Recolonisation potential

of

macroinvertebrates in the Lower Seine

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Contents

Summary

Aim of the European Water Framework Directive is to improve water bodies to such extend that their ecological functions ascribed are not impeded by anthropogenic influences. For heavily modified water bodies, like the Lower Seine, this means that its condition should meet the Good Ecological Potential by the year 2015. In order to describe this potential, it is essential to combine knowledge of the current situation with information from comparable river sections in undisturbed rivers, knowledge on recolonisation possibilities, and effects of river engineering on the former existing communities.

Based on the macroinvertebrate communities, three ecological zones can be distinguished in the today tidal freshwater section of the river Seine. These zones are about the same as those defined for the European Water Framework Directive. The most divers community of the whole tidal freshwater section was found in the most upstream zone. This community included some (pollution) sensitive species. Water quality in this part of the river is mediocre and the tidal currents are relatively low. The second zone is the river section between the river km's 247 and 288 (directly downstream of Rouen till Mesnil-sous-Jumièges). In this section the macroinvertebrate diversity has sharply dropped and sensitive species have disappeared. Water quality is insufficient, due to the industrial complexes in the vicinity of Rouen and the tidal currents are relatively high. The third zone was found between the river km's 292 and 324. In this river section the macroinvertebrate diversity is even lower compared with the second zone. Only a few species maintain populations in this harsh environment in which water quality is also insufficient and the tidal currents contain relatively high loads of suspended solids. The presence of only ten of disturbance sensitive macroinvertebrate taxa in the whole tidal freshwater section of the river Seine reflects the poverty of natural biotic and abiotic processes present in it. However, recolonisation potential is present in the tributaries and upstream sections.

Colonisation and recolonisation by aquatic macroinvertebrates strongly depends on three main processes of dispersal: drift, flying (for insects only) and human mediated dispersal. However, settlement is limited by the poor water quality, specially the oxygen content in the river, and absence of habitats due to embankments and river engineering.
The data analysed do not allow getting insight into what macroinvertebrate species recently invaded the tidal freshwater section of the river Seine. Main reason is that these animals were not identified to species level but to higher taxonomic groups. However, most of the nonindigenous species found during the June 2006 monitoring activities are recent invaders. Their number will increase mainly due to introductions from other river basins through canals connecting river basins. It should be taken into account that water and bottom quality improvement including nature development in the remaining floodplain will facilitate population development of these species as well.

Résumé

1. Introduction

The European Water Framework Directive (WFD) prescribes monitoring of several so-called "Water Quality Elements" (WQE's), in order to assess the ecological quality of water bodies. One of these elements is the composition and abundance of the macroinvertebrate fauna.

For each biological WQE assessment of the ecological quality should be based on a comparison between the actual situation and reference conditions described for each water body type (European Union, 2003). Since the Lower Seine was classified as a heavily modified water body, two reference conditions must be taken into account: the Maximum Ecological Potential (MEP) and Good Ecological Potential (GEP). Both conditions should be derived from the natural status.

Prior to the description of reference communities for a MEP or GEP, insight is needed into possibilities for flora and fauna to colonise or recolonise a water body. In this report these possibilities are discussed for macroinvertebrates in the tidal freshwater section of the Lower Seine. The report is the result of activity B of the project “Etat des peuplement benthiques dans la partie amont de l’estuaire”.

2. Methods

Results of several monitoring programs were used to develop knowledge about colonisation and recolonisation potential of macrozoobenthos communities in the tidal freshwater section of the river Seine. These results include data from monitoring activities in:

a. nine tributaries entering the main channel of the river Seine downstream the Poses weir (river km 202). These data, from the period 1992–2003, were made available by D.I.R.E.N. Haute Normandie;

b. the main channel of the river Seine upstream of the Poses weir. Data from 2005 also made available by D.I.R.E.N. Haute Normandie;

c. June 2006 when the river Seine was sampled between river km 203 and 324 in the framework of the current project. In this project 140 samples were taken:

   - 125 samples were taken from the intertidal, subtidal and deep bottom of the main channel;
   - 9 samples in the secondary channels upstream Rouen;
   - 4 samples in the outlet of the river Eure;
   - 2 samples in a streamlet flowing into the river Seine at river km 215.

All together the results of 221 samples were used (table 1).

Table 1
Overview of samples taken in the sampling programs.

Waterbody	Seine Aval	Andelle	Oison	Eure	Robec	Aubette	Cailly	Austreberthe	Rancon	Ste-Gertrude	Seine amont
Number of samples	140	4	12	11	10	6	10	12	6	5	5

Samples in the Seine-Aval all were taken in June 2006, in the tributaries in the period 1992–2003, and in the Seine-Amont in 2005.

3. Results

Based on the macroinvertebrate communities (sampling campaing june 2006) the three zones distinguished in the tidal freshwater section of the river Seine in the framework of the WFD also reflect ecological zones. The most upstream zone (I) is the river section confined by the Poses weir (river km 202) and river km 236 (in the vicinity of St-Etienne du Rouvray) (figure 1). The most divers community of the whole tidal freshwater section was found in this zone including some (pollution) sensitive species. Water quality in this part of the river is mediocre and the tidal currents are relatively low. The second zone (II) is the river section between the river km's 247 and 288 (directly downstream of Rouen till Mesnil-sous-Jumièges). In this section the macroinvertebrate diversity has sharply dropped and sensitive species have disappeared. Water quality is insufficient, due to the industrial complexes in the vicinity of Rouen and the tidal currents are relatively high. The third zone (III) was found between the river km's 292 and 324. In this river section the macroinvertebrate diversity is even lower compared with the second zone. Only a few species maintain populations in this harsh environment in which water quality is also insufficient and the tidal currents contain relatively high loads of suspended solids (table 2).

Figure 1
Map of the fresh water tidal part of the river Seine with indicated the three identified ecological zones (see text) (after Guézennec et al, 1999).

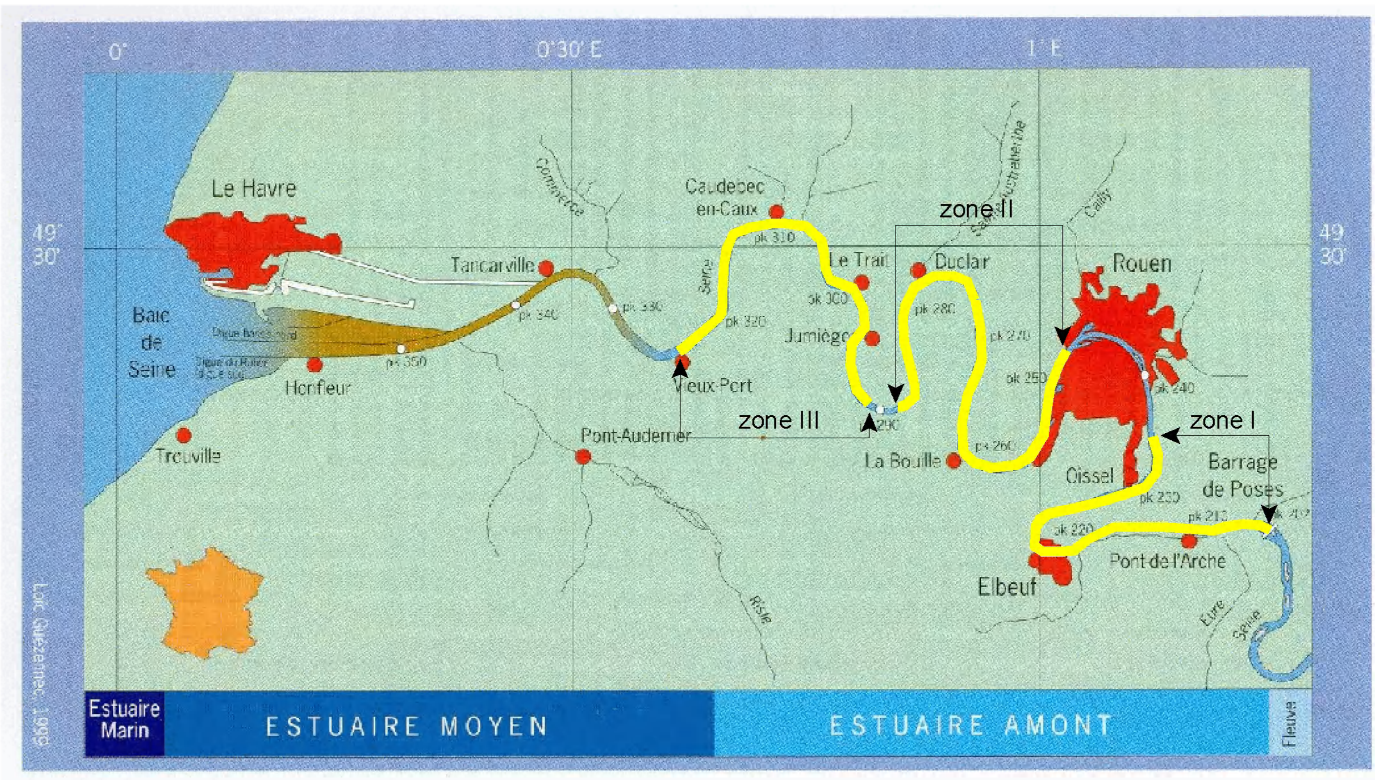

Table 2
Number of taxa per taxonomic group found in three ecological zones distinguished in the tidal freshwater section of the river Seine.

Taxonomic group	Number of taxa zone T1[A]	zone T1[B]	zone T2
Tricladida	3	3	1
Polychaeta	1	1	
Oligochaeta	15	14	10
Hirudinea	10	10	1
Mollusca	26	16	4
Crustacea	8	5	2
Ephemeroptera	3	1	
Plecoptera	1		
Heteroptera	2	1	
Coleoptera	3	3	1
Trichoptera	5	1	
Chironomidae	47	27	7
Total number of taxa	124	82	26

In order to improve the ecological quality of the river, first objective must be the reduction of waste water discharges by expanding the water purification capacity to such extend that the oxygen demand of the discharges does not significantly affect the oxygen content in the river. Physical restraints for macroinvertebrates are loss of intertidal habitats due to the embankments. During and after rehabilitation works in the Lower Seine species will colonize or recolonize the restored areas.
Colonisation and recolonisation by aquatic macroinvertebrates strongly depends on three main processes of dispersal: drift, flying (for insects only) and human mediated dispersal.

- **Drift** is the downstream displacement of macroinvertebrates. It is a natural process that can lead to massive displacement, especially at high discharges. Peak discharges in the Lower Rhine and Lower Meuse in February 1995 were among the highest of the 20th century. In erosion gullies formed along the main channel both rivers a total number of 565 living aquatic macroinvertebrate taxa were collected of which some had drifted for 500 km or more prior to stranding in the floodplain (Klink, 1999). These peak discharges reintroduced, for example, the dragonfly *Gomphus flavipes* lastly observed in the Netherlands in 1901.

- **Flying**: The East and West European lowland rivers contain a very similar insect fauna. Most groups of insects are good flyers that disperse very well by flying. Most vulnerable groups amongst them are the stone- and mayflies (Plecoptera and Ephemeroptera respectively) because of their sensitivity to pollution and habitat degradation. In addition, these insects are poor flyers. That is why most of them became extinct from the river Rhine in the late 19th century (Geijskes, 1948; Mol, 1985[a,b]), while reintroductions are very rare after improvement of the ecological quality of the river from the 1980's (Bij de Vaate *et al*., 1992).

- **Navigation** is the main vector in human mediated dispersal of aquatic animals in rivers. Most successful are species that are able to attach to ship's hulls. Navigation is also an important vector for the introduction of nonindigenous species. Intercontinental dispersals of these species mainly occur through transport in ballast water. Continental dispersals are mainly the result of interconnections of European rivers by shipping canals (Bij de Vaate *et al*., 2002). Also in this case animals are transported from one river basin to the other if attached to a ship's hull or as a result of water management in these canals. For example, in the Main-Danube Canal, connecting the Rhine and Danube basins, water level in the upper section is maintained with water supply from the Danube basin. This resulted in an annual flow of 150 million m^3 water from the Danube basin into the river Rhine (Tittizer, 1997). This especially facilitates dispersal of mobile animals (e.g., crustaceans) from the Danube basin towards the Rhine basin (figure 2). The canal has already been successfully traversed by some amphipod species such as *Dikerogammarus haemobaphes* (Schleuter et al. 1994), *D. villosus* (Bij de Vaate & Klink 1995), *Echinogammarus trichiatus* (Prodraza *et al*. 2001) and *Obesogammarus obesus* (Nehring, 2006), the isopod *Jaera istri* (figure 3)(Schleuter & Schleuter 1995), the mysid *Limnomysis benedeni* (Reinhold & Tittizer 1998), the polychaete *Hypania invalida* (Klink & Bij de Vaate1996), as well as the planarian *Dendrocoelum romanodanubiale* (Schöll and Behring 1998). All these Ponto-Caspian species including all other nonindigenous species occurring in the river Rhine are able to colonize the Seine basin directly through the Rhine-Marne Canal or through the existing European network of shipping canals.

Figure 2
Main corridors for range expansion of Ponto-Caspian macroinvertebrates (Bij de Vaate et al., 2002).

Table 3
Sensitive fauna elements in the tidal freshwater section of the river Seine, its tributaries and the neighbouring upstream section.

Taxonomic group	Taxa	Seine aval	Andelle	Oison	Eure	Robec	Aubette	Cailly	Austreberthe	Rancon	Ste-Gertrude	Seine amont
Mollusca	Acroloxus											+
	Ancylus	+	+	+	++	+++	++	+++	++	+++	++	
	Theodoxus		++		+++				+++	++	++	
	Pisidium											++
	Pseudanodonta											+
Hydracarina			+	++	+	++	++	++	+++	++	+++	
Ephmeroptera	Baetidae		+++	+++	+++	+++	+++	+++	++++	+++	+++	++
	Ephemerella	+	+++	++	++	+	++	+++	+++	++	+++	
	Ephemera		+		++			+				
	Ecdyonurus				+							
	Heptagenia	+		+	++							
Plecoptera	Leuctridae	+	++									
	Nemouridae									+	+	
Odonata	Calopteryx			+	+							
	Coenagron											++
	Orthretrum											+
	Platycnemis				+							+
Heteroptera	Aphelocheirus	+			++			+				
	Velia					+						
Coleoptera	Elmis	+	++	+++	+++		+	+	+	++	+	
	Esolus	+		++	++					+		
	Limnius	+	+++	+++	+++		+			+		
	Macronychus				+							
	Normandia			+								
	Oulimnius			+	++			+				
	Riolus		+	+	+		+			+		
	Stenelmis				+							
Trichoptera	Glossosomatidae					+	+++	+		+	++	
	Agapetus			+++	+		+++					
	Glossosoma				+							
	Beraeidae				+							
	Goeridae		+	+	+				+	+++		
	Hydroptilidae	+	++	++	++	+++	+++	++	++++	+	+++	
	Ithytrichia				+							
	Lepidostomatidae	+	+	+	++							
	Polycentropodidae											+
	Leptoceridae		+	+	++							
	Athripsodes				++							
	Mystacides				++							
	Triaenodes				+							
	Limnephilidae		+	++	+	+	+++	+	++			
	Odontocerum albicorne		+								+	
	Psychomyidae		+		+							
	Rhyacophila		+	+	+	+	+	+	++	+		
	Sericostomatidae		++		+		+		+	+		
Diptera	Simuliidae		++	++++	++++	+++	+++	++	+++	+++	++++	
	Athericidae			+								
Total number of taxa		10	20	21	33	10	14	13	12	16	11	8

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Figure 3
Jaera istri.

Data by courtesy of D.I.R.E.N. enable us getting insight in the recolonisation potential from the vicinity of the Lower Seine, which could happen by means of drifting and/or flying. Table 3 gives an overview sensitive taxa found in the main and secondary channels of the tidal freshwater section of the river Seine, its tributaries and the neighbouring upstream section. The group of *Chironomidae*, the most divers group of invertebrates has been left out since they were not identified.

Totally 46 sensitive taxa (probably >100 species) were found in the tributaries and the neighbouring upstream section. From the results of the June 2005 sampling it was concluded that ten of these taxa have a marginal existence in the tidal freshwater section of the river Seine. Of these taxa the mollusc *Theodoxus fluviatilis* is missing in the Seine-Aval. Also *Hydracarina* have not been found in the river. This group mainly contains of predators and their occurence depend on the presence of vegetation as their habitat. Of the mayflies, only *Ephemerella ignita* and *Heptagenia sulphurea* live in very small numbers in the upper section of the Seine-Aval. *Baetidae*, *Ephemera* and *Ecdyonurus* were only collected in the confluents. Of the two stoneflies, *Leuctra fusca* was found in the Seine-Aval near the confluence of the Andelle while *Nemoura* was only found in the Rancon and the Sainte Gertrude. However, both species are no characteristic inhabitants of large lowland rivers. They are inhabitants of smaller streams. The dragonflies *Calopteryx* and *Platycnemis* live close to the Seine Aval. The waterbug *Aphalocheirus aestivalis* was collected in the Seine-Aval and *Velia* lives in the Robec. Three genera of the critical beetles of the family *Elminthidae* live a marginal live in the Seine-Aval and five other genera live close by in the confluents (*Macronychus*, *Normandia*, *Oulimnius*, *Riolus* and *Stenelmis*).

The sensitive caddis flies (Trichoptera) are hardly able to develop viable populations in the Lower Seine. In the tributaries, however, many taxa have been found able to live the river as well. The rivers Andelle and Eure accomodate the richest Trichoptera fauna compared with the other tributaries taken into account. Of the dipterans the black flies (Simuliidae) are very common in the tributaries, but absent in the river where they can live under natural circumstances. The same is the case for snipe flies (Athericidae) which were only observed in the river Oison.
When water quality of the Seine-Aval improves, a lot of pollution sensitive taxa present upstream and in the tributaries are able to return by drifting or flying. However, for several taxa it will be hard to find a suitable habitat. For instance *Macronychus quadrituberculatus* (Coleoptera) and *Atherix ibis* (Athericidae) depend on the presence of dead wood (snag) being their habitat; a rare phenomenon in the current lower Seine.
Also a number of species that used to live in the river Seine will not return because they became extinct in Western Europe and are no good flyers in the case of insects. A well documented example is the mayfly *Prosopistoma foliaceum* (figure 4), that has become extinct in Western Europe in the 20th century and seems to disappear in Eastern Europe as well (Landa & Soldan, 1985). The same has also been observed for a number of stoneflies.

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Figure 4
Prosopistoma foliaceum
http://www.liis.lv/aizsargajamie/viendienites.htm.

The data analysed do not allow getting insight into what species recently invaded the tidal freshwater section of the river Seine. However, most of the nonindigenous species found during the June 2006 monitoring activities are recent invaders (Table 4). Their number will increase mainly due to introductions from other river basins. Water and bottom quality improvement including nature development in the remaining floodplain will facilitate population development of these species.

Table 4
Nonindigenous macroinvertebrates found during the June 2006 monitoring activities.

Taxonomic group	Species	Origin
Polychaeta	Hypania invalida	Ponto-Caspian area
Oligochaeta	Branchiura sowerbyi	probably East Asia
Tricladida	Dugesia tigrina	North America
Mollusca	Dreissena polymorpha	Ponto-Caspian area
	Corbicula fluminalis	East Asia
	Corbicula fluminea	East Asia
	Lithoglyphus naticoides	Eastern Europe
	Orconectes limosus	North America
Amphipoda	Crangonyx pseudogracilis	North America
	Dikerogammarus villosus	Ponto-Caspian area

4. Discussion

Intensive and exponential human use of European rivers started more than 500 years ago, and the basins lost, step by step, their naturalness and ecological integrity (Smits et al., 2000). Rivers were canalised for the purpose of navigation and regulated by weirs and sluices for water resource control and flood defence, habitats were fragmented and floodplain land was reclaimed for urban and industrial purposes. Rivers were treated as sewers carrying waste and drainage away from the urban environment (Walsh, 2000). In addition, from the early 1900's, major dam building activities started for both hydroelectric power and drinking water supply. Almost 80% of the total water discharge of the main European rivers is more or less strongly affected by flow regulation measures (Dynesius & Nilsson, 1994), and around 90% of the U.K. rivers are regulated as a result of those activities, while in a densely populated country like the Netherlands this percentage is close to hundred.
River degradation became particularly manifest following the industrial revolution in Europe. The river Thames in the U.K., for example, was already extremely polluted in the first half of the nineteenth century, culminating around the 1950's in public nuisance from hydrogen sulphide. Rehabilitation of the Thames water quality had already started from the late 1960's onwards, mainly by the enforced building of sewage treatment plants, exemplified, e.g. by a remarkable recovery of the fish fauna (Gameson & Wheeler, 1977). The river Rhine reached its worst level of pollution in the late 1960's and early 1970's, and significant improvement of the water quality took place in 1980's and early 1990's, although nutrient levels are still a problem (Tittizer & Krebs, 1996).
De Waal *et al*. (1995) gave a review of 66 river rehabilitation schemes recently carried out mainly in Western Europe. Human's most dramatic impact on fluvial systems is canalisation which involves the direct modification and shortening of the main river channel in the past. This could explain the high percentage (75%) of rehabilitation projects dedicated to channel morphology. Nature conservation and restoration was by far the most common objective of the rehabilitation projects (85%). A commonly cited constraint involves the inability to allow floodplain inundation because of the requirements to provide flood control. Another argument is the lack of control over floodplain land as a result of land ownership or because of urban areas occupying the floodplain area.

In order to restore the ecological integrity of large rivers, restoration including nature development has become an important issue from the end of the 1980's (Boon et al. 1992, Gore & Shields 1995, Sparks 1995, Nienhuis & Leuven 1999, Pedroli & Postma 1999). The Netherlands adopted a river management policy of habitat restoration by reconnecting floodplain habitats with the mainstream through restored floodpulses (figure 5). The general underlying assumption of this policy is that floodpulses (hydrodynamics) and morphological diversity arising from the flow pulse (morphodynamics) are the main driving forces for the formation of characteristic riverine habitats and associated life forms (e.g., Amoros & Roux, 1988; Junk *et al.*, 1989; Sedell *et al.*, 1989). Various habitat restoration projects have been developed with the aim of creating an ecological network along the Netherlands Lower Rhine and its tributaries, consisting of several large ecologically important reaches (1000-6000 ha each) with smaller areas in between. At present, about 7,500 ha of floodplain along the Lower Rhine and its tributaries have an important ecological function. The Netherlands river management policy aims to protect these areas including an additional rehabilitated area of 5,000 ha within the next 10-15 years (Van Dijk *et al.*, 1995).

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Figure 5
An example of nature development along the river Waal in the Netherlands, one of the distributaries in the Rhine delta.

For the recolonisation of riverine fauna one has to realise that natural riverine landscapes are dynamic, and biologically and spatially complex (Ward *et al.*, 2002). They are characterised by often extensive flood plains (e.g. Lewis *et al.*, 2000), a natural flow regime (Poff *et al.*, 1997), high hydraulic connectivity (Ward *et al.*, 1999), a successional landscape mosaic with high habitat heterogeneity (Wissinger, 1999), and a complex land-water coupling and exchange (Stanley, Fisher & Grimm, 1997). The interplay between these landscape elements has a direct bearing on the generation, distribution and maintenance of riverine biodiversity (Junk, 2000; Tockner *et al.*, 2000[a]). The riverine fauna also provides important feedbacks that can influence spatio-temporal dynamics of the landscape over long time periods (Naiman *et al.*, 2000).

Recently, also the importance of natural discharge fluctuations have been recognised in stream ecology (e.g., Stanley *et al.*, 1977; Tockner *et al.*, 2000[b]). For example, the extent of wetted areas can increase by orders of magnitude during the annual flood (Tockner *et al.*, 2000[a]), with concomitant effects on the distribution of aquatic and terrestrial organisms (e.g., Kohler *et al.*, 1999). Kohler *et al.* (1999) found that fish and macroinvertebrates were redistributed among floodplain ponds (temporary and permanent) during high waters. Consequently, the postflood community was affected strongly by

direct fish predation on invertebrate predators. This suggests that the mosaic of successional stages in flood plains may reflect deterministic biotic interactions a well as stochastic physical forcing.
However, the fauna, as ecological engineers, also engage in autogenic and allogenic processes that influence biodiversity (structural, functional, genetic), community assembly (life cycles, species traits, strategies), system functioning (nutrient cycling, energy flow), and consequent biotic feedbacks (dispersal, predator-prey interactions, migration) in riverine landscapes (Robinson *et al*., 2002).

The complex life cycles of many fauna of intact riverine landscapes infers that species loss translates to a loss of evolved morphologies, physiologies, behaviours and complex life cycles; that is, a loss in evolutionary trajectories. Ward *et al*. (1999), summarising many conceptual models regarding biodiversity, suggested that maximum biodiversity is maintained at intermediate disturbance and resource availability, levels typically found in intact riverine landscapes (e.g., Naiman *et al.*, 1988). Angermeier & Winston (1999) emphasised the importance of key landscape-scale features in conservation biology; the idea being that most species respond to changes in key environmental factors (Keddy, 1999). For example, because high ecotone/floodplain area ratios correlate strongly with high biodiversity (Brown, 1998), it follows that as the number and diversity of ecotones increases in regulated rivers the dynamic nature, integrity and biodiversity of these systems also will increase.

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Figure 6
Chelicorophium curvispinum.

The presence of only ten of disturbance sensitive macroinvertebrate taxa in the tidal freshwater section of the river Seine, having a marginal existence in it, reflects the poverty of natural biotic and abiotic processes present in that part of the river. Recolonisation potential is present in the tributaries and upstream sections. The most important supply of recolonizers is expected to arrive from upstream parts as was clearly demonstrated in the rivers Rhine and Meuse after peek discharges (Klink, 1999). However, the paradox is that with the ameliorating water quality, chances for nonindigenous nuisance species increase dominating the macroinvertebrate community (Den Hartog *et al*., 1992). Examples for the river Rhine are the Ponto-Caspian species *Chelicorophium curvispinum* (figure 6) and *Dikerogammarus villosus* (Rajagopal et al., 1999; Van der Velde et al., 2000; Van Riel et al., 2006[a], 2006[b]). In figure 7 recent developments of dominant species on an artificial substrate (figure 8) in the river Rhine at the Dutch-German border is shown for the period 1988-2003. Until 1991 the invaders did not seem hampering the colonisation of indigenous species. However, after that year clear impact has been demonstrated on indigenous species to colonize the substrate.

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Figure 7
Density of invaders and indigenous invertebrates on artificial substrate in the Lower Rhine at the Dutch-German border from 1988-2003.

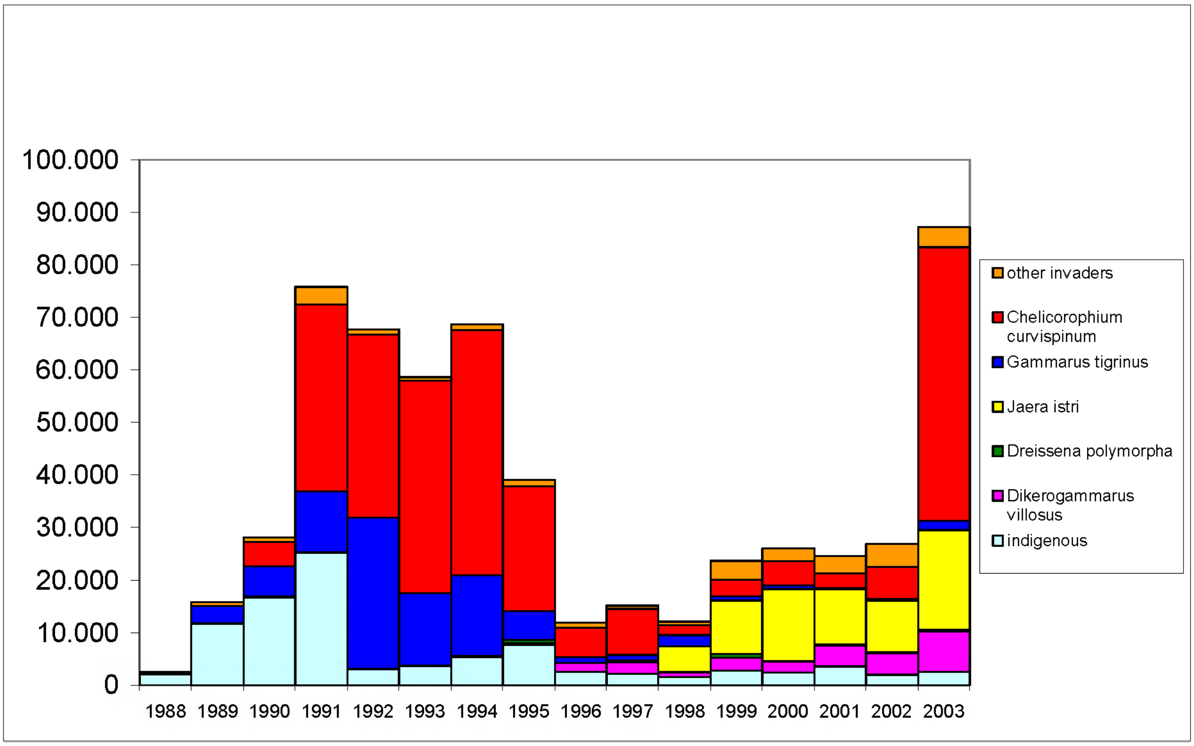

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Figure 8
The standardized artificial substrate (glass marbles) used in monitoring programs for large rivers

In general, community vulnerability to invasions is ascribed to combinations of several factors like the presence of vacant niches, habitat modification and disturbance before and during invasion. Although the link between the biodiversity of communities and their vulnerability to invasions remains to be proved, invasibility is known to increase if a community lacks certain species, which ought to be present under normal conditions. A new hypothesis linking the various explanations of increased invasibility is that of fluctuating resource availability such as an increased amount of unused resources (Davis et al. 2000).

The river Rhine is a good example of all these related factors. Pollution over a long period weakened the original communities and caused the loss of certain species, creating open niches for pollution-tolerant invaders. Water quality improvement led to a partial recovery of the original communities together with the establishment of previously disappeared and new invaders. A major disturbance like the Sandoz accident in 1986 subsequently led to invasions by many new species, which reached unprecedented densities. The fact that filter feeders are particularly abundant can be attributed to intense phytoplankton blooms due to eutrophication. Hardly any macrophytic vegetation is present in the Rhine channel to compete with phytoplankton for nutrients. Recolonisation after partial reduction of pollution in rivers modified by human activities seems to favour invaders more than indigenous species. These invaders then suppress the development of populations of indigenous species, although biodiversity increases (Van der Velde *et al.*, 2002).

Severe pollution can function as a barrier to the dispersal of invaders. An example is the Chicago connection between the Great Lakes and the Mississippi river, where the 1972 Clean Water Act provided subsequent improvements in municipal waste treatment. These resulted in improved water quality to such an extent that the zebra mussel (*Dreissena polymorpha*) and six other non-native "pest" species were able to spread from the Great Lakes to the Mississippi River (Stoeckel et al. 1996). *D. polymorpha* returned to the Rhine in the 1970's and 1980's, when cadmium concentrations in the water fell below 1 µg l^{-1} (accumulation in the mussel at that level was 40 µg g^{-1} DW) (Van Urk & Marquenie 1989).

The present day invasions of Ponto-Caspian invaders in Western Europe via the Main-Danube canal increases the likelihood that they will reach other harbours in Europe via ballast water transport because of the presence of many major ports in Western Europe (Bruijs et al. 2001). These species tolerate high temperatures and brackish water. The future will bring continued invasions, resulting in unstable communities with an accelerated turnover due to increasing propagule pressure combined with greater anthropogenic disturbance (Nilsson & Grelsson 1995; Stylinski & Allen 1999). This future scenario will cause a shift from battles between invaders and indigenous species towards battles among invaders of various origins.

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Annex

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