6 Invasions by alien macroinvertebrates and ecological rehabilitation: lessons from the Rhine

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Abstract
The large river Rhine has gone through periods of severe ecological deterioration due to human impact, alternating with periods of some ecological improvement. Measures taken since 1986 in the context of ecological rehabilitation programs have led to a dominance of alien macroinvertebrates, particularly crustaceans and molluscs, in the river's main channel. However, ongoing river engineering in the river channel and nature development in the remnants of its floodplain will cause the system to enter a phase of permanent disturbance. More invasions of macroinvertebrates are therefore likely, with a trend towards increasing similarity to the river Danube.

Introduction

From a economical point of view the Rhine is the most important river in Europe. The river's natural function is the discharge of melt water from the glaciers in the Alps and rain water from the river catchment. The meandering character of the natural lower river reaches creates many different habitats as sediments become differentiated by differences in flow rates, meanders become cut off by natural processes (oxbow lakes), and floods and seepage areas affect areas along the river. This has led to a high biodiversity in the river itself and its floodplain areas (Van der Velde *et al.* 2004). Habitat requirements to support the species-rich rheophilic flora and fauna are: a) relatively low water temperatures, b) a high oxygen supply, c) a regular food supply, c) various substrates differentiated into islands, sand and gravel banks, d) shallow sand and gravel banks for growth of benthic algae, the main food for grazers, e) water and bank vegetation, large woody debris (LWD), also for benthic algae production, providing attachment opportunities, spawning sites, shelter and food, f) floodplain forest for the reproduction of aquatic insects, shelter against sunlight and the production of LWD and other allochthonous litter.

The river is fed by streams in which the food source is mostly of terrestrial origin. It takes the form of wood and fallen leaves (coarse particulate organic matter (CPOM)), which is consumed by shredders such as insect larvae and by gammarids that digest the microbial fungi and bacteria that colonized the leaves in the water. These leaves also leach out dissolved organic matter (DOM), which can flocculate and be taken up by microbial organisms. Feces, fragments and flocs form fine particulate organic matter (FPOM) which fuels the higher order head streams and is the main food source for collectors (filter-feeders). As the stream widens in downstream direction, more light is able to reach the water surface, creating growth conditions for macrophytes, benthic algae and periphyton. This leads to more grazers in the system. In the lower reaches of the river collectors (filter-feeders and deposit feeders) dominate the system because of phytoplankton development, detritus supply and low flow rate. The various processes in the course of a river from small stream to large lowland river have been summarized in the River Continuum Concept (RCC).

As time went on, humans started to use the river for various other purposes leading to more and more anthropogenic influences by human activities. The river's economic functions now include navigation, fisheries, recreation, discharge of substances, provision of cooling water, drinking water production, electricity production, sediment extraction, and the use of river water for irrigation and to stop salt intrusion. Not only was the river used for economic functions, but the river floodplain was narrowed and the land thus obtained was protected by dikes to improve safety. The function of the river as a habitat for flora and fauna has always been neglected, until the 'Sandoz disaster', a chemical spill in 1986. After this disaster, plans have been developed and realized to achieve ecological rehabilitation of the river. The Rhine Action Program was the umbrella for these plans in the decade after the disaster. Macroinvertebrate studies started to examine the effect of anthropogenic influences, in order to provide a basis for management measures and to formulate political decisions. Much effort was put into monitoring activities to make results of ecological measures visible.

Deterioration

The various anthropogenic influences on river biotopes were several, all leading to a severe degradation of the ecological state of the river (Cioc 2002). Deforestation and agriculture led to increased erosion and sediment load as well as increases in nutrient and pesticide levels. Waste products of cooling water use (chlorination), industrialization and mining led to chemical often toxic water pollution such as heavy metals, organic substances and salt through discharge and atmospheric deposition. The sewer discharge in towns led to high levels of organic matter, oxygen depletion and high nutrient levels. High nutrient levels led to phytoplankton blooms diminishing transparency of the water. River engineering influenced water velocity and channel depth by normalization and canalization and by the construction of summer and winter dikes influencing flooding and sedimentation patterns.

In a natural river, the main channel meanders and is characterized by natural discharge, an open estuary, riffles, pools and sand banks. It has no sewer or navigation functions and no dikes or levees. Today, the river is characterized by fixed river beds, artificial meander cut-offs, (partly) partial dams, an estuary with many arms closed off by dams, a dredged river bed, sewage, a major navigation function and dikes and/or levees. This process has led to a reduced number of lotic and lentic biotopes, unnatural discharge levels, migration barriers, reduced species richness and a smaller floodplain (river forelands). These river forelands are also used as meadows for cattle. Canalization and meander cut-offs, normalization, bank protection, sand and gravel extraction are irreversible effects, whereas the effects of waste discharge can be reversed. Chemical pollution increased after the start of the industrial revolution, and after a pause during World War II increased again making the Rhine a severely polluted and degraded river, which was regarded the sewer pipe of Europe. Effects on macroinvertebrates were severe, greatly reducing the numbers in insect species, particularly rheophilous mayflies (Ephemeroptera), caddis fly larvae (Trichoptera) and midges (Chironomidae). The greatest reductions occurred in the numbers of species living on hard substrates (e. g. wood), in sand and in vegetation (Klink 1989; Van den Brink *et al.* 1990) (Figures 1 and 2). A species which became completely extinct was the largest mayfly in Europe, *Palingenia longicauda*, the last specimens of which were observed around 1915. It died out not only in the river Rhine but in nearly all large rivers in Europe, with the exception of the river Tisza, a tributary of the river Danube. Their larvae burrow into silty-clayey sediments making U-shaped burrows up to 15 cm length and 6-8 mm wide. Densities can reach 4000 specimens per m^2. The larvae live in the water for three years before they metamorphose into adults. Recolonisation of the Rhine by this species is not expected to take place, because of the changes in water quality, hydrology and morphology, and because the Tisza is too far away.

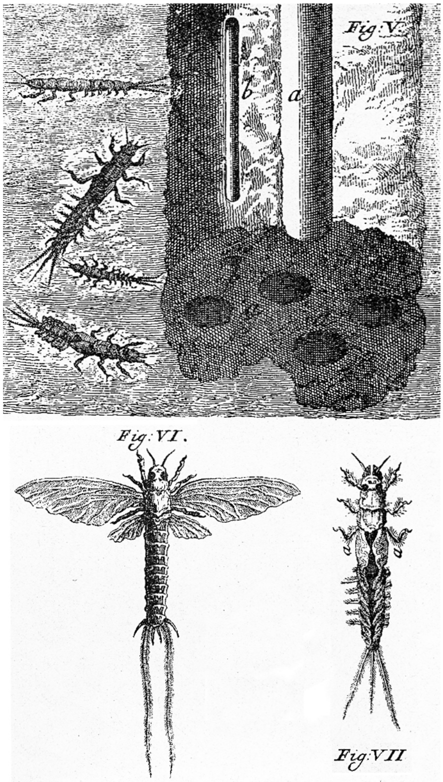

Figure 1 Example of a rheophilic burrowing filter-feeding mayfly species, Palingenia longicauda, which lived in the Rhine but is nowadays extinct. The drawings are made by Jan Swammerdam (1675).

Rehabilitation

Since 1970, however, the states along the Rhine have implemented measures to improve the water quality of the river. Between 1970 and 1990, this quality did indeed improve (Admiraal *et al.* 1993; Bij de Vaate *et al.* 2006). Concentrations of heavy metals like Cd and Hg, organic micropollutants and mineral oil were reduced to very low levels. Reduced concentrations of cholinesterase inhibitors led to the return of midges (Chironomidae) and caddis larvae (Trichoptera) in the river after 1976.

Minimum, average and maximum oxygen saturation values of the water increased to natural levels. On the other hand, average water temperatures in the Rhine have increased gradually by several degrees since 1911. Pesticides and other diffuse forms of pollution have remained, just like salt discharge, and the lack of habitat diversity has

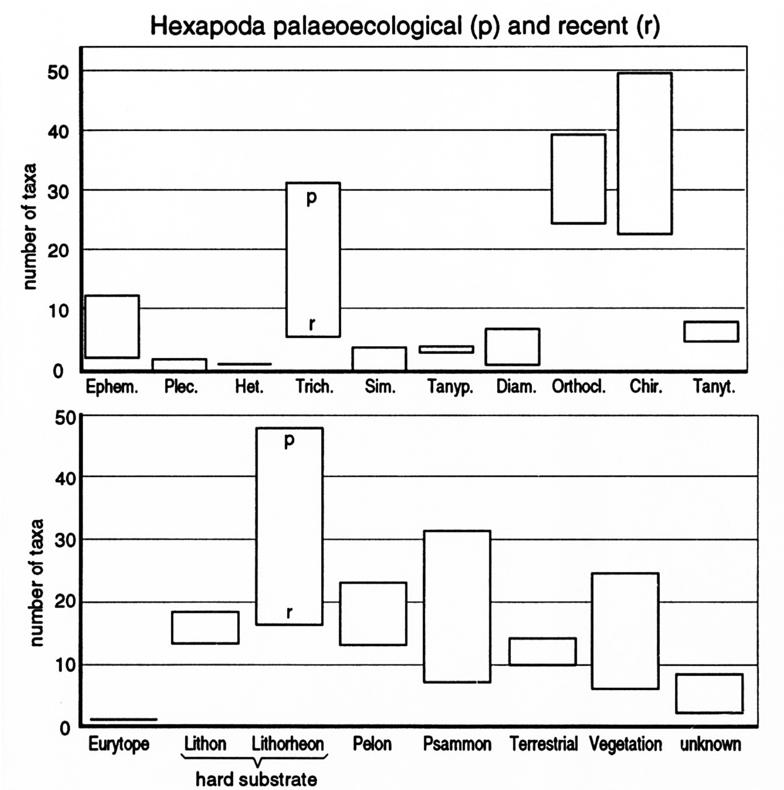

Figure 2 Reduction in insect species in the Rhine based on palaeoecological and recent data from Klink (1989). Above: taxa, Abbreviations: Ephem. = Ephemeroptera, Plec. = Plecoptera, Het. = Heteroptera, Trich. = Trichoptera, Sim. =Simuliidae, Tanyp. = Tanypodinae, Diam. = Diamesinae, Orthocl. = Orthocladiinae, Chir. = Chironomini, Tanyt. = Tanytarsini. Below: taxa grouped by habitat. P means palaeoecological figures, r means recent figures

also persisted. In 1995, 59-63 macroinvertebrate species were found per biotope (rip-rap, channel bottom, artificial substrate), 21 species per biotope were only found in a specific biotope. Nevertheless, a clear indication of the improvement of the circumstances for the sand inhabiting fauna is the recolonization in 1991 by the mayfly *Ephoron virgo* after almost 50 years of absence (Bij de Vaate *et al.* 1992).

Increasing invasions

Monitoring in the Rhine during the last decades has revealed that alien species, mostly crustaceans (Van der Velde *et al.* 2000) and molluscs have become dominant over native species, mostly insect species, numerically as well as in terms of biomass. Large rivers are normally insect-dominated. At the start of the water quality improvement campaign in 1970, the alien invaders were pollution-tolerant species. After the Sandoz accident in 1986, the invasion rate accelerated, as the river was invaded by Asiatic clams (*Corbicula fluminalis*, *C. fluminea*) in 1988, which moved in an upstream direction from the estuary (Bij de Vaate 1991), and by Ponto-Caspian macroinvertebrates, mostly crustaceans, invading in a downstream direction. The Ponto-Caspian invaders came from the Mittelland canal, which canal is connected with the Rhine and a series of canals connecting all south-north flowing rivers discharging into the Baltic and North Sea. After the opening of the Main-Danube canal in 1992, the invasion rate increased again, due to invasions by more and more Ponto-Caspian species. The increasing number of invasions is suggested to be the result of incomplete communities with vacant niches, due to major disturbances, viz. pollution followed by water quality improvement and then by a chemical spill, which cleared the river free of macroinvertebrates and eels over a stretch of hundreds of kilometers followed by further water quality improvements (Den Hartog *et al.* 1992). These invaders also cause disturbance leading to rapid turn-overs in the dominating species. Interactions between species of similar origin can quickly establish new communities, as new invaders are facilitated by the earlier invaders, a phenomenon which is known as invasional meltdown (Van der Velde *et al.* 2006 and literature therein). A series of Ponto-Caspian species invaded the Rhine through the Main-Danube canal, whereas only two alien species invaded the Danube through this canal.

Only a few invaders became highly dominant in the Rhine, and these are considered here in more detail. The North-American freshwater shrimp *Gammarus tigrinus* became very numerous after its appearance in the Rhine in 1982 together with the Ponto-Caspian Zebra mussel (*Dreissena polymorpha*), which returned to the river when cadmium concentrations in the water dropped in the 1970s and 80s (Van der Velde *et al.* 1991 and literature therein). After 1986, other Ponto-Caspian species invaded the Rhine, viz. the mudshrimp *Chelicorophium curvispinum* from the Mittelland canal followed by the freshwater shrimp *Echinogammarus ischnus* in 1989. After the opening of the Main-Danube canal new Ponto-Caspian species invaded the Rhine and became dominant, viz. the freshwater shrimp *Dikerogammarus villosus* in 1994/5, the isopod *Jaera istri* in 1995/7 and two mysid species in 1997 (Van der Velde *et al.* 2000). These dominant invaders had a large impact on the communities in the Rhine and can be regarded as ecosystem engineers.

Only two biotopes are present in the main channel, viz. sediment (sand and gravel) and stones (rip-rap, groynes). Densities of macroinvertebrates on the sand are low, the community being dominated by Asiatic clams. Densities on the stones, by contrast, are very high and there is severe competition for space. The impact of an invader on the communities can work in a bottom-up or top-down direction. Mutual interactions are responsible for species replacements and subsequent dominance.

The mudshrimp *Chelicorophium curvispinum* (Figure 3) changed the surface of the stones into muddy substrates by building the tubes in which they live (Figure 4). *C. curvispinum* is a filter-feeder taking advantage of algal blooms in the river due to eutrophication (Van den Brink *et al.* 1991, 1993). As densities ran into hundreds of thousands of individuals per square metre this mud layer became up to 4 cm thick, smothering Zebra mussels and other sessile organisms under the mud (Van der Velde *et al.* 1994, 1998). This led to a distinct reduction in biodiversity on the stones (Van der Velde *et al.* 2002). Predation is another way to dominate the communities. *Gammarus tigrinus* replaced the native *G. pulex* and later became replaced itself by *Dikerogammarus villosus*. Such replacement processes occur mainly by intraguild predation (IGP), which is a method used by generalists to exclude competitors through size-dependent predation, and which can be interspecific or intraspecific (cannibalism). This leads to avoidance of size classes of these species in space and/or time. Although freshwater shrimps are mainly omnivorous, *D. villosus* appeared to be the largest, most predatory and competitively strongest of the freshwater shrimps occurring in the Rhine. It not only replaced *G. tigrinus* (Van Riel *et al.* 2004) but was also responsible for a severe reduction in the densities of *C. curvispinum*, thus favouring the Zebra mussels and the freshwater limpets (*Ancylus fluviatilis*) (Van Riel *et al.* 2006). The appearance of this freshwater shrimp species prevents insect dominance in the Rhine because they form an easy prey. However, more and more Ponto-Caspian species can invade the Rhine in which predators and parasites of the invaders are already present, thus weakening their control over the communities till other invaders can take over this role. The decline of *C. curvispinum* conincided not only with the invasion of *D. villosus* but also with that of endo- and ectoparasites, other predatory macroinvertebrates and fish (Kelleher *et al.* 1998, 2000; Van Riel *et al.* 2003).

Discussion

The ecological rehabilitation scheme for the River Rhine has shown that recovery may be only partly successful. The greatest successes were obtained by improving the water quality. However, the river is still far from natural, due to irreversible anthropogenic changes relating to the large number of functions the river is expected to fulfil. Measures like habitat and the digging of new side channels are only possible in the river forelands. The river's navigation and discharge functions prevent continuing natural succession of the riparian forest, which leads to persistent human interference. It must be realized that the Rhine ecosystem has been destroyed over a period of more than a century, and it is not likely that it will return to its original state as long as human impact remains (Lenders *et al.* 1998). The canals connecting various river catchments which were in the past isolated from each other will remain and continue to be used as routes for more and more invading species, which are already underway. This will continue to change macroinvertebrate communities in the Rhine making them increasingly resemble those of the Danube (Bij de Vaate *et al.* 2002). Attempts have to be made to achieve a further reduction of pollutants from diffuse sources, while a further lowering of the salt concentrations can perhaps provide more chances for rheophilous insect species than for crustaceans. It is also to be expected that more and more thermophilous species will enter the Rhine. Native species will only return if more diverse habitats are created, increasing heterogeneity and providing more shelter options and a variety of food sources. Pollution Water quality improvement following pollution has also led to the invasion of alien species in other waters, as the barrier of polluted stretches was removed. Strayer *et al.* (2005) studied the Hudson River and state that restoration projects in large rivers are often accompanied by alien species in one way or another. The plans currently being implemented in The Netherlands, whose intention is to the river with more space to move in, will also lead to greater dynamics in the macroinvertebrate communities (increased turn-overs), with unpredictable outcomes. Larger numbers of these species will also invade our canals and lakes and can cause economical and ecological damage (Van der Velde 2001).

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Moeten deze figuren er ook nog in? Er wordt geen melding van gemaakt.

Fig. 3. The ponto-caspian mudshrimp *Chelicorophium curvispinum*: left side: female (above) and male (below), right side: mud tubes smothering the Zebra mussel (above) and copulatory behaviour in a mud tube.

Fig. 4. Groyne completely covered by mud tubes of *Chelicorophium curvispinum* becomes visible at low discharge of the Rhine.