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**Ecological impact of crustacean invaders: General
considerations and examples from the Rhine River**

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ABSTRACT

The paper reviews the impact of and success factors for crustacean invaders in aquatic systems. As an example, recent invasions of crustaceans in the Rhine River are considered in more detail. In this river, 19 crustacean invaders have been recorded since 1800, with the rate of invasion increasing in recent years. Two species (rule of ten) appear to be most successful: the amphipods *Gammarus tigrinus* and *Corophium curvispinum*. Their success is not due to one factor but to a combination of behavioural, physiological and environmental factors. The outcome of interspecies competition may also be the result of this combination of factors. *G. tigrinus* has been found to be very resistant to invasions by other gammarids, but *Dikerogammarus villosus* may be able to compete with it successfully under present day conditions. When in very high densities, *C. curvispinum* is able to change its habitat conditions, which appears to depend on water flow, chlorophyll-*a* concentrations and water quality. At these high densities, it accumulates so much mud on the stones that the macroinvertebrate community changes to a mud community with a reduced range of species compared to the previous situation. *Dreissena polymorpha* is out-competed under such circumstances, a case of spatial competition by 'swamping'. Both successful amphipods exert extensive influence on the food chain, not only horizontally (competition, swamping), but also vertically, with predators switching diets at each successful invasion.

1 INTRODUCTION

Invasion by exotic species is considered to be one of the major threats to biodiversity worldwide, with preponderance on plants and vertebrates. Two aquatic macroinvertebrates currently receiving much attention with respect to invasions are the predatory cladoceran *Bythotrephes cederstroemi* and the Zebra mussel *Dreissena polymorpha*, both invading the Great Lakes in the USA (Morton 1997). Historically, many unintentional and intentional introductions or immigrations of such aquatic organisms have been reported in the literature. Most introductions are not very successful, in the sense that those species are caught only incidentally, are restricted to certain habitats, often occupying under-utilized niches like cooling water discharge areas, or showing populations remaining small with negligible effect on the ecosystem. Sometimes, however, such species can threaten endangered or protected indigenous species, e.g. by hybridization, predation or competition. Many invasions, however, are reflections of other changes rather than being agents of change themselves and in such cases, biological invasions can be regarded as indicators of environmental change (Vitousek et al. 1996). Biological invasions can also lead to interactions between species that often have never met before and to replacement of autochthonous species by exotic relatives (Conlan 1994). An explosive and catastrophic growth in the population size of invaders can cause drastic changes in an ecosystem as a whole due to depressed local populations, individual species extinction and influence on vertical and horizontal food-chain processes, even leading to a restructuring of the ecosystem. Even then, in most cases, there is a lack of evidence that such an invasion has a significant ecological impact. This is due to the unpredictable nature of invasions, which means that pre-invasion data are usually not available. The speed with which changes can occur is such that changes immediately after the start of the invasion are missed. The impact of a mass invader is usually large at its population peak, after which the population fluctuates and other factors influencing the communities may mask the effect of the invasion.

Mass invasions attract special attention when they cause economic problems, while concern is also aroused by related problems of ecological changes, possible genetic influences on native species and the introduction into native populations of non-endemic pathogens; even human health may be endangered (Sinderman 1992). Economic problems caused by crustaceans are mostly related to professional and recreational fishery (crayfish, Chinese mitten crab (*Eriocheir sinensis*), Spiny water flea (*Bythotrephes*), aquaculture (crabs), damage to crops, especially rice, by crayfish, damage to ditch walls, stream banks and shorelines (burrowing crayfish, the isopod *Sphaeroma*, Chinese mitten crab) and biofouling (barnacles, woodboring isopods). The Chinese mitten crab is also a second intermediate host to the Oriental liver fluke (*Paragonimus westermanii*); eating raw or inadequately cooked infected crabs can infect the human host. Some snail species are the first intermediate hosts; if these species are not present the cycle can not be completed (Cohen & Carlton 1995).

Among the invertebrates, crustacean species are often important and successful invaders; their success is only rivaled by some mollusk species (Morton 1997). Kinzelbach (1995) mentions 20 crustacean species (four of them classified as successful to extremely successful) as exotic invaders in Central and Western European inland waters, as well as 15 mollusk species (seven of them successful to extremely successful) and 8 species belonging to other groups of macroinvertebrates. Glassner-Shwayder (1996) mentions five crustaceans as belonging to the most important invaders with respect to ecological and economic impact in the United States. For British marine waters, Clare Eno et al. (1997) recorded 30 exotic macroinvertebrate species, of which 9 were Mollusca, 8 were Annelida and 7 were Crustacea.

Cohen & Carlton (1995) compared the numbers of introduced marine, estuarine and freshwater species in four regional studies and found Crustacea always to rank number one or two in the list of introduced macroinvertebrate species. In freshwater areas (Great Lakes, Hudson River), mollusk species outnumber crustacean species, while in estuarine and marine environments (Baltic and Swedish coast, San Francisco Bay) crustacean species outnumber mollusks.

2 SUCCESS FACTORS

Exotic crustacean invasions occur only when natural barriers to dispersal are circumvented due to human activities. Human impact can lift barriers for dispersal in several ways:

- By the construction of canals, rivers and lakes, linking large catchment areas,

- By the construction of a web of smaller waters like ditches and ponds which can facilitate further local dispersal,
- By the construction of harbors at river mouths and the discharge of ballast water by ships, allowing the introduction of estuarine and other brackish water tolerant species,
- By the increase in transcontinental as well as local shipping, especially over the last fifty years, that has increased the number of immigrant species (Cohen & Carlton 1998),
- By intentional introduction of species, for example as fish food or for aquaculture purposes,
- Through escapes from aquaculture, aquaria, garden ponds etc., and
- By trade and transport, which may facilitate the dispersal of species, either unintentionally, for example the non-target species transported with plants and animals transplanted for aquaculture ('hitchhikers'), or intentionally, for example, species collected and discarded afterwards.

3 WHAT DETERMINES SUCCESS?

In spite of increased opportunities for the immigration of exotic species, not all are successful. To explain this phenomenon, the rule of ten was formulated (Williamson 1996). This states that only ten percent of the established immigrant species can develop populations dense enough to turn them into pests. Species that were successful during a previous invasion on one continent have also proved successful as they entered new areas on another continent. This means that such species become cosmopolitans, making ecosystems all over the world more and more similar with respect to species composition.

Successful invasions by new species usually proceed via a number of stages. The initial introduction must occur across a natural barrier. Enormous spatial leaps may be made, e.g. from one continent to another. Subsequently, the invasive species must be able to settle or adapt to the habitat in a new area that is conducive to its survival. As a next stage, it must be able to reproduce and complete its life cycle. The species will then spread over the new range successfully, usually by gradual local dispersal but also by jumps aided by transport means. It will show exponential population growth, to densities sometimes higher than ever recorded, followed by somewhat lower steady-state fluctuations.

Attempts have been made to define the possible factors likely to be important for successful invasions. These include:

- Invader properties, adaptations, genetic characteristics, mode of reproduction, growth rate and dispersive capability,
- Competition, predation, diseases and parasites, and
- Climate match, habitat modification, vacant niche and ancestral habitat.
- With respect to invader properties, the qualities of successful crustacean invaders are generally in accordance with those of so-called opportunistic species, often also termed r-strategists. Morton (1997) summed up the qualities for mollusk invaders. In a similar way, we can list the qualities for crustacean invaders:
 - Short life span and generation time,
 - Rapid growth with early sexual maturity,
 - High fecundity,
 - Female able to colonize alone,
 - Larger than most relatives,
 - Euryoecious (the ability to colonize a wide range of habitat types),
 - Eurytopic (a wide range of physiological tolerances),
 - Wide genetic variability and phylogenetic plasticity,
 - Gregarious behaviour,
 - Suspension feeding, omnivorous,
 - An ability to repopulate defaunated habitats, following population crashes caused by extreme disturbances,
 - Some form of association with human activities.

Success by exotic invaders can also be explained by a lack of native competitors, predators, diseases and/or parasites, allowing uncontrolled population expansion. Lack of predators and parasites can make the performance of crustacean invaders much better than that of their native conspecifics, as has been

found for the European green crab (*Carcinus maenas*) on the east coast of the USA (Torchin et al. 1998). On the other hand, exotic invaders may import diseases to which they are more tolerant than their indigenous relatives. An example is the introduction into Europe of a fungus called crayfish pest (*Aphanomyces astaci*) via the American crayfish, *Orconectes limosus*. The indigenous crayfish *Astacus astacus* turned out to be very susceptible to this pest.

Furthermore, immigrant species appear to be successful especially in regions with a climate similar to where they originate. Range extension can also be aided by human modification of habitats, which may mean that new species are preadapted due to the resulting similarity to their ancestral habitat and so colonize very quickly, while indigenous species simultaneously are weakened by the modifications. Sometimes a new niche is exploited because no equivalent indigenous species are present. Pollution calamities in rivers, for example, can create open space for new colonizers, giving newcomers a great opportunity to colonize. Persistent pollution can also create such empty niches.

Rivers provide interesting case studies with respect to invasions of exotic invaders because they are migration channels that have been modified in several ways. Exotic invaders can intrude in rivers from various sources: from estuaries or harbors in the upstream direction, or from one river catchment to another in the downstream direction. This process of internationalization of the actors in the food web is occurring in rivers and lakes all over the world, often involving the same or related invading species.

4 THE RHINE: A MODIFIED RIVER SYSTEM

The Rhine is a regulated ecosystem, having long been subject to anthropogenic influences on its physical, chemical and biotic characteristics (Van der Velde et al. 1991, Admiraal et al. 1993). The physical variety of the Rhine has been greatly reduced by changes to the river's geomorphology and hydrology. The river, especially the Lower Rhine, is now extremely normalized with high current velocities causing very low connectivity with its floodplain waters. The main river bed has been fixed by stone groynes, and the banks of the various branches have also often been protected against erosion by stones. Water quality has been degraded over the last century; the Rhine is highly eutrophic, due to nutrient-rich discharges from agricultural, municipal and other sources in the entire drainage area, leading to high phytoplankton productivity in the Lower Rhine (De Ruyter van Steveninck et al. 1992). Temperature, salinity and pollutant concentrations have also increased (Den Hartog et al. 1992). Recent improvements in water quality, such as higher oxygen levels and reduced concentrations of ammonium, heavy metals (Table 1) and cholinesterase inhibitors, have led to the establishment of more and more exotic invaders, which now dominate the Rhine, having replaced indigenous species (Kureck 1992, Bij de Vaate & Greijdanus-Klaas 1993, Van den Brink et al. 1996).

Furthermore, the estuary of the rivers Rhine and Meuse in the Netherlands has been closed by dams provided with sluice gates that caused the disappearance of the former brackish water gradient (Smit et al. 1997). The disappearance of estuarine conditions caused large changes in the communities, such as the amphipod fauna (Platvoet & Pinkster 1995). The former estuary has filled up with Rhine water, and only two amphipod species were able to profit from the new situation: *Gammarus tigrinus* and *Corophium curvispinum*, both exotic species.

Shipping traffic on the Rhine is very intensive; it is a major transport route from the harbors of Rotterdam and Amsterdam to Germany, France and Switzerland. Shipping provides great opportunities for the transport for immigrant estuarine species from the harbors upstream. In the interest of shipping, the Rhine has also been connected upstream to eastern rivers (Ems, Weser, Oder, Wista) by canals like the Mittelland Canal. However, one of the most important connections is the Main-Danube Canal, a canal completed and officially opened in September 1992, which links the Rhine catchment area via the Main tributary with the Danube River (Tittizer 1996a) (Fig. 1). This has created a migration route from the Black Sea to the North Sea, allowing Ponto-Caspian species to migrate westwards, while species from the Rhine can invade the Danube, such as the freshwater shrimp *Atyaephyra desmaresti* (Tittizer 1996b, Moog et al. 1999, Wittmann et al. 1999). The water transfer is from the Danube to the Main, which is towards the Rhine, but vessels can also transport exotic invaders in the opposite direction.

Sometimes a pollution calamity can free a niche, which may be of advantage for new colonizers. In the Rhine, a chemical spill known as the Sandoz accident occurred in November 1986 (Heil 1990). From Basel downstream, a stretch of 400 km was virtually cleared of macroinvertebrates (Güttinger & Stumm

1990). Measures have subsequently been taken to improve the water quality and to provide ecological rehabilitation (IRC 1987, 1992). This gradual improvement of the water quality has led to a greater biodiversity in the river.

Table 1. Water quality data (annual mean values) for the Rhine at Lobith (Rijkswaterstaat, RIWA).

	1987			1988			1989		
	mean	min.	max.	mean	min.	max.	mean	min.	max.
<i>General</i>									
Discharge (m ³ /sec)	2860	1370	7640	2820	1180	10270	1820	855	4530
Water temperature (°C)	12.3	0.8	22.1	13.7	5.9	23.1	14.1	5.7	23.8
Dissolved oxygen (mg/l)	9.3	6.2	13.0	9.3	6.2	12.3	9.2	7.1	11.4
Oxygen saturation (%)	85	70	126	88	50	111	89	68	126
pH	7.7	7.3	8.5	7.7	7.5	8.0	7.7	7.4	8.5
Suspended matter (mg/l)	40	19	130	45	21	112	34	23	57
Chlorophyll-a (µg/l)	12	BDL	63	22	BDL	92	30	BDL	150
<i>Nutrients</i>									
Ammonium (mg/l N)	0.56	0.07	2.33	0.34	BDL	0.76	0.34	0.02	1.11
Total nitrogen (mg/l N)	1.5	0.8	3.3	1.4	1.0	1.8	1.4	1.0	2.4
Nitrate (mg/l N)	4.0	2.7	5.1	3.7	2.6	4.9	4.5	3.1	5.9
Orthophosphate (mg/l P)	0.19	0.11	0.35	0.15	0.05	0.26	0.13	0.02	0.21
Total phosphate (mg/l P)	0.38	0.26	0.71	0.34	0.25	0.46	0.34	0.24	0.43
<i>Inorganic substances</i>									
Conductivity (20°C, mS/m)	NA			80	48	120	89	54	135
Chloride (mg/l)	140	50	212	150	67	214	182	95	321
Sulphate (mg/l)	66	51	84	63	47	89	NA		
Sodium (mg/l)	81	51	114	79	39	118	98	52	178
Potassium (mg/l)	5.7	3.6	7.5	6.0	4.1	7.8	7.0	5.3	10.7
Calcium (mg/l)	76	61	95	81	45	106	84	69	110
Magnesium (mg/l)	11	3.8	13	11	8.3	14	12	9.7	14
Total hardness (mmol/l)	NA			NA			NA		
<i>Heavy metals</i>									
Iron (mg/l)	1.41	0.72	4.65	1.36	0.79	4.13	1.07	0.77	2.10
Cadmium (µg/l)	0.10	0.04	0.44	0.10	0.04	0.38	0.11	0.05	0.27
Copper (µg/l)	5.3	3.4	10.9	5.1	0.7	10.1	6.0	4.0	8.3
Mercury (µg/l)	0.05	BDL	0.29	0.05	BDL	0.18	0.05	0.02	0.16
Lead (µg/l)	4.0	1.8	10.8	3.4	0.6	6.8	4.9	2.2	8.2
Nickel (µg/l)	3.9	1.7	8.2	3.7	2.2	5.9	4.6	2.5	8.0
Selenium (µg/l)	NA			NA			NA		
Zinc (µg/l)	34	4	73	34	13	57	31	19	46

NA = data not available, BDL = below detectable level.

5 CRUSTACEAN INVADERS IN THE RHINE

Remaining pollution levels and habitat changes have in recent years led to rising numbers of crustacean immigrants in the Rhine (Van den Brink et al. 1990). Major potential causes include the altered ionic composition of the river water as a result of mining activities, especially discharge from French potassium mines; thermal pollution canceling out the effects of severe winters; and the fact that crustaceans show greater tolerance to all sorts of pollution than insects and, to a lesser degree, mollusks, as has often been demonstrated for originally estuarine and brackish water species.

Table 1. Continued.

	1990			1991			1992		
	mean	min.	max.	mean	min.	max.	mean	min.	max.
<i>General</i>									
Discharge (m ³ /sec)	1860	900	7030	1750	790	6710	2010	870	4920
Water temperature (°C)	14.3	2.7	23.0	13.9	3.4	23.9	13.7	5.3	23.8
Dissolved oxygen (mg/l)	9.8	7.5	11.6	9.4	6.7	12.7	9.6	6.9	11.7
Oxygen saturation (%)	94	70	118	91	73	122	89	79	102
pH	7.7	7.5	8.2	7.8	7.5	8.4	7.6	7.3	7.8
Suspended matter (mg/l)	34	BDL	130	32	10	53	29	19	60
Chlorophyll-a (µg/l)	23	BDL	105	27	BDL	97	13	BDL	52
<i>Nutrients</i>									
Ammonium (mg/l N)	0.39	0.04	1.16	0.42	0.07	1.18	0.30	0.09	1.11
Total nitrogen (mg/l N)	1.3	0.7	2.1	1.5	0.1	2.1	1.2	0.6	2.2
Nitrate (mg/l N)	4.1	2.6	6.1	3.8	2.2	5.0	3.9	2.6	5.3
Orthophosphate (mg/l P)	0.11	BDL	0.20	0.08	0.02	0.17	0.09	0.02	0.17
Total phosphate (mg/l P)	0.30	0.24	0.43	0.27	0.18	0.46	0.24	0.17	0.38
<i>Inorganic substances</i>									
Conductivity (20°C, mS/m)	89	50	130	90	48	125	82	54	115
Chloride (mg/l)	187	85	266	199	89	322	163	74	266
Sulphate (mg/l)	NA			NA			NA		
Sodium (mg/l)	99	43	154	105	41	164	87	42	139
Potassium (mg/l)	7.0	4.6	9.9	7.1	4.3	9.6	6.4	4.4	9.0
Calcium (mg/l)	88	66	98	89	65	100	80	58	100
Magnesium (mg/l)	11	8.4	13	12	8.3	14	10	9.0	13
Total hardness (mmol/l)	NA			NA			2.4	1.8	3.1
<i>Heavy metals</i>									
Iron (mg/l)	1.13	0.58	2.70	0.99	0.57	1.85	0.96	0.44	1.73
Cadmium (µg/l)	0.10	0.05	0.21	0.10	BDL	0.24	0.06	0.04	0.09
Copper (µg/l)	5.7	0.7	11.0	6.5	4.5	8.7	5.8	4.3	9.1
Mercury (µg/l)	0.04	0.02	0.11	0.05	BDL	0.14	0.05	0.02	0.09
Lead (µg/l)	5.1	2.0	12.7	4.6	BDL	6.7	4.0	2.6	6.1
Nickel (µg/l)	3.8	1.9	6.2	4.6	3.3	6.4	4.0	3.0	7.4
Selenium (µg/l)	NA			< 2.0	< 2.0	< 2.0	< 2.0	< 2.0	< 2.0
Zinc (µg/l)	46	14	184	30	6	98	23	15	38

NA = data not available, BDL = below detectable level.

In the near future, many species can be expected to migrate to the Rhine via the Main-Danube Canal, especially those Ponto-Caspian species which are already observed in the Upper Danube, like the amphipods *Obesogammarus obesus*, *Echinogammarus trichiatus* and *Corophium sowinskyi* (Jazdzewski & Kónopacka 1993, Weinzierl et al. 1996, 1997). This route to the Rhine has already been successfully traversed by some amphipod species such as *Dikerogammarus haemobaphes* and *D. villosus*, as well as the isopod *Jaera istri* and the mysid *Limnomysis benedeni* (Schleuter et al. 1994, Bij de Vaate & Klink 1995, Schleuter & Schleuter 1995, Tittizer 1995, Reinhold & Tittizer 1998).

The following exotic crustaceans, grouped by origin, have been found in the Rhine.

Table 1. Continued.

	1993			1994			1995		
	mean	min.	max.	mean	min.	max.	mean	min.	max.
<i>General</i>									
Discharge (m ³ /sec)	2010	1200	10940	2530	1100	8100	2790	1080	11890
Water temperature (°C)	13.8	6.0	22.8	15.2	4.7	26.0	13.4	5.3	24.4
Dissolved oxygen (mg/l)	10.0	8.2	11.4	9.5	6.3	11.9	10.0	8.1	11.9
Oxygen saturation (%)	93	77	149	97	75	145	98	86	120
pH	7.8	7.6	7.9	7.7	7.3	8.6	7.7	7.5	7.9
Suspended matter (mg/l)	33	18	130	31	5	98	35	14	140
Chlorophyll-a (µg/l)	19	BDL	135	6.8	BDL	41	8.0	BDL	57
<i>Nutrients</i>									
Ammonium (mg/l N)	0.25	0.09	0.68	0.17	0.02	0.51	0.15	BDL	0.56
Total nitrogen (mg/l N)	1.2	0.3	2.7	1.1	0.4	4.9	0.9	0.2	2.5
Nitrate (mg/l N)	3.7	2.4	5.2	3.4	2.4	4.3	3.3	2.2	4.5
Orthophosphate (mg/l P)	0.08	BDL	0.12	0.08	BDL	0.14	0.08	BDL	0.17
Total phosphate (mg/l P)	0.22	0.15	0.58	0.21	0.10	0.44	0.20	0.10	0.46
<i>Inorganic substances</i>									
Conductivity (20°C, mS/m)	80	58	100	74	47	90	71	38	99
Chloride (mg/l)	144	85	194	120	64	170	116	49	190
Sulphate (mg/l)	65	45	93	63	36	80	59	42	83
Sodium (mg/l)	81	47	106	70	33	90	67	28	100
Potassium (mg/l)	6.0	4.3	7.5	5.4	3.9	6.7	5.4	3.9	7.2
Calcium (mg/l)	80	60	97	75	59	91	76	51	95
Magnesium (mg/l)	11	8.8	14	11	8.5	18	11	7.3	15
Total hardness (mmol/l)	2.5	1.9	3.0	2.3	1.8	2.9	2.3	1.6	2.9
<i>Heavy metals</i>									
Iron (mg/l)	1.05	0.55	4.70	1.10	0.56	2.95	1.33	0.60	6.10
Cadmium (µg/l)	0.05	BDL	0.11	0.07	BDL	0.27	0.07	0.04	0.23
Copper (µg/l)	5.2	3.6	8.8	4.9	2.5	8.2	4.6	3.2	10.2
Mercury (µg/l)	0.03	0.02	0.08	0.02	BDL	0.06	0.02	BDL	0.09
Lead (µg/l)	4.6	2.3	17.8	4.3	1.7	9.6	3.7	0.9	13.5
Nickel (µg/l)	3.8	2.3	10.0	3.8	1.6	8.7	2.9	1.7	8.0
Selenium (µg/l)	< 2	< 2.0	< 2.0	BDL	BDL	2.0	BDL	BDL	BDL
Zinc (µg/l)	23	10	38	25	5	105	21	10	58

NA = data not available, BDL = below detectable level.

5.1 Northern-Europe

5.1.1 *Bythotrephes longimanus* (Cladocera)

This species was recorded for the first time in 1987 in the untreated water storage reservoirs of the drinking water companies de 'Brabantse Biesbosch' in the Netherlands. Since then it has been found in numbers reaching 10,000 per m³. From 1988, it has been found in Lake Volkerak-Zoommeer. Peak abundances of *Bythotrephes longimanus* and *Leptodora kindti*, which is a native predatory cladoceran, seem to lead to drastic decreases in the abundance of daphnids, especially in July. Copepod densities were also slightly lower after the invasion. *Leptodora* abundance is not affected by *Bythotrephes*. Perhaps both species are controlled by fish. The impact of *B. longimanus* has not been as profound as that of *B. cederstroemi* in the Great Lakes of the USA.

Table 1. Continued.

	1996			1997		
	mean	min.	max.	mean	min.	max.
<i>General</i>						
Discharge (m ³ /sec)	1760	1010	4360	1910	930	6930
Water temperature (°C)	13.1	2.1	23.2	14.1	1.1	24.5
Dissolved oxygen (mg/l)	10.5	7.1	13.8	10.1	7.0	14.2
Oxygen saturation (%)	98	84	120	99	82	127
pH	7.8	7.4	8.1	7.8	7.6	8.5
Suspended matter (mg/l)	29	3	120	31	1	310
Chlorophyll-a (µg/l)	8.6	BDL	57	9.6	BDL	63
<i>Nutrients</i>						
Ammonium (mg/l N)	0.22	0.03	0.98	0.10	0.01	0.39
Total nitrogen (mg/l N)	0.8	0.1	1.6	0.8	0.1	2.7
Nitrate (mg/l N)	3.6	2.3	4.8	3.2	0.9	4.5
Orthophosphate (mg/l P)	0.10	0.03	0.14	0.10	0.01	0.20
Total phosphate (mg/l P)	0.22	0.13	0.51	0.21	0.11	0.46
<i>Inorganic substances</i>						
Conductivity (20°C, mS/m)	NA			NA		
Chloride (mg/l)	155	71	249	147	58	246
Sulphate (mg/l)	65	43	88	60	45	86
Sodium (mg/l)	85	45	127	80	44	112
Potassium (mg/l)	6.1	4.2	7.6	6.3	4.5	8.0
Calcium (mg/l)	82	69	98	85	69	105
Magnesium (mg/l)	11	8.9	14	12	9.1	13
Total hardness (mmol/l)	2.5	2.1	3.0	2.6	2.1	3.2
<i>Heavy metals</i>						
Iron (mg/l)	1.23	0.51	3.08	1.16	0.80	2.07
Cadmium (µg/l)	0.07	0.01	0.16	0.06	0.01	0.17
Copper (µg/l)	5.2	2.3	7.0	5.0	3.4	8.3
Mercury (µg/l)	0.04	0.01	0.22	0.04	0.02	0.07
Lead (µg/l)	4.5	1.9	10.8	3.9	2.1	8.3
Nickel (µg/l)	3.1	1.6	6.2	3.5	1.6	5.9
Selenium (µg/l)	0.4	BDL	1.1	0.2	BDL	0.4
Zinc (µg/l)	41	2	100	24	10	60

NA = data not available, BDL = below detectable level.

B. longimanus must have reached the Netherlands via long distance dispersal, because the species is present in the catchment area of the Rhine in the Alps (though not that of the Meuse), but also in north-eastern Germany, Poland, Belarus, the Baltic states, Scandinavia (Norway and Sweden), Great Britain, and Ireland. In the Rhine catchment area, *B. longimanus* is known to be present in Lake Constance (Bodensee), which means that specimens drifting in the river could arrive in the Netherlands within 5-10 days. A few specimens have been found in the Dutch part of the Maas River (Meuse). Although it cannot be ruled out that water birds have introduced the species into the basins, it is likely that resting eggs were transported downstream and hatched in standing waters like the storage basins and the slow flowing parts of the river. *Bythotrephes* specimens caught in the river had only one lateral spine on the caudal spine, indicating that they had not yet molted. *B. longimanus* can reproduce parthenogenetically.

Large populations of *B. longimanus* occur in the storage basins and in Lake Volkerak-Zoommeer, both large and deep artificial lakes (5-27 m) containing river water. These man-made lakes house few predatory fish, so that zooplankton is well developed. In spite of their eutrophic character, sedimentation processes make the water clear, which makes it easier for *B. longimanus* to detect its prey. This type of water did not occur in the Netherlands in the past, so *B. longimanus* has made use of a totally new, man-made opportunity to settle (Ketelaars & Van Breemen 1993, Ketelaars et al. 1993, Ketelaars & Gille 1994).

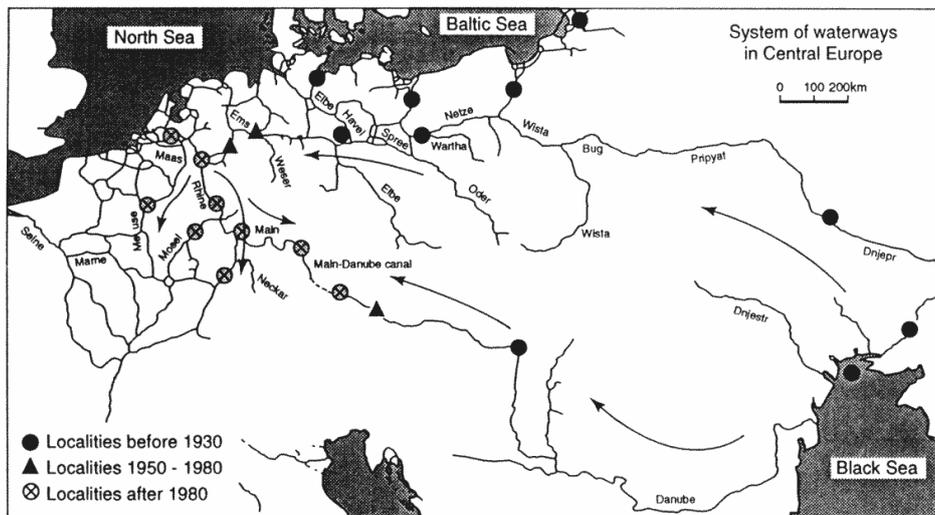


Figure 1. Major rivers systems to the east of the Rhine, with canals linking the rivers and the main dispersal routes of *Corophium curvispinum* (from Tittizer et al. 1994).

5.2 Southern Europe

5.2.1 *Atyaephyra desmaresti* (Decapoda)

This freshwater shrimp originates from the Mediterranean, from where it has spread actively over Europe by using the canals that connect European river basins, including that of the Rhine. The species invaded the Main-Danube Canal in 1994 and the Danube River basin in 1998 (Moog et al. 1999, Wittmann et al. 1999). In the Netherlands, it was first noted in 1915; it is now widespread in the rivers, canals and lakes. In harsh winters, the numbers of records are low, reflecting its southern origin (Van den Brink & Van der Velde 1986b). The species is phytophilous, eurythermous and brackish water tolerant (Tittizer 1996b).

5.2.2 *Echinogammarus berilloni* (Amphipoda)

This amphipod species originates from the Mediterranean. According to Pinkster (1973), it is a typical species of middle courses of streams and rivers. It is an active migrant, which has made use of canals to reach the Rhine. It is found in the Rhine from Dusseldorf to Basel, where it occurs in low densities, and in the Mosel (Moselle), a tributary of the Rhine. It is salt tolerant and eurythermous (Tittizer 1996b).

5.2.3 *Orchestia cavimana* (Amphipoda)

This species from Mediterranean-Ponto-Caspian origin was already recorded in the Rhine (Waal) near Tiel in 1898, from where it spread over the Netherlands, where it is still a common species. Via the Scheldt (1906) in Belgium, it reached the Seine (1913) from where it migrated via the Rhine-Marne Canal to the Mosel and hence to the Upper Rhine (1937). From there, it spread downstream to the Middle and Lower Rhine in 1962-1971 (Kinzelbach 1972). Its mode of dispersal is unknown. The species inhabits the littoral margins of the river and lakes ('spray zone') and flood marks where organic matter accumulates between stones or macrophytes that have washed ashore, etc. Its food consists of organic matter like macrophyte tissue, sponge tissue, diatoms, bluegreen and green algae. Organic water pollution seems to be a factor favoring this species, although it behaves as a terrestrial species and the animals only seek the water to escape from enemies. In fact, it invaded an empty space, where only some insect species can also occur (Kinzelbach 1972). According to Den Hartog (1963), the occurrence of *O. gammarella* may limit *O. cavimana* at the isohaline of 1.8‰ chloride at high tide in the estuaries.

5.2.4 *Proasellus meridianus* and *Proasellus coxalis* (Isopoda)

Both species immigrated from the western Mediterranean and were perhaps introduced by ships in the 20th century. *P. meridianus* was first found in the Lower Rhine in 1948. It spread along the river and inhabits slow flowing waters as well as still waters. Both species are known from the entire Rhine. They feed on detritus and dead plant material. Both species are salt tolerant (Tittizer 1996b).

5.3 Ponto-Caspian

5.3.1 *Corophium curvispinum* (Amphipoda)

This tube-building species has been extending its range to the west since the start of 20th century via the rivers Pripyat and Wista and their interlinking canal systems. In 1987 it was found in the German and Dutch parts of the Rhine (Van den Brink et al. 1989; Scholl 1990a, Tittizer et al. 1990). The Rhine was reached via the Havel-Spree area, Mittelland Canal and Dortmund-Ems Canal (Tittizer 1996b), from where it spread along the whole river and its tributaries (Bobbe 1994). The Main-Danube Canal has been colonized by this species from two directions, viz. from the rivers Rhine (1987) and Main (1988) and from the Upper Danube (1959); it was found in this canal in 1993 (Tittizer 1996b).

Dispersal routes for *C. curvispinum* include the ballast water in ships. Great Britain was probably reached in 1918 via the ballast water in ships trading with ports on the Elbe River in northern Germany (Harris 1991) and via rivers connected. Dispersal modes include ballast water, ships' hulls and drift or active migration (Harris 1991). With respect to dispersal speed, its spread over Europe was similar to that of the zebra mussel (*D. polymorpha*), but at a much slower rate (Fig. 1).

Reproduction occurs via a brood pouch with a maximum clutch of 42 eggs. The breeding season is strongly correlated with high water temperatures. Reproduction begins in March and continues until October (Rajagopal et al. 1999b).

In the Lower Rhine, there are three generations per year (Van den Brink et al. 1993, Rajagopal et al. 1999a). The life span of the animals is less than eight months. Populations may reach densities of hundreds of thousands of individuals occurring on one m² of hard substrate. It is now the dominant macroinvertebrate on stones in the Rhine (Van den Brink et al. 1993, Rajagopal et al. 1999a, b).

The food of this filter feeder consists of phytoplankton and detritus (Van den Brink et al. 1991, 1993). Eutrophication favors high population densities of the species (Waterstraat & Kohn 1989), which requires a constant supply of food and silt particles (Muskó et al. 1998). *C. curvispinum* builds its mud tubes on hard substrates such as stones and wooden piles, as well as on aquatic macrophytes (Crawford 1937, Entz 1949, Muskó 1990, 1992, 1994, Sebestyen 1938, Van den Brink et al. 1991). *C. curvispinum* can also be found in the sediment (juveniles) or swimming in the water at lower densities.

According to Crawford (1937), the species is variable, adaptable and widely distributed and found in salt, brackish and fresh water. Several varieties have been described, including one freshwater adapted variety (var. *devium* Wundsch). The species occurs up to a salinity of 6‰ (Romanova 1975). With respect to salinity, *C. curvispinum* var. *devium* needs ion-rich, hard freshwater with a minimum [Na⁺] of 0.5 mMol L⁻¹ (Harris & Aladin 1997). Taylor & Harris (1986a, b), Harris & Bayliss (1990) and Harris (1991) demonstrated that *C. curvispinum* is leakier to Na⁺ and Cl⁻ and water than freshwater gammarid species. There is considerable physiological variability within populations of *C. curvispinum* from various localities with respect to the retaining and replacing of Na⁺ and Cl⁻. Its adaptation to freshwater by means of a lower permeability than the other varieties must have evolved very recently. At higher salinities, the 'freshwater form' will possibly compete with brackish water *Corophium* species, like *C. lacustre* and *C. multisetosum* (Herbst & Bäche 1993).

C. curvispinum in tubes consume twice the amount of oxygen consumed by specimens outside the tubes (Muskó et al. 1995, 1998, Harris & Muskó 1999). Much oxygen seems to be required to irrigate the tubes. At low oxygen levels, the animals leave the tubes and begin to swim. In order to obtain enough oxygen while in their tubes, they need current or wave action.

Rather high water temperatures seem to be required. Jazdzewski & Konopacka (1990) mentioned the co-existence of *E. ischnus*, *C. curvispinum* and *D. polymorpha* in a heated lake in Poland with a temperature amplitude of 7.0-31.8°C. *C. curvispinum* is absent at heavy organic pollution and low oxygen levels (Jazdzewski 1980, Harris & Muskó 1999).

Parasites are unknown, while predators include birds, fish, crayfish and other predatory macroinvertebrates (Biró 1974, Van den Brink et al. 1993, Marguillier et al. 1998, Kelleher et al. 1998, 1999).

5.3.2 *Dikerogammarus haemobaphes* (Amphipoda)

This gammarid species migrated from the Upper Danube (1976), via the Main-Danube Canal (1993) and the Main (1993) to the Rhine (1994). *D. haemobaphes* is an euryoecious species occurring on stones, macrophytes and filamentous algae in large rivers and lakes (Kititsyna 1980, Muskó 1993, Tittizer 1996b). This species is brackish water tolerant up to 8‰ (Ponomareva 1975) and is able to endure a wide range of temperature variations (6-30°C) (Kititsyna 1980). It normally reproduces from April to October, but does so all the year round in the warm water of the cooling water discharge of an electric power plant (Kititsyna 1980). In Lake Balaton, this species reproduces from May to the end of August on submerged macrophytes (Muskó 1993). Its food consists of various plant material (diatoms, filamentous algae and detritus) (Ponyi 1961, Romanova 1963). Because of its high reproduction capacity, suggestions have been made to cultivate *D. haemobaphes* as fish food (Vorob'eva & Nikonova 1987).

5.3.3 *Dikerogammarus villosus* (Amphipoda)

D. villosus took the same immigration route as *D. haemobaphes*, viz., from the Upper Danube (1992), along the Main-Danube canal (1993) and the Main (1994) to the Rhine (1995). This actively migratory and euryecious species inhabits large rivers and lakes (Tittizer 1996b). It is more salt-tolerant than *D. haemobaphes* (Bij de Vaate & Klink 1995 and literature therein). Since its arrival in the Upper Danube, *D. villosus* has outcompeted *D. haemobaphes*, which was successful and numerous before (Weinzierl et al. 1996). *D. villosus* has an enormous reproductive capacity, as was shown in the lower reaches of the Don River. In a frost-free brook, it appeared to reproduce all the year round (Mordukhai-Boltovskoi 1949). Its food includes both plant and animal food and sometimes it even eats the conspecific newborns and weak adults (Mordukhai-Boltovskoi 1949). In the Lower Rhine, it reaches its highest densities on hard substrates, where it is already an important contributor to dietary biomass offish (Kelleher et al. 1998).

5.3.4 *Echinogammarus ischnus* (Amphipoda)

E. ischnus was first recorded from the Rhine in 1989, reaching densities of 100 ind. m⁻² of hard substrate. The species was already present in northern German canals from 1900. At the end of the 1980s, there were reports from the Rhine-Herne Canal and from the Wesel-Dattel Canal (Scholl 1990b). In 1991, it was found in the Dutch part of the Rhine (Van den Brink et al. 1993). *E. ischnus* migrated to the Main-Danube Canal (1995) via the Upper Danube (1989). The species is salt tolerant and eurythermous (Tittizer 1996b). Present-day densities in the Lower Rhine are below 50 individuals per m² of hard substrate.

5.3.5 *Hemimysis anomala* (Mysidacea)

This euryhaline species was recorded from stony banks of the Neckar River and the Middle Rhine in 1997 (Schleuter et al. 1998). The way the species entered the Rhine is unclear. It may have entered either from the Baltic Sea or from the Danube. It seems possible, however, that it came from the Danube via the Main-Danube Canal (Wittmann et al. 1999). Perhaps it arrived via the ballast water in a ship from the Baltic Sea. In the Netherlands, the species was recently found in a small artificial lake not far from the Noordzeekanaal near Amsterdam (Faasse 1998). Specimens were also found in fish taken from the Lower Rhine in 1997, so it is possible that the species was overlooked for some years because of its habit to hide in and near cavities in stony banks of lakes and rivers and because of its nocturnal activity pattern. Its impact on the river communities is unknown, but in the Biesbosch reservoirs it became very numerous as a voracious predator on zooplankton and also an omnivorous feeder (Ketelaars et al. 1999).

5.3.6 *Limnomysis benedeni* (Mysidacea)

This species could have reached the Rhine via the Danube, where it has spread upstream to reach the Upper Danube in 1994, via the Main-Danube Canal (Wittmann 1995). *Limnomysis* was discovered in

1997 in a side channel of the middle Rhine with some *Myriophyllum spicatum* (Geissen 1997). Recently it was also found in a river-connected sandpit (1997) and a floodplain pond (1998) along the Waal River, as well as in the Lek River (1998). The Waal and Lek are both side branches of the Rhine, and in the Zuiderdiep, which is connected with the Haringvliet, the regulated estuary of the Waal and Meuse (Kelleher et al. 1999b). In 1998, it was discovered in the Main-Danube Canal (Reinhold & Tittizer 1998). Its discovery in the Netherlands preceded that in the Middle Rhine by some months (Kelleher et al. 1999b).

Vessels seem to be the most likely dispersal mode, in view of the widespread localities in the Rhine. In contrast to *H. anomala*, *L. benedeni* is associated to aquatic vegetation and can be considered to be potamophilous, phytophilous and salt tolerant.

5.3.7 *Jaera istri* (Isopoda)

This species inhabits hard substrates in estuaries and rivers in the littoral zone. This isopod came from the Danube and migrated upstream, via the Main-Danube Canal (1993) to the Main (1995), then to the Rhine (1995) and subsequently further downstream (Tittizer 1996b). In 1997, the species was also recorded from the Lower Rhine branches in the Netherlands (Kelleher et al. 1998). Population densities have been increasing on hard substrates. The animals may spread by means of vessels. Its food consists of algae, plant remains and detritus (Tittizer 1996). The species is salt tolerant.

5.4 East Asia

5.4.1 *Eriocheir sinensis* (Decapoda)

The Chinese mitten crab lives most of its life in freshwater but reproduces in the sea. It migrates actively into the river via the estuaries. In the Yangtse-Kiang, it migrates 1300 km upstream. It is dispersed via the ballast water in ships and is widespread in the USA (Cohen & Carlton 1995).

In the Netherlands, it was first recorded in 1929 and spread quickly over the country, even over land, also invading the Rhine-Meuse estuaries. From the estuaries, the animals migrate far upstream into Germany; it has even been recorded north of Basel (Tittizer 1996b). The crabs are omnivorous. Sometimes they develop very dense populations, perhaps competing for food with fish. The species is salt tolerant and eurythermous (Tittizer 1996b).

5.5 North America

5.5.1 *Callinectes sapidus* (Decapoda)

The adult Blue crab is an omnivorous inhabitant of estuaries on the east coast of North America, where it can live in nearly fresh to hyposaline water. Just as the Chinese mitten crab, females migrate to the sea for reproduction, while juvenile animals migrate into the estuaries. The species tolerates a temperature range of 2-35°C, but the animals are only active above 15°C. It seems that this species was introduced in the Netherlands by ballast water in ships in 1932 (Adema 1991). Its present distribution includes the Noordzeekanaal, which is connected with the Rhine via the Amsterdam-Rhine Canal. However, it has not yet been observed in either the Rhine estuaries (mostly blocked by dams) or the river itself.

5.5.2 *Crangonyx pseudogracilis* (Amphipoda)

This amphipod species has inhabited central and southern England and Wales since 1975, from where it spread to the north, and Ireland. In 1979, it was discovered in the north of the Netherlands (Province of Groningen) (Pinkster et al. 1992). *C. pseudogracilis* reproduces mainly in the warm summer months; its reproductive cycle is slower than that of *G. tigrinus* and *G. pulex* (Pinkster & Platvoet 1983). The species is euryoecious inhabiting all types of water ranging from fresh or brackish, clean or polluted. In the Dutch part of the Rhine, the species has been discovered once, in a temporary backwater near Millingen aan de Rijn, where three specimens were collected (Bij de Vaate & Klink 1995). The species is steno-philous (Garland 1981) and thermophilous (Sutcliffe & Carrick 1981).

5.5.3 *Gammarus tigrinus* (Amphipoda)

Sexton first described this species in Britain in 1939, in brackish water and ion-rich polluted water. It was later found to have originated from the USA. This species was introduced into Germany in the Weser and Werra Rivers as fish food, because of its tolerance to salinated and ion-rich polluted water. Specimens from Britain were released in these rivers in 1957 and a mass development began. The species cleans the water of detritus and dead animals, but it is also very rapacious and voracious, attacking wounded or weakened fish (Schmitz 1960).

G. tigrinus was first recorded in the Netherlands in lake IJsselmeer in 1960, where it was also introduced in low numbers by a fisheries institute (Pinkster & Stock 1967). It may also have been released into the IJsselmeer by ballast water in ships from Germany (Nijssen & Stock 1966). From the IJsselmeer it spread quickly over the Netherlands, establishing populations in still as well as flowing water. In 1973, it was recorded from the Haringvliet, the estuary of the Meuse and Rhine (Dieleman & Pinkster 1977). Since 1982/83, it has been found in the Lower Rhine itself (Berndt 1984, Pinkster et al. 1992).

Dispersal takes place via an existing network of canals and rivers by active migration (e.g. Northern Ireland, Germany and The Netherlands) and by human interference (Pinkster et al. 1980) as well as ballast water in ships (Hynes 1955, Jazdzewski 1980). Its dispersal speed has been calculated as up to 40 km per year (Pinkster et al. 1980). Allelic frequencies (PGI, MPI and PGM) have demonstrated that *G. tigrinus* populations from Germany and the Netherlands show considerable genetic differences reflecting different origins (Bulnheim 1985). There has, however, been a second invasion into the Netherlands from Germany, as was proven by electrophoretic tests (Pinkster et al. 1992).

With respect to reproduction, 15-16 generations are theoretically possible during one year (Pinkster 1975). Females attain sexual maturity beyond 4 mm body length, and only 27-29 days are required to reach this maturity at 20°C. Reproduction stops below 5°C (Pinkster et al. 1992). The highest density of *G. tigrinus* ever found was 24,000 ind. m⁻² of bottom in the Frisian lake Tjeukemeer (Chambers 1977). In the Rhine, *G. tigrinus* has been found in densities of thousands per m² of hard substrate. In recent years, populations have declined, probably due to the invasion of *D. villosus*. *G. tigrinus* is omnivorous, feeding on animals, algae, plants and detritus, and functions both as a primary and secondary consumer of the first and second order. *G. tigrinus* tolerates a salinity of 1-16‰ (Dorgelo 1974) and a temperature of up to 30°C (Savage 1982). It prefers well aerated water. Principally a brackish water species, it has successfully invaded freshwater habitats. Furthermore, it is pollution tolerant (Streit & Kuhn 1994).

As regards pathogens, one fungus, *Saprolegnia* sp., affects *G. tigrinus* but not *G. pulex* (Dieleman & Pinkster 1977). Fish are its main predators, and the species is often introduced as a feeding supplement.

5.5.4 *Orconectes limosus* (Decapoda)

O. limosus originates from the eastern United States. In 1890, 100 specimens were released into fish ponds near Berlin (Germany), from where the species spread via the Mietzel River to the Oder, Warthe and Netze Rivers. It was also introduced in France. Until 1940, the western border of its geographical area was the Elbe. In the Netherlands, the species actively migrated via the Meuse from Belgium, as well as from Germany via the Twente Canal (Geelen 1975). Since the first half of the 20th century, it has spread over the whole of Europe (Tittizer 1996b), including the Rhine. It feeds on macroinvertebrates, detritus, algae and macrophytes.

This crayfish species is well adapted to pollution and low oxygen concentrations, and is immune to the crayfish pest that wiped out the indigenous *Astacus astacus*. Although it is also found in lakes, it prefers canals and rivers. It is euryecious and salt tolerant (Tittizer 1996b).

5.5.5 *Rhithropanopeus harrisi* (Decapoda)

This species originates from brackish water and estuaries on the North-American east coast. It was present in The Netherlands in the second half of the 19th century, and was even regarded as an endemic species from the Zuiderzee, being described as a new species in 1874. It must have been introduced via ballast water in ships. It is a common species of brackish water (Adema 1991), migrating into the river from the estuary. It has been recorded several times in the estuary as well as upstream in the Lower Rhine itself, until just across the German border near Rees, although in very low numbers (Den Hartog et al. 1989, Van der Velde et al. 1990, Fontes & Scholl 1994, Bij de Vaate & Klink 1995).

6 IMPACT

Of the 19 crustacean species recorded from the Rhine, two species (10%; rule of ten) can be regarded as particularly successful, in the sense of having established high density populations over long stretches of the river, viz., *G. tigrinus* and *C. curvispinum*. Why have other species been less successful? The reasons for the limited success of an invader may be suboptimal conditions, poor adaptation to present conditions leading to reduced fitness, severe interspecific competition, lack of food, heavy predation or combinations of all of these factors. Most crustacean invaders of the Rhine show brackish to hard water adaptations, are euryecious, tolerant to pollution in general and thermophilous. With respect to feeding habits they are omnivores, deposit or filter feeders. They may also be successful invaders because they possess a brood pouch, which means that one female can establish a population. The brood pouch protects the eggs at an early stage against environmental changes and perhaps also against the influence of pollution. Dick et al. (in press) have shown that *Crangonyx pseudogracilis* females alter their brood care activities in response to dissolved oxygen and temperature fluctuations, and this species is a successful invader of such waters.

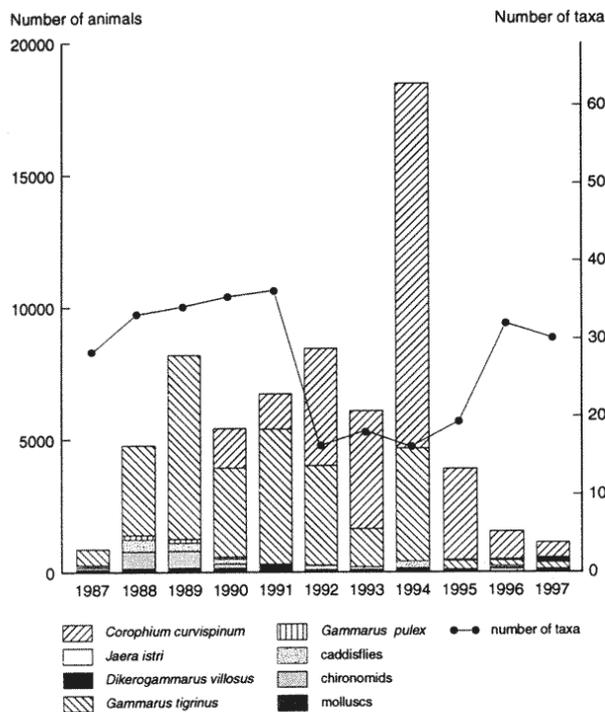


Figure 2. Development of the macroinvertebrate fauna on standardized artificial substrates (for a description of the method see De Pauw et al. 1994, Pashkevich et al. 1996) over the years in the Rhine near Lobith (the Netherlands) starting in 1987 (after the Sandoz accident and the first year that *Corophium curvispinum* was recorded). Numbers of animals from two artificial substrate samplers are averaged; numbers of taxa are total numbers from both samplers. Observations have been carried out in September.

Invasions of gammarids in the Rhine have led to the replacement of one gammarid species by another, viz. *G. pulex* by *G. tigrinus*, probably as a result of competitive displacement and intraguild predation. Pinkster (1975) and Pinkster et al. (1977) recorded the displacement of several native *Gammarus* species by the invasion of *G. tigrinus*. One factor in this process is the enormous reproductive capacity of *G. tigrinus* in oligohaline water as compared to that of *G. zaddachi*, *G. duebeni* and *G. pulex*, as was demonstrated by Pinkster et al. (1977). However, severe and prolonged winters can reduce the populations of *G. tigrinus* (Pinkster et al. 1992). Another factor explaining its success compared to *G. pulex* is a better tolerance of salt pollution, which means a lower energy demand due to ionic regulation and consequently

a better competitive strength at high ionic concentrations (Koop 1997). Dick & Platvoet (1996) found that *G. tigrinus* excluded *G. pulex* from oligohaline water and freshwater with a high conductivity, whereas *G. pulex* excluded *G. tigrinus* in freshwater with a low conductivity. Between these two species there is frequent mutual predation of moulting individuals. In fresh water, *G. pulex* showed significantly higher predation frequencies on *G. tigrinus* than vice versa. In oligohaline water, however, there was no clear difference in predation frequencies between *G. tigrinus* and *G. pulex*. Dick & Platvoet (1996) developed a model for interactions with relevant population parameters, which could identify the complex switches in species dominance with transient periods of co-existence. The intensity of gammarid species interactions thus seems mediated by behavioural, physiological and environmental factors (Dick & Platvoet 1996).

Streit & Kuhn (1994) demonstrated that *G. tigrinus* is much more tolerant to organophosphorus insecticides than *G. pulex* and *G. fossarum*. This means that the latter species could be competitively weakened by pesticides, another factor that could explain the dominance of *G. tigrinus* in the Rhine and the disappearance of *G. pulex*.

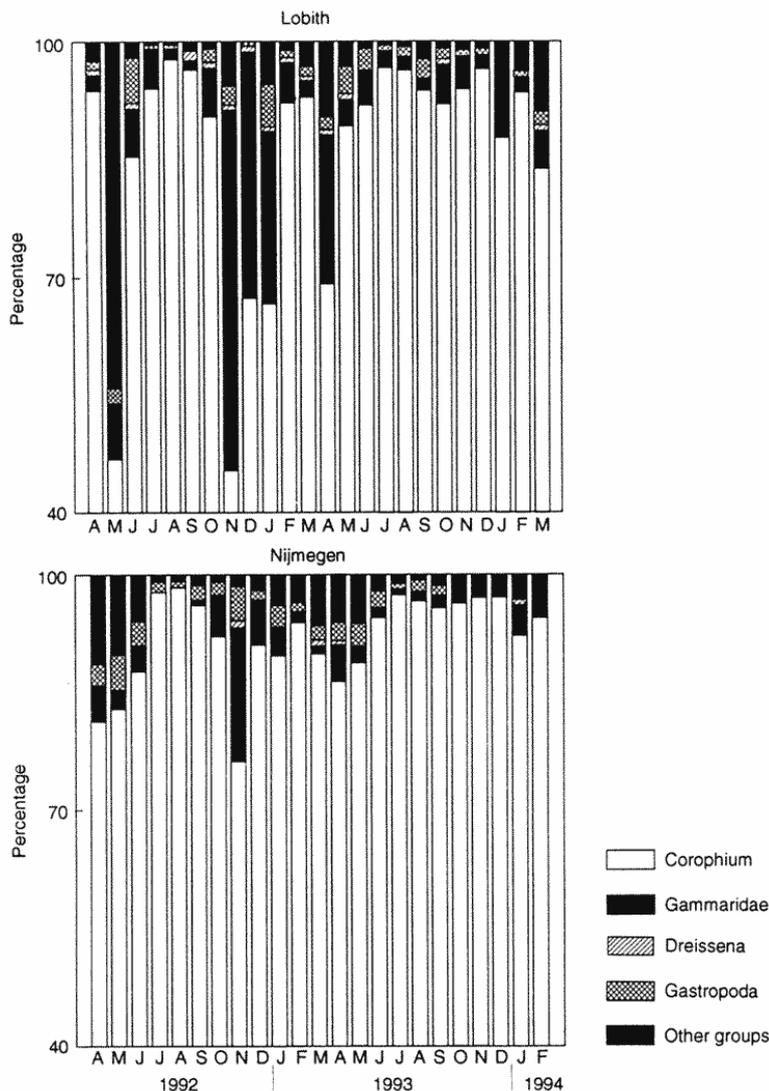


Figure 3. Seasonal variations in population density percentages of various macroinvertebrates from April 1992 to March 1994 on stones ($n = 5$) of groynes in the Lower Rhine at Lobith and Waal at Nijmegen, the Netherlands.

The next gammarid species invading the Rhine was *Echinogammarus ischnus*, which was, however, unable to develop very dense populations. It may be hindered by *C. curvispinum*, which could prevent its success as a stone dweller by covering the stone surfaces in mud and by reducing the supply of the Zebra mussel (*D. polymorpha*). That *E. ischnus* is capable of outcompeting other gammarid species has recently been demonstrated by its invasion of the Great Lakes. In 1995, *E. ischnus* reached the Great Lakes in the US, probably via ballast water (Witt et al. 1997). It outcompeted *G. fasciatus*, that had previously increased in abundance by hiding and feeding in the mussel beds built up after the invasion of the Zebra mussel (*D. polymorpha*) (Dermott et al. 1998 and literature therein). Waterstraat & Kohn (1989) and Kohn & Waterstraat (1990) mentioned that *E. ischnus* is closely associated with *Dreissena* clumps in Lake Kummerow (Germany). It seems that *E. ischnus* dominates in spite of its somewhat lower fecundity and life span than *G. fasciatus*, being more of a specialist on rocky habitats than *G. fasciatus*. In dense submerged vegetation or quiet, turbid water, *E. ischnus* shows low densities and here *G. fasciatus*, well equipped to cling to vegetation, is more numerous; *Cladophora* growing on rocks favours *G. fasciatus* (Dermott 1998, Dermott et al. 1998). This means that successful invasions clearly depend on the properties of the invader, which must have an advantage in some habitats compared to the properties of indigenous species. This example is also a good demonstration of a habitat being conditioned for *E. ischnus* by an earlier Ponto-Caspian invader, the Zebra mussel.

E. ischnus is able to outcompete other gammarid species especially in stony habitats. In addition to the above-mentioned factors, it is possible that *G. tigrinus* and the later invasion of *D. villosus* have prevented its further success in the Rhine or that *D. villosus* outcompeted *G. tigrinus*, which allowed a third subdominant gammarid, in this case *E. ischnus*, to settle in the deeper parts of the river.

All *Gammarus* species can prevent successful invasion by *Crangonyx pseudogracilis*; Dick (1996) found that this species is preyed upon heavily by *G. pulex* as well as *G. tigrinus*, regardless of the molt state of the victims; frequencies of predation upon reproductive females were high, reaching 70%. Until now, this species has not been successful in the Rhine.

The most promising species with respect to recent success is *D. villosus*, which is a much larger amphipod than the other species. It is currently developing very dense populations. *D. villosus* is suspected to be more predatory than the other gammarids. Isotope analysis ($\delta^{15}\text{N}$) has indicated that they are active at the same trophic level as fish species (Marguillier 1998). Dick (1996) mentioned that differences in predatory/survival abilities of gammarid species are influenced by body size, with larger species and sexes preying upon the smaller. So *D. villosus* may have considerable impact on the *G. tigrinus* population (Fig. 2). *D. villosus* may dominate the stone communities and *G. tigrinus* the sandy communities, as *G. tigrinus* is still dominant in the river-connected sandpits in the Rhine (Kelleher et al. 1998). As more gammarid species enter the Rhine system, the outcome of subsequent invasions will be unpredictable in the long term. However, the history of invasions over the last decade has generated data sets that will allow some assessment of their initial impact; such data were not available for the initial colonizers like *C. curvispinum* and *E. ischnus*. The co-existence of various gammarid species in the Rhine is made possible by differences in habitat selection and differential predation and competitive interactions.

By far the most successful invasion is that of the tube-building corophiid *C. curvispinum*. This species shows many of the properties mentioned in Section 3. Recorded for the first time in the Rhine in 1987, it developed very dense populations within a few years (Fig. 2), so that it became the most numerous macroinvertebrate on the stones along the river (Fig. 3). Due to its tube building, it fixes much mud on the stones, altering the stone communities (Fig. 4). Monitoring data on artificial substrates over the years have shown that the macroinvertebrate species richness was reduced at the highest densities of *C. curvispinum* (Fig. 2). According to Kinzelbach (1997), *C. curvispinum* also outcompetes the freshwater isopod *Asellus aquaticus* and several species of chironomid larvae. As a result, the numbers of their predators, like leeches, have decreased. What was clear from the beginning was the strongly negative influence of *C. curvispinum* on another Ponto-Caspian invader, the Zebra mussel (*D. polymorpha*), which was already present in high numbers in the Rhine (Van den Brink et al. 1991, 1993, Van der Velde et al. 1994, 1998).

At other localities, for example, in Lake Balaton, the Zebra mussel and *C. curvispinum* may have arrived about the same time during their expansion from the Ponto-Caspian region (1932 and 1935, respectively). Sebestyén (1938) noted that where *D. polymorpha* was present, *C. curvispinum* was also present, so these species seem to be associated in some way. It is therefore interesting that in the Rhine, *C. curvispinum* 'swamps' *D. polymorpha* and reduces its populations. *C. curvispinum* simply changes the

habitat so that the Zebra mussel disappears. Amounts of mud fixed on the stones are clearly correlated with the densities of *C. curvispinum* (Fig. 5). Sometimes in summer, the mud layer can be 4 cm thick (Paffen et al. 1994). By a thick layer of mud especially in the summer months, when densities of *C. curvispinum* were at a peak, Zebra mussel larvae lack bare stone surfaces to settle, and adult Zebra mussels were smothered to death. Jantz (1996) found that at high densities of *C. curvispinum*, there was a shift in the Zebra mussels' size classes, from high frequency of specimens with a shell length of 5-15 mm to a predominance of specimens smaller than 5 mm, while many overgrown dead specimens were found. The reduction of the Zebra mussel populations by *C. curvispinum* can be regarded as a case of spatial competition.

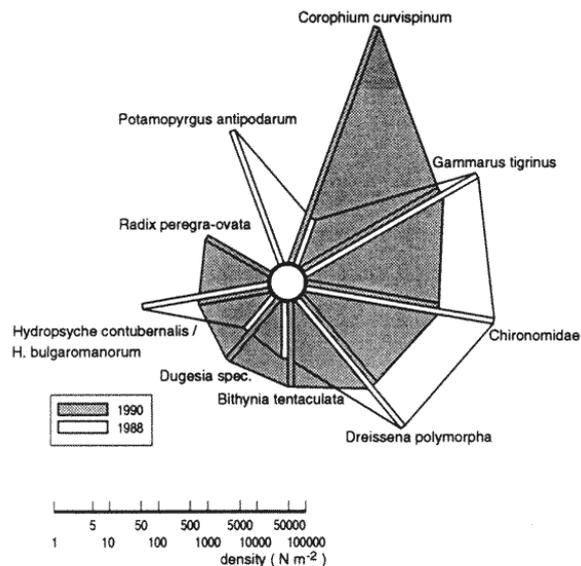


Figure 4. Changes in the densities of the major macroinvertebrates on stones in the Rhine at the start of the population explosion of *Corophium curvispinum* and afterwards (data from Van den Brink et al. 1993).

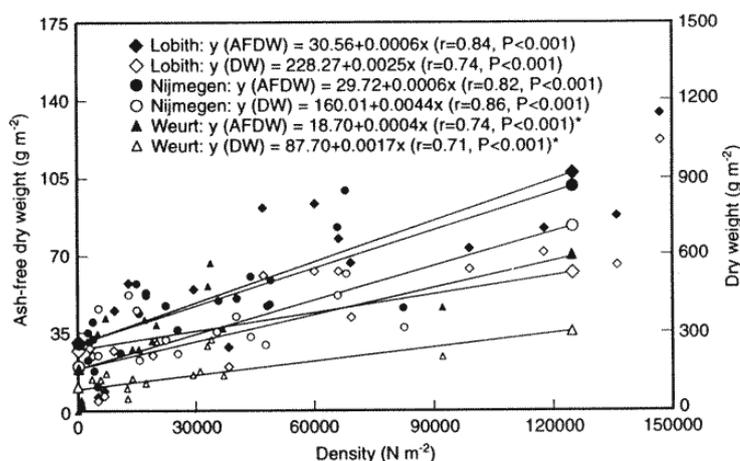


Figure 5. Population densities of *Corophium curvispinum* and muddy tube material (dry weight and ash-free dry weight) on stones at Lobith and Nijmegen and on long-term cumulatively exposed tiles at Weurt (Maas-Waal Canal), the Netherlands.

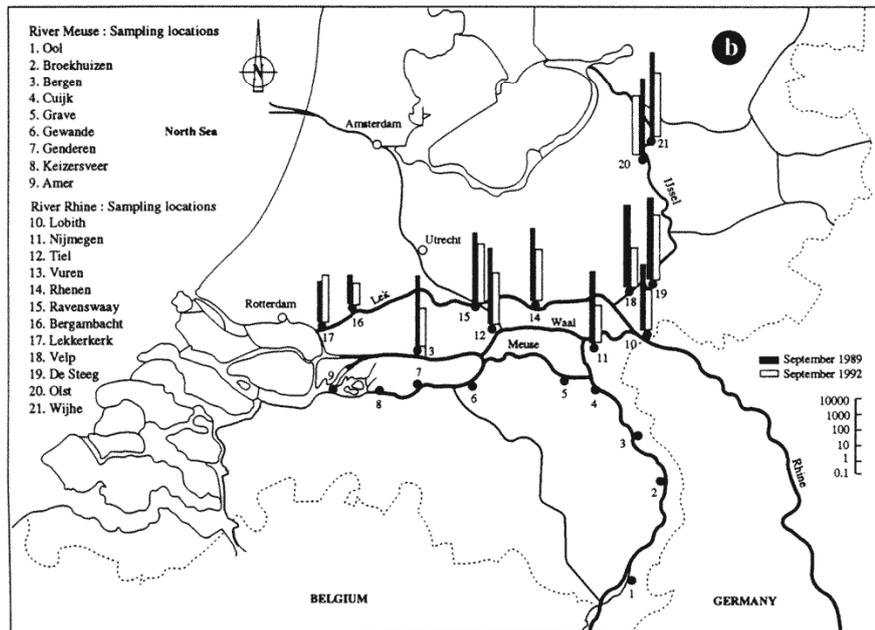
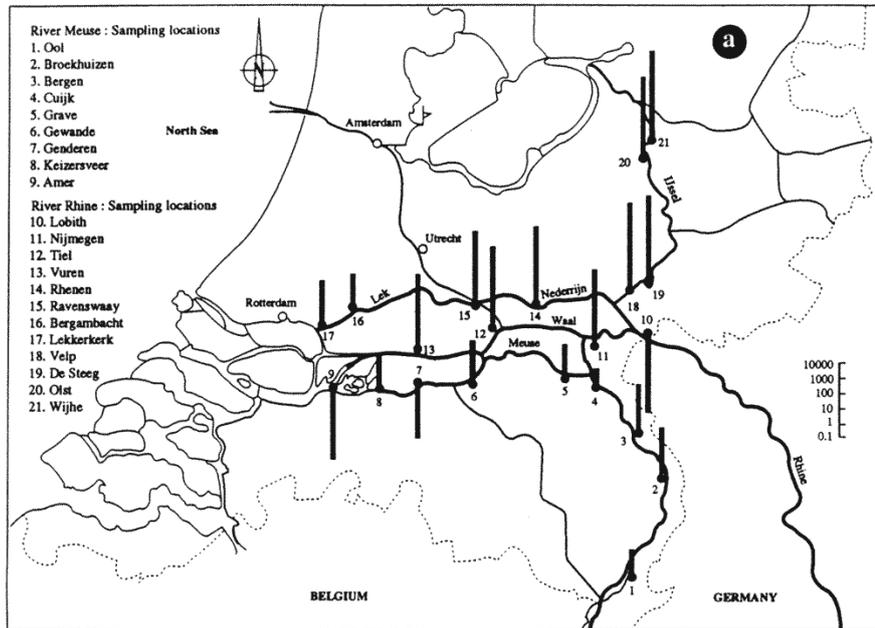


Figure 6. Map showing the sampling localities in the Rhine and Meuse in the Netherlands. A) Mean population densities of *Corophium curvispinum* (individuals per m² stone surface at 1 m depth) at different sampling localities in the Rhine and Meuse during September 1993. B) Mean population densities of *Dreissena polymorpha* (individuals per m² stone surface at 1 m depth) at different sampling localities in the Rhine, before (September 1989) and after (September 1992) the population explosion of *C. curvispinum*.

With respect to food competition between these two species in the Rhine, stable isotope analysis showed very similar values for $\delta^{13}\text{C}$ (carbon source) and $\delta^{15}\text{N}$ (trophic level) for the stone-dwelling *C. curvispinum*, *D. polymorpha* and the sand dwelling Asiatic clams (*Corbicula fluminea*, *Corbicula fluminalis*), indicating a common diet of phytoplankton and particulate organic matter (POM) among these filter feeding animals (Marguillier 1998). This means that competition between the Zebra mussel and *C. curvispinum* can also be regarded as a case of interspecific exploitative competition, although competition for space seems to be the main aspect. Van den Brink et al. (1991, 1993) found detritus as well as planktonic algae in the digestive tract of *C. curvispinum*. The mean number of eggs per brood of *C. curvispinum* during the season showed a positive correlation with chlorophyll-*a* in the Rhine (Rajagopal et al. 1999b). The growth rate of *C. curvispinum* was positively correlated with the temperature, but increased growth rate correlated with an increase in chlorophyll-*a* concentrations (Rajagopal et al. 1999a). This means that the high densities of *C. curvispinum* in the Rhine can arise due to high chlorophyll-*a* concentrations in the eutrophicated river. In 1994, *C. curvispinum* reached a peak density (Fig. 2) but chlorophyll-*a* concentrations dropped to a low level and remained low in 1995 and 1996 (Table 1). This drop in chlorophyll-*a* concentrations may have been caused by the reduced levels of nutrients, especially phosphate (in 1986 annual mean total phosphate was 0.45 mg l^{-1} , range $0.12\text{-}0.78 \text{ mg l}^{-1}$) leading to decreased planktonic algal development. Although *C. curvispinum* remained the dominant macroinvertebrate on the stones, its densities decreased in these years. At the same time macroinvertebrate species richness increased after the decline of *C. curvispinum* (Fig. 2), but this was mainly due to the occurrence of new hard substrate exotics.

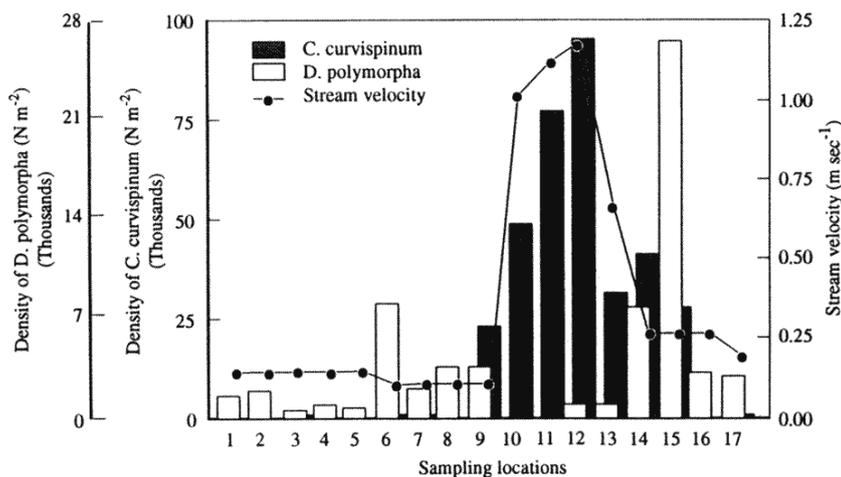


Figure 7. Relationships between population densities of *Corophium curvispinum* and *Dreissena polymorpha*, with average stream velocities at different locations along the rivers Rhine and Meuse in the Netherlands (for sampling locations see Fig. 6).

Another factor that appeared to be important in the development of a high density population able to outcompete the Zebra mussel is stream velocity (Van der Velde et al. 1998). A high stream velocity favors *C. curvispinum* by transporting silt and planktonic algae, as well as causing high oxygen levels, which are necessary for metabolism. This is clearly illustrated by investigations along the longitudinal axis of the Rhine and Meuse (Figs 6-8). From these results, it can be concluded that a low stream velocity, such as that in the Meuse, prevents the building up of highly dense populations of *C. curvispinum* (Fig. 7). However, the water quality of the Meuse could also be a limiting factor because Na^+ concentrations are low and near the tolerance limit of *C. curvispinum* (Van der Velde et al. 1998). In the Meuse, *D. polymorpha* is one of the dominant macroinvertebrates on the stones. In the Rhine stream velocity drops downstream, allowing *D. polymorpha* to maintain its dominant position at downstream sites (Fig. 8).

As pointed out above, mass invaders influence both horizontal (competition, swamping) and vertical food chain processes. *G. tigrinus* and *C. curvispinum* both play an important role in the food web of the Rhine and are consumed by fish. Kelleher et al. (1998) found that Perch (*Perca fluviatilis*) and Eel (*Anguilla anguilla*) consume both amphipod species. Eels foraging at groynes appear to have switched their diet completely from *G. tigrinus* to *C. curvispinum*. Perch, being more active hunters on mobile prey, maintain a preference for *G. tigrinus*. In river-connected sandpits, eels consume more *G. tigrinus* and *O. limosus* than *C. curvispinum* in terms of biomass. In another study in the Rhine, Ruffe (*Gymnocephalus cernuus*), Perch and juvenile Pike-perch (*Stizostedion lucioperca*) were found to feed on *G. tigrinus* and *D. villosus* as well as on *C. curvispinum*. Besides these percids, Eel and Roach (*Rutilus rutilus*) were also found to feed on *C. curvispinum* (Kelleher et al. 1999a).

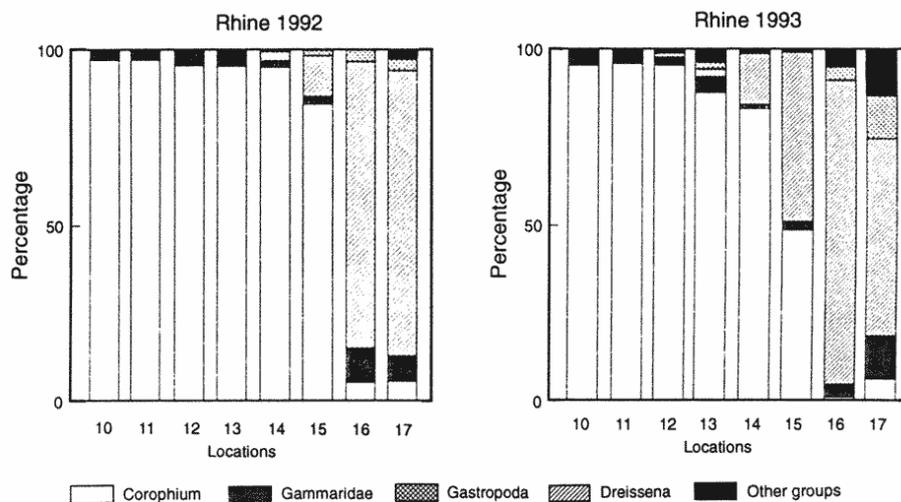


Figure 8. Population densities (in percentages) of different macroinvertebrates on stones ($n = 3-5$) from the groynes at different locations along the Rhine in the Netherlands (for location see Fig. 6) during September 1992 and September 1993.

This means that there is a rapid flux in exotic species composition in the food base of these predatory species with differential preferences. *D. villosus* seems set to become the next important food for many of these species, because of its increasing population and because it is bigger than the other amphipod species (Kelleher et al. 1998). Diet switching can be important as a controlling factor of the amphipod populations, since predation pressure on these exotic amphipods can change rapidly. If a predator switches to another additional prey, the other prey species may suffer less from predation and their population could increase again.

In summary, it can be stated that gammarids and tube-building corophiids have different strategies for coping with their competitors. Gammarids show aggressive behaviour against their relatives, while tubicolous corophiids like *C. curvispinum* introduce mud to their habitat and so prevent the development of other competitors. The outcome is in both cases not only dependent on behavior but also on physiological as well as environmental factors, as was illustrated above. This means that the success of crustacean invaders can be explained by linking detailed information on behavior and physiology to monitoring of the macroinvertebrate communities and environmental factors.

Continuous biological monitoring in the Rhine can provide data with respect to successive invasions, their interactions and their impact in relation to water quality changes. Further improvement of the water quality may change the outcome of the competition between the crustacean invaders. A decrease in salt concentration when the French potassium mines become exhausted, probably in 2004, may have a strong impact especially on the crustaceans in the river. Thus, the changes in the Rhine and other rivers can be regarded as large-scale ecological experiments.

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