.8	25.11.2004	10	D. Bernauer
Branchiura sowerbyi (Beddard, 1892)	351.9	25.11.2003	2	D. Bernauer
	351.9	30.04.2004	1	D. Bernauer
	359.5	25.11.2003	3	D. Bernauer
	362.6	22.04.2003	5	D. Bernauer
	364.9	29.11.2004	8	D. Bernauer
	364.9	22.04.2003	2	D. Bernauer
	364.9	25.07.2003	7	D. Bernauer
	365.3	26.11.2003	5	D. Bernauer
	376.0	30.04.2004	10	D. Bernauer
	376.0	23.04.2003	2	D. Bernauer
	376.4	24.07.2003	3	D. Bernauer
	376.4	25.11.2003	11	D. Bernauer
	376.5	23.04.2003	2	D. Bernauer
	399.5	25.11.2003	14	D. Bernauer
	399.5	29.04.2004	6	D. Bernauer
	399.5	23.11.2004	8	D. Bernauer
Caspiobdella fadejewi (Epshtein, 1961)	393.5	29.04.2004	1	D. Bernauer
Chelicorophium curvispinum (G.O. Sars,1895)	354.7	29.11.2004	3	D. Bernauer
	358.9	29.11.2004	6	D. Bernauer
	359.0	23.04.2003	19	D. Bernauer
	359.0	26.11.2003	615	D. Bernauer
	359.6	22.04.2003	52	D. Bernauer
	359.6	22.04.2003	256	D. Bernauer
	359.6	25.07.2003	21	D. Bernauer
	359.6	22.04.2003	187	D. Bernauer
	359.6	30.04.2004	27	D. Bernauer
	359.6	29.11.2004	315	D. Bernauer
	362.6	30.04.2004	970	D. Bernauer
	363.5	23.04.2003	97	D. Bernauer
	364.0	29.11.2004	360	D. Bernauer
	364.0	23.04.2003	78	D. Bernauer
	364.9	25.07.2003	18	D. Bernauer
	364.9	30.04.2004	21	D. Bernauer
	364.9	29.11.2004	2300	D. Bernauer

	365.3	26.11.2003	357	D. Bernauer
	365.9	22.04.2003	74	D. Bernauer
	368.5	26.11.2003	21	D. Bernauer
	370.1	25.07.2003	77	D. Bernauer
	374.0	25.07.2003	13	D. Bernauer
	374.0	30.04.2004	220	D. Bernauer
	375.7	23.04.2003	43	D. Bernauer
	376.0	23.04.2003	73	D. Bernauer
	376.0	24.07.2003	12	D. Bernauer
	376.0	25.11.2004	97	D. Bernauer
	376.0	30.04.2004	21	D. Bernauer
	376.4	23.04.2003	103	D. Bernauer
	376.4	25.11.2003	69	D. Bernauer
	376.4	25.11.2004	410	D. Bernauer
	376.5	23.04.2003	26	D. Bernauer
	376.5	24.07.2003	47	D. Bernauer
	380.8	25.11.2004	531	D. Bernauer
	385.5	29.04.2004	63	D. Bernauer
	390.0	13.08.2004	600	D. Bernauer
	391.3	23.11.2004	2100	D. Bernauer
	392.5	23.11.2004	780	D. Bernauer
	393.5	23.04.2003	49	D. Bernauer
	393.5	24.07.2003	435	D. Bernauer
	393.5	24.07.2003	105	D. Bernauer
	394.3	13.08.2004	27	D. Bernauer
	394.3	23.11.2004	1240	D. Bernauer
	398.9	29.11.2004	7	D. Bernauer
	399.3	23.11.2004	81	D. Bernauer
	399.5	29.04.2004	615	D. Bernauer
Chelicorophium robustum (G.O. Sars, 1895)	359.6	30.04.2004	5	D. Bernauer
	359.6	29.11.2004	76	D. Bernauer
	376.4	25.11.2004	1	D. Bernauer
Corbicula fluminalis (O.F. Müller, 1774)	359.6	22.04.2003	2	D. Bernauer
	362.6	22.04.2003	27	D. Bernauer
	362.6	29.11.2004	6	D. Bernauer
	364.9	22.04.2003	14	D. Bernauer
	375.7	23.04.2003	2	D. Bernauer
	376.0	23.04.2003	6	D. Bernauer
	376.0	25.11.2004	64	D. Bernauer
	376.0	30.04.2004	16	D. Bernauer
	376.5	24.07.2003	24	D. Bernauer
	393.5	23.04.2003	25	D. Bernauer
	393.5	25.11.2003	56	D. Bernauer
Corbicula fluminea (O.F. Müller, 1774)	358.9	29.11.2004	2	D. Bernauer
	359.0	25.07.2003	39	D. Bernauer
	359.5	25.11.2003	245	D. Bernauer

	359.5	30.04.2004	2	D. Bernauer
	359.5	29.11.2004	92	D. Bernauer
	359.6	22.04.2003	450	D. Bernauer
	362.6	22.04.2003	420	D. Bernauer
	362.6	29.11.2004	30	D. Bernauer
	364.9	22.04.2003	470	D. Bernauer
	364.0	23.04.2003	36	D. Bernauer
	365.3	26.11.2003	11	D. Bernauer
	365.9	22.04.2003	9	D. Bernauer
	368.5	26.11.2003	67	D. Bernauer
	370.1	25.07.2003	48	D. Bernauer
	375.7	23.04.2003	8	D. Bernauer
	376.0	23.04.2003	33	D. Bernauer
	376.4	24.07.2003	18	D. Bernauer
	376.4	25.11.2003	215	D. Bernauer
	376.4	25.11.2004	138	D. Bernauer
	376.5	24.07.2003	1400	D. Bernauer
	376.5	25.11.2003	60	D. Bernauer
	380.8	25.11.2004	50	D. Bernauer
	385.0	24.07.2003	15	D. Bernauer
	385.5	29.04.2004	8	D. Bernauer
	391.3	23.11.2004	2	D. Bernauer
	393.5	23.04.2003	970	D. Bernauer
	393.5	24.07.2003	42	D. Bernauer
	393.5	25.11.2003	1500	D. Bernauer
	394.3	23.11.2004	295	D. Bernauer
	399.5	24.07.2003	28	D. Bernauer
	399.5	25.11.2003	105	D. Bernauer
	399.5	29.04.2004	62	D. Bernauer
	399.5	23.11.2004	52	D. Bernauer
Cordylophora caspia (Pallas, 1771)	368.5	25.07.2003	1	D. Bernauer
Crangonyx pseudogracilis (Bousfield, 1958)	375.7	23.04.2003	2	D. Bernauer
	376.0	25.11.2004	1	D. Bernauer
Dendrocoelum romanodanubiale (Codreanu, 1949)	365.3	26.11.2003	1	D. Bernauer
	391.3	23.11.2004	13	D. Bernauer
	398.9	29.11.2004	2	D. Bernauer
Dikerogammarus villosus (Sovinskij, 1894)	354.7	29.11.2004	300	D. Bernauer
	355.8	25.07.2003	480	D. Bernauer
	358.5	30.04.2004	147	D. Bernauer
	358.9	29.11.2004	210	D. Bernauer
	359.0	23.04.2003	117	D. Bernauer
	359.0	25.07.2003	203	D. Bernauer
	359.0	26.11.2003	540	D. Bernauer
	359.5	25.07.2003	67	D. Bernauer
	359.5	25.11.2003	24	D. Bernauer

359.6	22.04.2003	475	D. Bernauer
359.6	22.04.2003	146	D. Bernauer
359.6	30.04.2004	21	D. Bernauer
359.6	29.11.2004	129	D. Bernauer
359.6	25.07.2003	210	D. Bernauer
359.6	22.04.2003	970	D. Bernauer
359.9	22.04.2003	163	D. Bernauer
360.3	22.04.2003	203	D. Bernauer
360.3	30.04.2004	445	D. Bernauer
362.6	27.01.1900	39	D. Bernauer
362.6	30.04.2004	33	D. Bernauer
363.5	23.04.2003	785	D. Bernauer
364.0	29.11.2004	136	D. Bernauer
364.9	25.07.2003	715	D. Bernauer
364.0	23.04.2003	1850	D. Bernauer
364.9	30.04.2004	34	D. Bernauer
364.9	29.11.2004	548	D. Bernauer
365.3	26.11.2003	367	D. Bernauer
365.9	22.04.2003	178	D. Bernauer
366.4	22.04.2003	2100	D. Bernauer
368.5	26.11.2003	815	D. Bernauer
370.1	25.07.2003	1150	D. Bernauer
370.1	30.04.2004	15	D. Bernauer
374.0	25.07.2003	2750	D. Bernauer
374.0	30.04.2004	394	D. Bernauer
375.7	23.04.2003	135	D. Bernauer
375.7	24.07.2003	321	D. Bernauer
376.0	23.04.2003	137	D. Bernauer
376.0	24.07.2003	81	D. Bernauer
376.0	30.04.2004	417	D. Bernauer
376.4	23.04.2003	18	D. Bernauer
376.4	24.07.2003	423	D. Bernauer
376.4	25.11.2004	53	D. Bernauer
376.5	23.04.2003	63	D. Bernauer
376.5	24.07.2003	465	D. Bernauer
376.5	25.11.2003	189	D. Bernauer
380.8	25.11.2004	178	D. Bernauer
385.0	24.07.2003	36	D. Bernauer
385.5	29.04.2004	920	D. Bernauer
390.0	13.08.2004	540	D. Bernauer
391.3	23.11.2004	215	D. Bernauer
392.5	23.11.2004	278	D. Bernauer
393.5	23.04.2003	203	D. Bernauer
393.5	24.07.2003	870	D. Bernauer
393.5	24.07.2003	135	D. Bernauer
393.5	25.11.2003	48	D. Bernauer
394.3	13.08.2004	36	D. Bernauer
394.3	23.11.2004	110	D. Bernauer
398.9	29.11.2004	60	D. Bernauer

	399.3	23.11.2004	97	D. Bernauer
	399.5	25.11.2003	63	D. Bernauer
	399.5	29.04.2004	1230	D. Bernauer
Dreissena polymorpha (Pallas, 1771)	354.7	29.11.2004	700	D. Bernauer
	358.9	29.11.2004	235	D. Bernauer
	359.0	26.11.2003	140	D. Bernauer
	359.5	29.11.2004	750	D. Bernauer
	362.6	22.04.2003	154	D. Bernauer
	364.9	22.04.2003	275	D. Bernauer
	364.9	25.07.2003	2900	D. Bernauer
	364.9	30.04.2004	6	D. Bernauer
	364.9	29.11.2004	1700	D. Bernauer
	365.3	26.11.2003	214	D. Bernauer
	365.9	22.04.2003	455	D. Bernauer
	367.4	25.07.2003	27	D. Bernauer
	370.1	25.07.2003	13	D. Bernauer
	374.0	25.07.2003	109	D. Bernauer
	374.0	30.04.2004	92	D. Bernauer
	375.7	23.04.2003	124	D. Bernauer
	376.0	23.04.2003	12	D. Bernauer
	376.0	25.11.2004	280	D. Bernauer
	376.4	23.04.2003	365	D. Bernauer
	376.4	25.11.2003	8	D. Bernauer
	376.5	23.04.2003	350	D. Bernauer
	376.5	24.07.2003	1900	D. Bernauer
	376.5	25.11.2003	14	D. Bernauer
	380.8	25.11.2004	82	D. Bernauer
	391.3	23.11.2004	375	D. Bernauer
	393.5	23.04.2003	156	D. Bernauer
	393.5	24.07.2003	1700	D. Bernauer
	393.5	24.07.2003	167	D. Bernauer
	393.5	25.11.2003	375	D. Bernauer
	398.9	29.11.2004	2	D. Bernauer
	392.5	23.11.2004	1400	D. Bernauer
	399.3	23.11.2004	6	D. Bernauer
	399.5	25.11.2003	27	D. Bernauer
Dugesia tigrina (Girard, 1850)	358.9	29.11.2004	1	D. Bernauer
	359.6	25.07.2003	6	D. Bernauer
Echinogammarus berilloni (Catta, 1878)	351.9	26.08.2003	79	D. Bernauer
Echinogammarus ischnus (Stebbing, 1899*)*	354.7	29.11.2004	54	D. Bernauer
	355.8	25.07.2003	2	D. Bernauer
	358.5	30.04.2004	21	D. Bernauer
	358.5	29.11.2004	190	D. Bernauer
	359.0	23.04.2003	9	D. Bernauer
	359.0	25.07.2003	5	D. Bernauer

	359.5	25.07.2003	18	D. Bernauer
	359.6	22.04.2003	12	D. Bernauer
	359.6	29.11.2004	31	D. Bernauer
	359.6	25.07.2003	2	D. Bernauer
	362.6	30.04.2004	11	D. Bernauer
	364.9	29.11.2004	7	D. Bernauer
	365.3	26.11.2003	2	D. Bernauer
	365.9	22.04.2003	6	D. Bernauer
	366.4	22.04.2003	114	D. Bernauer
	368.5	26.11.2003	45	D. Bernauer
	374.0	30.04.2004	117	D. Bernauer
	376.0	23.04.2003	2	D. Bernauer
	376.0	30.04.2004	15	D. Bernauer
	376.0	25.11.2004	6	D. Bernauer
	380.8	25.11.2004	24	D. Bernauer
	385.0	24.07.2003	13	D. Bernauer
	385.5	29.04.2004	63	D. Bernauer
	391.3	23.11.2004	9	D. Bernauer
	392.5	23.11.2004	11	D. Bernauer
	393.5	25.11.2003	5	D. Bernauer
	394.3	13.08.2004	3	D. Bernauer
	394.3	23.11.2004	9	D. Bernauer
	399.5	25.11.2003	3	D. Bernauer
	399.5	29.04.2004	2	D. Bernauer
Echinogammarus trichiatus (Martynow, 1932)	355.8	25.07.2003	3	D. Bernauer
	358.5	30.04.2004	21	D. Bernauer
	359.5	25.11.2003	3	D. Bernauer
	359.6	22.04.2003	3	D. Bernauer
	362.6	30.04.2004	6	D. Bernauer
	364.0	29.11.2004	14	D. Bernauer
	364.9	30.04.2004	6	D. Bernauer
	364.9	29.11.2004	590	D. Bernauer
	365.9	22.04.2003	3	D. Bernauer
	367.4	25.07.2003	4	D. Bernauer
	370.1	25.07.2003	15	D. Bernauer
	375.7	24.07.2003	11	D. Bernauer
	376.5	25.11.2003	3	D. Bernauer
	380.8	25.11.2004	76	D. Bernauer
	392.5	23.11.2004	254	D. Bernauer
	393.5	24.07.2003	19	D. Bernauer
	399.5	29.04.2004	21	D. Bernauer
Gammarus tigrinus (Sexton, 1939)	376.0	25.11.2004	19	D. Bernauer
Hemimysis anomala (G.O. Sars, 1907)	364.0	29.11.2004	2	D. Bernauer
	394.3	23.11.2004	1	D. Bernauer
Hypania invalida (Grube, 1860)	355.8	25.07.2003	11	D. Bernauer

	358.5	30.04.2004	3	D. Bernauer
	358.9	29.11.2004	1	D. Bernauer
	359.0	23.04.2003	3	D. Bernauer
	359.0	25.07.2003	32	D. Bernauer
	359.0	26.11.2003	4	D. Bernauer
	359.5	25.07.2003	21	D. Bernauer
	359.6	22.04.2003	165	D. Bernauer
	359.9	22.04.2003	11	D. Bernauer
	362.6	22.04.2003	61	D. Bernauer
	364.0	29.11.2004	34	D. Bernauer
	364.9	25.07.2003	18	D. Bernauer
	364.9	29.11.2004	97	D. Bernauer
	365.3	26.11.2003	24	D. Bernauer
	365.9	22.04.2003	116	D. Bernauer
	366.4	22.04.2003	2	D. Bernauer
	370.1	30.04.2004	5	D. Bernauer
	375.7	23.04.2003	6	D. Bernauer
	375.7	24.07.2003	15	D. Bernauer
	376.0	23.04.2003	2	D. Bernauer
	376.0	24.07.2003	11	D. Bernauer
	376.0	30.04.2004	6	D. Bernauer
	376.4	25.11.2003	10	D. Bernauer
	376.5	23.04.2003	13	D. Bernauer
	376.5	24.07.2003	117	D. Bernauer
	380.8	25.11.2004	4	D. Bernauer
	385.5	29.04.2004	17	D. Bernauer
	390.0	13.08.2004	85	D. Bernauer
	391.3	23.11.2004	9	D. Bernauer
	393.5	23.04.2003	21	D. Bernauer
	393.5	24.07.2003	63	D. Bernauer
	394.3	13.08.2004	19	D. Bernauer
	399.5	25.11.2003	107	D. Bernauer
	399.5	29.04.2004	5	D. Bernauer
Jaera istri (Veuille, 1979)	354.7	29.11.2004	2750	D. Bernauer
	355.8	25.07.2003	60	D. Bernauer
	358.5	30.04.2004	34	D. Bernauer
	358.9	29.11.2004	930	D. Bernauer
	359.0	23.04.2003	75	D. Bernauer
	359.0	25.07.2003	52	D. Bernauer
	359.0	26.11.2003	1230	D. Bernauer
	359.6	22.04.2003	630	D. Bernauer
	359.6	25.07.2003	72	D. Bernauer
	359.6	29.11.2004	155	D. Bernauer
	359.9	22.04.2003	74	D. Bernauer
	360.3	22.04.2003	10	D. Bernauer
	362.6	30.04.2004	178	D. Bernauer
	363.5	23.04.2003	1020	D. Bernauer
	364.0	23.04.2003	52	D. Bernauer

	364.0	29.11.2004	560	D. Bernauer
	364.9	30.04.2004	13	D. Bernauer
	364.9	29.11.2004	86	D. Bernauer
	365.3	26.11.2003	255	D. Bernauer
	365.9	22.04.2003	15	D. Bernauer
	366.4	22.04.2003	11	D. Bernauer
	368.5	26.11.2003	12	D. Bernauer
	370.1	25.07.2003	215	D. Bernauer
	374.0	25.07.2003	275	D. Bernauer
	374.0	30.04.2004	4600	D. Bernauer
	375.7	23.04.2003	113	D. Bernauer
	376.0	24.07.2003	12	D. Bernauer
	376.0	25.11.2004	8	D. Bernauer
	376.4	23.04.2003	35	D. Bernauer
	376.4	24.07.2003	24	D. Bernauer
	376.5	23.04.2003	142	D. Bernauer
	376.5	24.07.2003	74	D. Bernauer
	380.8	25.11.2004	2100	D. Bernauer
	385.0	24.07.2003	17	D. Bernauer
	385.5	29.04.2004	425	D. Bernauer
	390.0	13.08.2004	390	D. Bernauer
	391.3	23.11.2004	12 000	D. Bernauer
	392.5	23.11.2004	780	D. Bernauer
	393.5	23.04.2003	136	D. Bernauer
	393.5	24.07.2003	240	D. Bernauer
	394.3	13.08.2004	12	D. Bernauer
	394.3	23.11.2004	345	D. Bernauer
	398.9	29.11.2004	21	D. Bernauer
	399.3	23.11.2004	157	D. Bernauer
	399.5	29.04.2004	17 000	D. Bernauer
Limnomysis benedeni (Czerniavsky, 1882)	358.5	30.04.2004	2	D. Bernauer
	364.9	25.07.2003	37	D. Bernauer
	364.9	29.11.2004	2	D. Bernauer
	375.7	23.04.2003	29	D. Bernauer
	375.7	24.07.2003	7	D. Bernauer
	376.0	30.04.2004	62	D. Bernauer
	380.8	25.11.2004	24	D. Bernauer
	393.5	24.07.2003	2	D. Bernauer
	393.5	25.11.2003	54	D. Bernauer
Lithoglyphus naticoides (C. Pfeiffer, 1828)	359.0	26.11.2003	9	D. Bernauer
	359.5	25.11.2003	21	D. Bernauer
	359.5	29.11.2004	30	D. Bernauer
	364.9	22.04.2003	53	D. Bernauer
	365.3	26.11.2003	1	D. Bernauer
	375.7	24.07.2003	3	D. Bernauer
Menetus dilatatus (Gould, 1841)	359.0	26.11.2003	1	D. Bernauer

	359.5	29.11.2004	8	D. Bernauer
Orchestia cavimana (Heller, 1865)	364.9	25.07.2003	12	D. Bernauer
	364.9	29.11.2004	2	D. Bernauer
	399.5	29.04.2004	69	D. Bernauer
Orconectes immunis (Hagen, 1870)	376.4	21.07.2005	2	D. Bernauer
Orconectes limosus (Rafinesque, 1817)	376.0	24.07.2003	1	D. Bernauer
	376.4	24.07.2003	1	D. Bernauer
	364.0	29.11.2004	1	D. Bernauer
Pectinatella magnifica (Leidy, 1851)	376.0	30.04.2004	2	D. Bernauer
Physella acuta (Draparnaud, 1805)	359.6	25.07.2003	370	D. Bernauer
	370.1	25.07.2003	6	D. Bernauer
	375.7	23.04.2003	3	D. Bernauer
	375.7	24.07.2003	7	D. Bernauer
	376.0	24.07.2003	8	D. Bernauer
	376.0	30.04.2004	14	D. Bernauer
	376.4	24.07.2003	6	D. Bernauer
	380.8	25.11.2004	8	D. Bernauer
	394.3	23.11.2004	10	D. Bernauer
	399.5	29.04.2004	2	D. Bernauer
Physella heterostropha (Say, 1817)	367.4	25.07.2003	4	D. Bernauer
Procambarus clarkii (Girard, 1852)	351.9	26.08.2003	2	D. Bernauer
Potamopyrgus antipodarum (Gray, 1843)	355.8	25.07.2003	123	D. Bernauer
	359.0	25.07.2003	146	D. Bernauer
	358.5	30.04.2004	4	D. Bernauer
	359.0	13.08.2004	2	D. Bernauer
	359.5	29.11.2004	57	D. Bernauer
	359.6	25.07.2003	231	D. Bernauer
	359.9	22.04.2003	22	D. Bernauer
	360.3	29.11.2004	2	D. Bernauer
	364.0	23.04.2003	34	D. Bernauer
	364.9	25.07.2003	47	D. Bernauer
	364.9	29.11.2004	12	D. Bernauer
	365.3	26.11.2003	35	D. Bernauer
	367.4	25.07.2003	9	D. Bernauer
	368.5	26.11.2003	6	D. Bernauer
	370.1	25.07.2003	7	D. Bernauer
	375.7	24.07.2003	126	D. Bernauer
	376.0	24.07.2003	8	D. Bernauer
	376.0	25.11.2004	3	D. Bernauer
	376.4	24.07.2003	7	D. Bernauer
	376.5	24.07.2003	34	D. Bernauer

	380.8	25.11.2004	6	D. Bernauer
	391.3	23.11.2004	51	D. Bernauer
	392.5	23.11.2004	5	D. Bernauer
	393.5	24.07.2003	63	D. Bernauer
	394.3	23.11.2004	245	D. Bernauer
	399.5	25.11.2003	17	D. Bernauer
Proasellus coxalis (Herbst, 1956)	359.3	30.07.2003	1	D. Bernauer
Viviparus viviparus (Linnaeus, 1758)	362.6	22.04.2003	2	D. Bernauer
	364.9	30.04.2004	3	D. Bernauer
	376.4	23.04.2003	3	D. Bernauer
	380.8	25.11.2004	5	D. Bernauer
	399.5	29.04.2004	2	D. Bernauer

*Full reference to the data: Bernauer D and Jansen W (2006) Recent invasions of alien macroinvertebrates and loss of native species in the upper Rhine River, Germany, Aquatic Invasions 1(2): 55-71
**For geographic coordinates of the sampling location see Annex 1