Historical Change of Large Alluvial Rivers: Western Europe
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The Lower Rhine: Palaeoecological Analysis

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INTRODUCTION

This chapter reviews the first few years of palaeoecological river research, by means of insect remains, in the Netherlands. In 1983 the first floodplain samples from the River Rhine were analysed and since then, progressively, we have been building up biological evidence concerning the history of the river. As is symptomatic of any new development in science, numerous questions arise from the analysed material and very few answers can be given. Nevertheless, it has become clear that palaeoecological river research has considerable scope.

HISTORICAL DATA ON THE INSECT FAUNA OF THE RHINE

Data on the insects inhabiting the Rhine in the past are very scarce. From the most comprehensive record of riverine insects (Albarda, 1889) it is apparent that the characteristic riverine Ephemeroptera, Plecoptera, Odonata and Trichoptera were still present in the 19th century. The best example of the Ephemeroptera is *Palingenia longicauda*, which burrowed into the clay banks in large numbers: it was last recorded in 1907 (Mol, 1985). The Plecoptera in the Rhine included the genera Oemopteryx, Isoperla and Chloroperla. These stoneflies became extinct in the early decades of this century (Geijskes, 1940). *Gomphus flavipes*, a mud-dwelling dragonfly, was last collected in 1902 (Geijskes and Van Tol, 1983). The Trichoptera included, among others, *Cheumatopsyche lepida*, *Lepidostoma hirtum*, *Psychomyia pusilla* and many *Hydropsyche* species. The first two species have not been collected during the 20th century. The last record of *Psychomyia pusilla* dates back to 1933 (Fischer, 1934). Very little is known about the Diptera. Van Der Wulp (1877) notes that adult Simuliidae (only four species described) were very common on places near the rivers Rhine and Meuse. The chironomids mentioned in his work cannot be assigned to the typical river fauna.

From the early records it can be concluded that in the second half of the 19th century and the first few decades of the 20th century a dramatic decline was observed in the larger insects. The river Rhine today is deprived of Ephemeroptera (except *Caenis* species), Plecoptera, Anisoptera and Simuliidae. Apparently Trichoptera have been absent from the Rhine for a long period of time, too. From 1978 on, however, a remarkable return of *Hydropsyche contubernalis* and some other caddisflies has been observed (Van Urk, 1984).

CHEMICAL CHANGES IN THE RHINE

Evidence that early pollution of the Dutch rivers did not go unnoticed can be found in the following quotation from Velsen (1768):

> 'Our people have always been utterly indifferent to a vital part of this country, the rivers. We used them and abused them as we pleased, without any supervision whatsoever. If the rivers were to die tomorrow not a soul would care or be grieved. Instead of worshipping her as gods or saints, we treat them as sewers, in which anyone may freely dispose of his wastes. This is what has caused their abominable state.'

Most probably the pollution referred to above was predominantly organic. Large-scale mining activities did not start until the middle of the 19th century, and it was not until the 20th century that steel production became a major industry and pesticides based on mercury and arsenic were commonly used. In Figure 1 the history of heavy metal pollution is inferred from analyses of old river sediments and soil samples from a branch of the Lower Rhine. Organic pollution in former times has been deduced from the population

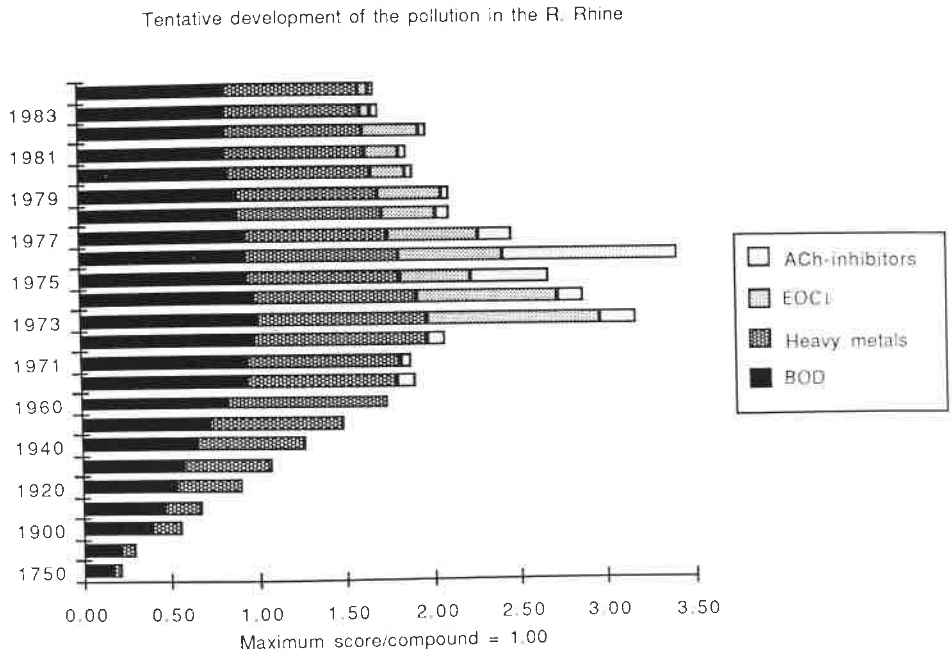

FIGURE 1. Tentative compilation of the pollution history of the Rhine derived from direct and indirect evidence

statistics of the Netherlands. The first decades of the 20th century were characterized by the onset of a steep rise in organic and heavy metal pollution in the Rhine.

Since the Second World War an entirely new branch of industry has added its own characteristic compounds to the environment. With the development of the petrochemical industry the family of chlorinated hydrocarbons (DDT, PCBs, drins and dioxins) have been released into the river. In the 1960s and 1970s acetylcholinesterase inhibitors were used as insecticides, resulting in concentrations in the Rhine of up to 50 $\mu g\, l^{-1}$ (Greve, 1980). The initial rise in chlorinated hydrocarbons (as EOCl) is not known as no analyses were made until 1973. In the mid nineteen seventies, however, concentrations as high as

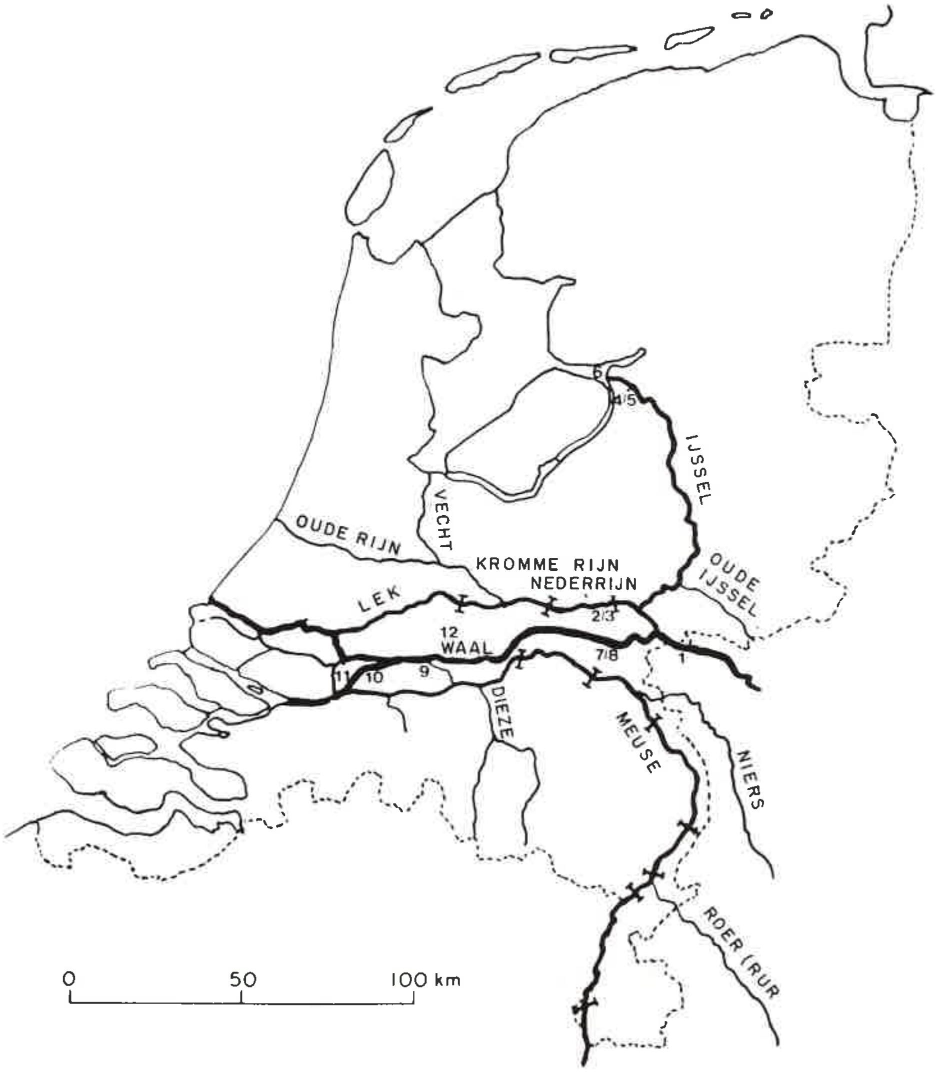

FIGURE 2. The Rhine–Meuse river system in the Netherlands. The sampling sites are numbered as in Table 1

TABLE 1. Sampling sites by type and date of sedimentation/sampling

Number	River	Type	Date
1	Rhine	Floodplain deposit	–1745
2	Nederrijn	Floodplain deposit	–1880
3	Nederrijn	Exuviae sampling	1981
4	IJssel	Sediment core	?
5	IJssel	Exuviae sampling	1986
6	IJssel	Sediment core	?
7	Waal	Exuviae sampling	1985
8	Waal	Suspended solids ($\geq 100\,\mu m$)	–1984
9	Boven Merwede	Floodplain deposit	1914
10	Nieuwe Merwede 9	Sediment core	? 5140 BP
11	Nieuwe Merwede 12	Sediment core	?
12	Schoonrewoerdse Wiel	Sediment core	1750–1984

$30\,\mu g\,l^{-1}$ were measured (Greve, 1980). Concurrently, the pollution of the Rhine reached its maximum. Subsequently, improvements in oxygen content and a decline in micropollutants have been observed. The return of caddisflies in the Rhine, notably *H. contubernalis* could be the result of this improvement (Becker, 1987).

Localities and methods

The sampling sites used in this survey of the Lower Rhine are shown in Figure 2 and listed in Table 1.

The sediment samples were collected in three different ways. First, sediment cores from the river-bed were taken by means of a mudcorer installed on a research vessel. The core from Schoonrewoerdse Wiel (nr. 12) was taken by means of scuba gear. Secondly, floodplain deposits were collected with hand auger equipment for soil research. The augers were drilled into the soil until a layer of coarse sand was met, indicating the former river-bed. Since these layers contain hardly any remains of invertebrates, the samples were taken from the silt layer directly on top of the sand. Thirdly, suspended solids were collected from the river itself by means of a driftnet (mesh $100\,\mu m$). To compare these data with the present situation, monthly exuviae collections were carried out at three sampling stations from May to October by means of a driftnet (mesh $500\,\mu m$).

The deposits were sieved over a mesh of $100\,\mu m$ and the macroinvertebrate remains were handpicked under a magnification of 40–80 and preserved in ethanol 70 per cent. Only five insect orders were found in sufficient numbers for sample comparison. Distribution of aquatic Coleoptera remains was too local to take them into consideration, while no Odonata remains were found. Of the non-insect groups, mollusc shells appeared to be absent in all but a few samples, while Tricladida, Oligochaeta and Hirudinea remains were not found at all. The Tricladida and Hirudinea contain no chitinous parts that stay intact in the sediment. The chitinous parts of the Oligochaeta (chaetae and cuticular penis sheaths in some Tubificidae) must have been lost in sieving or overlooked during sorting with this magnification. Curiously no remains of Isopoda or Amphipoda were recognized.

The following groups are considered and identified according to the selected parts: Ephemeroptera (mandibles); Plecoptera (maxilla); Heteroptera (tergites); Trichoptera (frontoclypeus); and Diptera (headcapsule).

The remains of the insects were identified by means of the available literature on the various groups. As single references rarely provided complete identification by means of the selected parts a wide variety of special articles was consulted. The remains that could not be identified in this way were compared to the material in reference collections. If this was not successful, the taxa were drawn and given a tentative name (for example Chironomini gen. no. 1).

Abandoned main channels were selected for the dating of the floodplain deposits. As old river maps show, the filling of these channels is a process that may take no more than a few decades. The layer directly above the coarse sand (assumed to represent the former channel bed) was taken for analyses of the remains as described and dated according to the period that the river abandoned that particular course. The estimated age of the sediment remains is the youngest possible age because the sediment contains an unknown fraction of older resuspended deposits. The inferred age of the sediment, therefore, is an underestimation of the average age of the sediment. The sediment cores from the present river-bed have not been dated, because no old river maps could be applied to the coring sites, and no sequential isotope decay series has been found or is expected to be found in the fluctuating sedimentation and resuspension environment that take place in rivers.

The identified remains were treated as units. This means that a mandible of a mayfly was counted as one mayfly. Mathematically this is not correct, since one mandible stands for only one half of one of the 25 instars that mayflies usually have. The one part = one specimen approach was chosen instead of the mathematically correct alternative because if not the numbers of hemimetabolic insects would have been too low to differentiate in statistical analyses. The homometabolic insect remains were treated similarly except the Chironomidae in which especially half headcapsules of the Orthocladiinae were found, which were counted as half specimens. The exuviae collections were summarized over the period of sampling (May–October). Finally, the counts in the sediment samples and the exuviae collections were recalculated to a total of 500 specimens and $\ln(x+1)$ transformed for factor and cluster analyses. These analyses were done by the statistical package SYSTAT (Wilkinson, 1986).

RESULTS

A total of approximately 15 000 insect remains covering 167 taxa were found in 52 samples from sediment cores, floodplain deposits and coarse suspended solids, while exuviae collections contained a little over 13 000 specimens comprising 66 taxa. From the statistical analyses it appears that subsamples from the same sediment core are always more closely related to each other than to samples from other cores or floodplain deposits, even in cores of 3 m long. In addition to the sedimentation process in the abandoned channels referred to earlier, the analyses of the insect remains also show that sediment cores from the river-bed may represent only very brief periods of time.

The names of the taxa in Figure 3 represent separate clusters by their most differentiating taxon. The bold-faced characters indicate the status of the clusters according to historical and recent documentation (e.g. the *Nanocladius* cluster includes species that have invaded the rivers). The distance from the clusters to the origin is a relative scale of abundance.

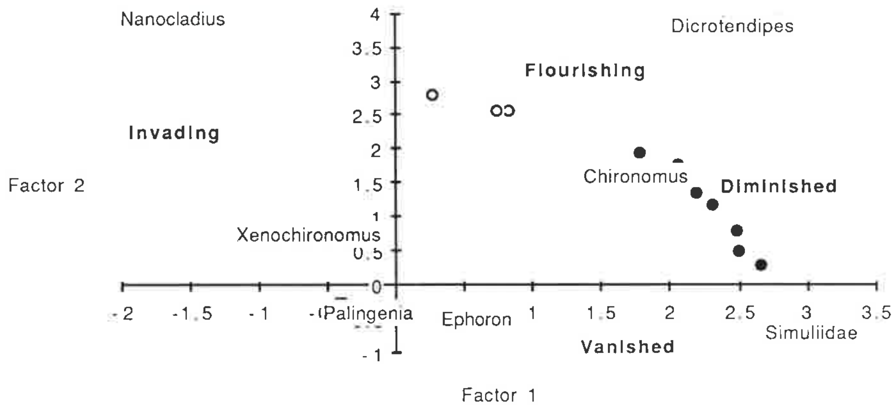

FIGURE 3. Changes of the insect fauna of the Rhine. The open circles are exuviae samples and the solid circles are samples from sediment cores and floodplain deposits

The first quadrant of Figure 3 contains taxa that are abundant in both sediment and exuviae samples. The *Dicrotendipes* cluster stands for *Dicrotendipes nervosus* and the *Cricotopus/Orthocladius* aggregate (not subdivided in the remains). They are under-represented in the sediment samples but are 'flourishing' so to speak in the present Rhine. In the exuviae collections *Cricotopus bicinctus* is by far the most abundant representative of the Cricotopus/Orthocladius aggregate. The Chironomus cluster includes *Chironomus* spp., *Cricotopus* sg. *Isocladius*, *Cryptochironomus* spp., *Glyptotendipes gr. pallens*, *Hydropsyche contubernalis*, *Parachironomus arcuatus*, Pentaneurini (not identifiable to a generic level) and *Polypedilum scalaenum*. This cluster stands for species that are still plentiful in the Rhine but not as abundantly as in the sediment samples. Despite the spectacular return of *Hydropsyche contubernalis* in the Rhine since 1978/1979 (Van Urk, 1984), their relative abundance in the sediments has not been equalled (yet).

The second quadrant consists of two discrete clusters of species which have largely vanished from the Rhine. The Simuliidae cluster includes (besides Simuliidae) *Microtendipes gr. chloris* and *Procladius* spp. Neither Simuliidae and *Microtendipes gr. chloris* were found in exuviae samples at all, while *Procladius* appeared to be extremely rare in the exuviae collections, in contrast to the sediment samples. The *Ephoron virgo* cluster differs from the Simuliidae cluster only in that the 30 taxa involved are less abundant. These taxa are frequently found in the sediment samples but are absent or extremely rare in the exuviae collections. The taxa concerned are mainly riverine Ephemeroptera and Trichoptera (e.g. Ephemera, Ephemerella, Baetis spp. Heptageniidae, Leptophlebiidae and *Brachycentrus subnubilus*, *Cheumatopsyche lepida*, *Hydropsyche pellucidula*, *Lepidostoma hirtum*, *Psychomyia pusilla*), the adults of which were all collected on the river banks in the last century (Albarda, 1889). Noteworthy is the occurrence of *Byssodon maculatum* (Simuliidae). It is uncertain if the species was ever caught alive in the Netherlands since the only encountered record may well refer to *Byssodon maculatum* and *Wilhelmia equina* (Van Der Wulp, 1877). According to Rubsow (1964), *Byssodon maculatum* inhabits large lowland rivers from Western France (River Seine) to the ultimate eastern part of the USSR (River Kolima). Even in the Mississippi this malicious biting blackfly has been collected.

The third quadrant contains only the Palingenia cluster. It contains 98 of the total of 167 taxa. The cluster lies close to the origin, which means that the species involved are not abundant and infrequently met in the dataset. Most of its species are extinct in the Rhine, including *Palingenia longicauda* itself, *Aphelocheirus aestivalis* and *Potamanthus luteus*. Species characteristic for large rivers are some sand-dwelling chironomid taxa (*Beckidia zabolotzkyi*, *Chernovskiia 'macrocera'*, *Paratendipes connectens 3 Lipina*, *Paratendipes intermedius*, *Robackia demeijerei* and *Potthastia gaedii*). They have not been collected alive in the Dutch rivers. Another chironomid (*Symposiocladius lignicola*) has recently been described (Cranston, 1982). The larvae burrow into submerged wood and are thus confined to snag habitats. The Trichoptera in this cluster are *Chimarra marginata*, Goeridae, Hydroptilidae, Micrasema spp., *Odontocerum albicorne*, *Oligoplectrum maculatum* and Rhyacophila sp. These taxa are not characteristic of lowland rivers and predominantly live upstream. It is uncertain if these species have actually ever inhabited the Lower Rhine.

The clusters in the fourth quadrant contain species that rarely occur in the sediment samples and can therefore be characterized as invaders. They all belong to the Chironomidae. The Nanocladius cluster includes Nanocladius spp., *Rheocricotopus chalybeatus*, Rheotanytarsus spp. and *Parachironomus longiforceps*. The Xenochironomus cluster includes the less abundant midges *Synorthocladius semivirens* and *Xenochironomus xenolabis*. Their absence in all but a few (recent?) sediment samples may be due to the physical changes taking place in the Rhine. Two of the most conspicuous changes are the increasing the water temperatures and the changing habitats.

Possible effects of long-term changes in water temperature

Climatic conditions have changed and thermal pollution has increased. This combination has so far caused a rise of 2.5 °C in the average temperature of the Rhine since 1908 (Department of Public Works, 1851–. . .; RIWA (Cooperating Rhine and Meuse Water Supply Companies), 1983). Also, observations of ice formation in the Rhine over the last two centuries (Figure 4) show that there has been a steady increase in the temperature of

FIGURE 4. Number of days with ice in the Rhine at the German–Dutch border since 1780

the river since the middle of the last century. The documented invasion of the freshwater shrimp (*Atyaephyra desmaresti*: Decapoda) in the Rhine can be considered as biological evidence for rising winter temperatures (Van Den Brink and Van Der Velde, 1986). The species has a southern European distribution and was first collected in the Netherlands in 1915 (Redeke, 1936).

Other species for which the rise in temperature may have been beneficial are the 'invaders' *Rheocricotopus chalybeatus*, *Nanocladius rectinervis* and the *Rheotanytarsus* species. They are very abundant in the Rhine today, and can well add up to 60 per cent of the total insects in the exuviae collections. *Rheocricotopus chalybeatus* has a southern distribution. In Europe, the species does not occur in Scandinavia (Fittkau and Reiss, 1978), but is very common in the River Po in Italy (Rossaro, 1984) and the Llobregat in Spain (Prat *et al.*, 1984). The species has also been collected in Lebanon (Moubayed and Laville, 1983) and Syria (Reiss, 1986). *Nanocladius rectinervis* roughly follows the same distribution pattern as *Rheocricotopus chalybeatus*. In Europe, the genus Rheotanytarsus is restricted to the area south of Scandinavia (Fittkau and Reiss, 1978). The distribution area of *R. photophilus* is not clear. Another species (*R. rhenanus*) has recently been described by Klink (1983), who collected the species not only in Dutch rivers but also in the rivers Meuse in S. Belgium, Lahn (W. Germany), Loire (France) and Tisza (Hungary). Saxl (personal communication) collected material from the River Krems (Austria), and Moubayed (personal communication) caught the species in Lebanese rivers. No collection sites north of the Netherlands are known at the moment. Future research may produce evidence that the expansion of these species to the north is due to the rise in river temperatures. It should be more interesting, though, to trace species showing a reverse trend, which would allow us to monitor the negative effects of thermal pollution. The Rhine is unsuitable for such research, however, because of the other profound changes that have taken place.

Changing habitats in the Rhine and their effect on the insect fauna

The original habitats of the 'natural' River Rhine can be deduced at least to some extent from the insect remains and historical research. The river-bed must have been a gradient passing from coarse sands in the erosive zones to silt in the depositional areas. Stones did not occur in the natural river-bed. Part of the banks may have been covered with vegetation, with dead trees providing snag habitats. The biological importance of the snag habitat has been pointed out by Bencke *et al.* (1984). The historical struggle of man against wood debris in rivers has been described in a case study by Triska (1984).

The changes which have affected the Rhine habitats have been discussed in the previous chapter but in brief the following has happened. The natural forests along the Rhine must have been cleared long ago, but the low-lying parts of the floodplains were partly covered by stands of willow until the late 19th/early 20th century. Jetties consisting of basalt blocks were built from the second half of 19th century. Recently part of the banks are protected by stones to prevent erosion from the increasingly powerful cargo vessels. In consequence, the habitat distribution in the Rhine has changed completely. The vegetation and snag habitats have been replaced by heavy boulders and the gradients in the composition of the river-bed have disappeared because of the jetties.

The overall impact of changed habitats on the insect fauna can be derived from Figure 5. The sediments contain 20–55 per cent of bottom-dwelling insect remains, while

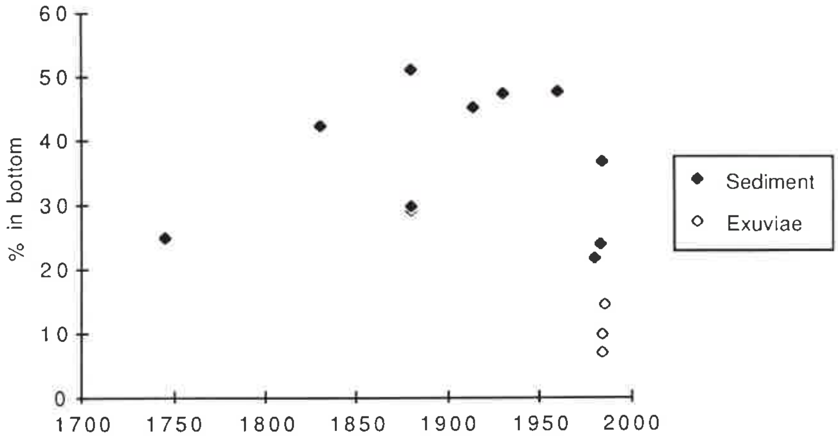

FIGURE 5. Relative abundance of benthic insect fauna in relation to the relative age: sediment (old), exuviae (recent)

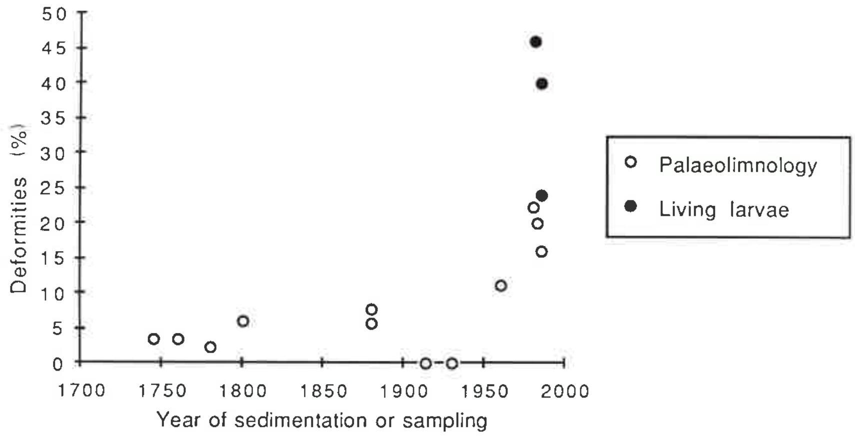

FIGURE 6. The incidence of deformities in the headcapsules of *Chronomus* larvae, in relation to inferred (probably underestimated) sediment age

in the recent situation not more than 15 per cent of the insect fauna lives in the bottom. The 'invader' species *Parachironomus longiforceps* and *Xenochironomus xenolabis* may have benefited from these altered habitats. The former live in colonies of Bryozoa (Ertlova, 1974). The latter inhabit sponges (Pagast, 1934). In the present Rhine both Bryozoa and Porifera are confined to the stones on the banks and jetties. To what extent the natural snag provides a suitable habitat for these colonies is still uncertain. Unlike the supposed thermophilic invaders, the distribution area of these midges and their hosts extends into Scandinavia.

Incidence of deformities in headcapsules of mud-dwelling *Chironomus* larvae

Although marked physical changes have taken place in the river-bed of the Rhine, mud habitats still exist and these are preferred by *Chironomus* larvae. Unfortunately heavy metals

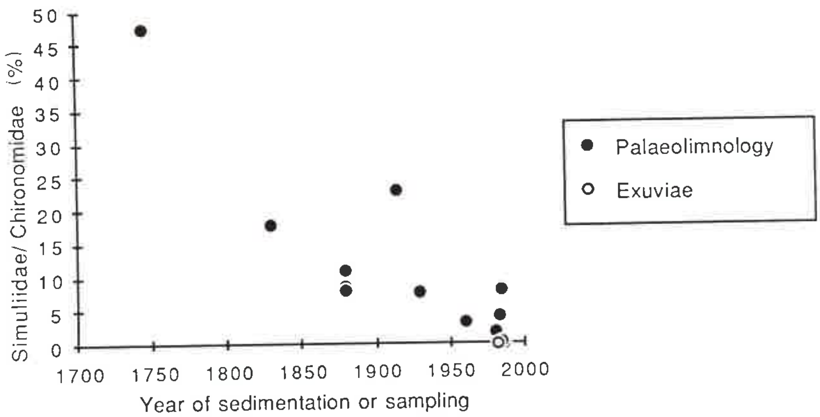

FIGURE 7. Changes in Diptera composition in the Rhine according to sediment samples and recent exuviae collections. Ages are probably underestimates

and other pollutants are accumulating in this sediment. According to Cushman (1984), Hamilton and Saether (1971), Warwick (1985) and Wiederholm (1984), the incidence of deformities in the headcapsules of *Chironomus* larvae is strongly propagated by xenobiotic pollutants. The most suspect compounds are heavy metals and chlorinated hydrocarbons. However, causal relationships between particular pollutants and deformities are not yet known. In the Rhine deformities of up to 40 per cent are not exceptional (Van Urk and Kerkum, 1986).

Comparison of the percentage of deformities in the sediment samples with recently collected living larvae, as shown in Figure 6, reveals a trend in the incidence of head deformities and the (underestimated) age of the sediment. Despite the lack of reliable sediment dating, it is obvious that deformities occurred as early as the 18th century, but that the sharp increase was only generated in this century. The rise in heavy metal concentrations (Figure 1) is strikingly similar to this rise in deformity rates. The relationship has yet to be proven by laboratory research, as concurrently with the rise in heavy metals the levels of other pollutants have been increasing too. Phenol pollution in the early 1900s, for instance, was traced because salmon meat tasted 'carbolic' (Van Drimmelen, 1982).

Changes in the Diptera fauna of the Rhine

One of the most striking discrepancies found between the sediment samples and exuviae collections is the absence of Simuliidae in the present Rhine (see Figure 7). The habitat of Simuliidae is solid substrate in the current, a habitat which is heavily propagated by the presence of jetties. The cause of their extinction is unknown but it could be related to the quality of the suspended solids, their food source. Another factor adversely affecting their existence is fluctuating current velocities. In the case of the Rhine, instantaneous fluctuations are generated by the wave action from boats, especially around the jetties. Future research on the sensitivity of Simuliidae to chemical and physical factors can provide valuable information on the threshold levels of these factors. Such information is crucial if the restoration of the Rhine ecosystem is to be attempted.

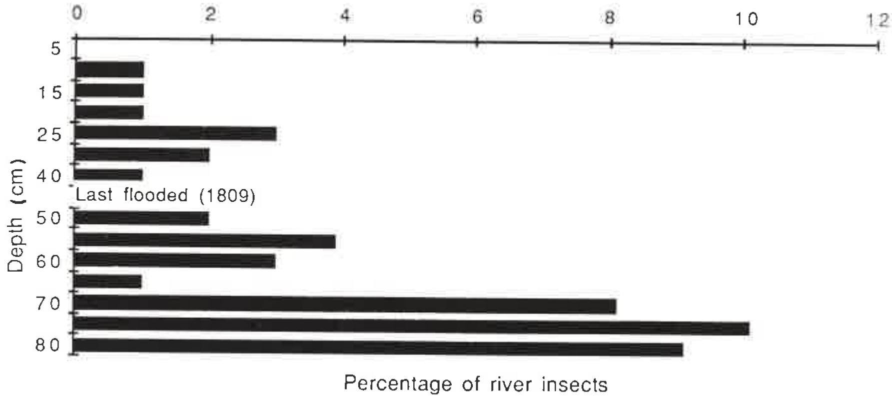

FIGURE 8. The percentage of typical river insects in the sediment core from L. Schoonrewoerdse Wiel. The 35 cm layer was discarded as no subfossil insects were found

FLOODPLAIN STRATIGRAPHY BASED UPON TWO CORES OF DIFFERENT ORIGIN

Description of a sediment core from a lake generated by a dykeburst

In the Netherlands most large rivers were embanked as early as the 13th century (Pons, 1957). When a river bursts through a short stretch of dyke, the result is a large eddypool which creates localized scour and leaves a small lake. In this way many dozens of lakes—called 'Wielen'—were generated by the Rhine. The Schoonrewoerdse Wiel (1573) is one of the larger ones, with an area of approximately 0.25 km^2 and a depth of 8 m. It was flooded several times in the past. It is not known how often this occurred, but in 1672 it was part of the Dutch 'waterlinie', a strip of land inundated as a defence against the army of Louis XIV of France. The Wiel has not flooded again since 1809, although it remained connected to a branch of the R. Rhine by means of a ditch. For the past 30 years it has been completely isolated.

In 1984 a sediment core (length 80 cm) was taken from the deepest part of the Wiel by means of scuba gear. One half of the core was dated by means of Pb-210, and its phytoplankton analysed. The other half was processed for insect analyses. The core covers the period from approximately 1750 to 1984. In Figure 8 the percentage of typical river insects is shown against the depth of the sample (depth 0–5 cm is the top). Despite a sharp decline in the riverine insects (Simuliidae, Heptageniidae and Hydropsychidae, as well as some rheophilic Chironomidae) the indirect influence of the river is still notable, even at a depth of 10 cm (1972). This core reveals that large areas of the western part of the Netherlands evolved by slow vertical accretion of Rhine sediments.

Description of a river deposit in the freshwater tidal belt in the western part of the Netherlands

In 1986 two sediment cores were taken from the Nieuwe Merwede (Figure 2; Table 1). The genesis of this tidal area is discussed by Van Urk (1984) and will only be summarized

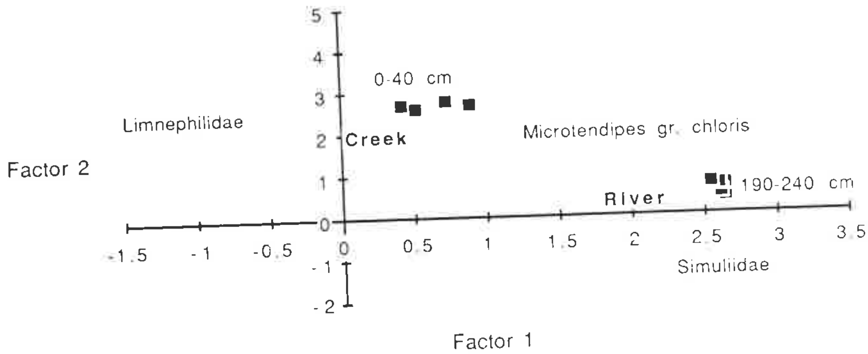

FIGURE 9. Factor analysis of the samples and insects in a sediment core from the Nieuwe Merwede

here. In 1421 there was a disastrous flood in the southwestern part of the Netherlands (the Saint Elizabeth flood). The River Merwede completely washed away a vast area of land. In the following centuries sedimentation progressed and resulted in the formation of a dense system of small and large creeks. A century ago this system was cut through by a newly dug river called the Nieuwe (New) Merwede. The sediment composition in the core is roughly as follows:

0–40 cm:predominantly coarse sand with pieces of wood
40–190 cm:peat and clay in varying quantities
190–240 cm:predominantly fine sand clay

In Figure 9 the insect analyses have been summarized by means of a factor analysis. The most striking feature of the analysis is the clear separation between the upper and lower part of the core. The peat in between hardly contains any insect remains. The Simuliidae cluster represents river-inhabiting taxa and apart from Simuliidae includes *Harnischia* sp., *Potthastia gaedii*, *Stenochironomus* sp., *Hydropsyche contubernalis*, *Polypedilum scalaenum* and a score of less abundant taxa. The Limnephilidae cluster includes *Micropsectra* sp., *Zavrelia pentatoma*, *Glyptotendipes pallens*, *Chaetocladius* spp., *Metriocnemus* with three species, *Bryophaenocladius* sp. and *Limnophyes* sp. The first two representatives in particular can reach high abundances in small slow-flowing streams in the eastern part of the Netherlands. The latter four genera (all Orthocladiinae) are (semi)terrestrial, which may be evidence that the creek was a very shallow one, with parts becoming dry temporarily. The cluster between these two extremes is either formed by taxa which occur in both large rivers and small streams (e.g. *Microtendipes gr. chloris*), or by taxa that cannot properly be identified in the samples (e.g. Pentaneurini).

According to geological studies (Zonneveld, 1960; Verbraeck, 1970; Verbraeck and Bisschops, 1980; Berendsen, 1982) peat formation and river deposits alternate in Holocene sediments in the western part of the Netherlands. The bulk of peat formed in the subboreal (2000–5000 BP) as part of the so-called Hollnd peat, which has a widespread lateral extension throughout the western part of the country. The age of the river deposit at the bottom of the core has not been established, but it is probably several thousands of years. (the peat has an age of 5140 ± 40 BP). The insects in this deposit may be considered as the inhabitants of the natural Rhine or Meuse. As pointed out above, in the natural Rhine the number of insects that inhabited the bottom compares to those that inhabited the solid substrate, which also is the case in these deposits with an even distribution over both types of habitats (45 per cent each). If its estimated age is correct, the natural swamp forests near the river must have consisted mainly of Alnus. On the lower parts, willow coppice must have grown. The higher parts were covered with Quercus, Ulmus, Fraxinus and Corylus (Zonneveld, 1960; Van Der Woude, 1981).

The tidal creek deposit at the top of the core is of unknown age but could date from after the Saint Elisabeth flood (1421) when the numerous smaller and larger tidal creeks were formed. This deposit reveals that these creeks used to be inhabited by caddisflies (Limnephilidae). This is an important fact, as Van Urk (1984) found a distinct absence of Trichoptera in these tidal creeks. From this evidence, it may be concluded that the absence of Trichoptera must be entirely due to river pollution, as the morphology of the creeks is still quite natural.

CONCLUSION

In this palaeoecological study the lack of a reliable dating method of river sediment cores was a major problem. For the time being this problem can be partly overcome by collecting floodplain deposits, with minimum ages determined from old maps. Palaeoecology in large rivers appears to be a powerful instrument, however, in generating the species composition of former insect faunas and in revealing the differences between a former and the present situation.

As a consequence of large-scale chemical and physical changes which have taken place in the Rhine, the insect fauna of the river has changed completely. Eighty to one hundred insect taxa have disappeared from the river over the last few centuries (see appendix). The changes in habitats documented in the literature are reflected by these changes in the insect fauna. Three important changes of individual taxa are:

- the propagation of species with a southern distribution possibly caused by the long-term rise in water temperature;
- a positive relationship between the deformities of headcapsules and the heavy metal content of the river sediment; and
- the decline and extinction of Simuliidae—once abundant—over the last few centuries.

This study can be considered as the initial phase of palaeolimnological river research in the Netherlands. The changes observed in the Rhine by means of sediment analyses still stand fairly isolated, since no direct links can be made with causal factors. Research needs to focus on establishing these links. A possible approach is to relate the biological characteristics in the sediment to the levels of persistent pollutants. Another line of approach would be to determine the sensitivity spectra of the extinct indicator species still living in other rivers. These spectra would help greatly if we want to restore the Rhine into a suitable ecosystem for these species.

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APPENDIX 1. LIST OF TAXA IN THE SEDIMENT AND EXUVIAE COLLECTIONS

Key: E = Eurytope
L = Lithon
LR = Lithorheon
P = Pelon
PS = Psammon
T = Terrestrial
V = Vegetation
? = Unknown

Taxon	Habitat	Palaeo	Recent
EPHEMEROPTERA			
Baetidae	LR	+	
Caenis sp.	L	+	+
Cloeon sp.	L	+	+
Ecdyonurus sp.	LR	+	
Ephemera sp.	PS	+	
Ephemerella sp.	LR	+	
Ephoron virgo	PS	+	
Heptagenia sp.	LR	+	
Leptophlebiidae	V	+	
Palingenia longicauda	P	+	
Potamanthus luteus	LR	+	
Raptobaetopus tenellus	PS	+	
Rhithrogena sp.	LR	+	
PLECOPTERA			
Nemouridae	LR	+	
Perlidae	LR	+	
HETEROPTERA			
Aphelocheirus aestivalis	LR	+	
TRICHOPTERA			
Athripsodes aterrimus	V	+	
Athripsodes sp.	V	+	
Brachycentrus subnubilus	LR	+	
Ceraclea sp.	LR	+	+
Cheumatopsyche lepida	LR	+	
Chimarra marginata	LR	+	
Cyrnus sp.	L	+	+
Ecnomus tenellus	L	+	+
Glossosomatidae	LR	+	
Goeridae	LR	+	
Hydropsyche angustipennis	LR	+	
Hydropsyche contubernalis	LR	+	+
Hydropsyche pellucidula	LR	+	
Hydropsyche saxonica	LR	+	
Hydropsyche sp.	LR	+	+
Hydroptilidae	V	+	
Lepidostoma hirtum	LR	+	
Leptoceridae	V	+	
Limnephilidae	PS	+	
Lype sp.	L	+	
Micrasema sp.	LR	+	

Taxon	Habitat	Palaeo	Recent
Molanna sp.	PS	+	
Mystacides longicornis	V	+	
Neureclipsis bimaculata	L	+	+
Notidobia ciliaris	PS	+	
Odontocerum albicorne	LR	+	
Oecetis sp.	V	+	
Oligoplectrum maculatum	LR	+	
Phryganea bipunctata	V	+	
Polycentropus flavomaculatus	LR	+	
Psychomyia pusilla	LR	+	
Rhyacophila sp.	LR	+	
Sericostoma sp.	PS	+	
SIMULIIDAE			
Byssodon maculatum	V	+	
Eusimulium sp.	LR	+	
Prosimulium sp.	LR	+	
Simuliidae gen. 1	LR	+	
CHIRONOMIDAE-TANYPODINAE			
Labrundinia sp.	?	+	
Pentaneurini	?	+	+
Procladius sp.	P	+	+
Tanypus sp.	P	+	+
DIAMESINAE			
Diamesa carpatica	LR	+	
Diamesa sp.	LR	+	
Monodiamesa bathyphila	PS	+	
Potthastia gaedii	P	+	
Potthastia longimana	P	+	
Prodiamesa olivacea	P	+	+
Syndiamesa sp.	LR	+	
ORTHOCLADIINAE			
Acricotopus lucens	V	+	
Brillia longifurca	LR	+	+
Brillia modesta	LR	+	+
Bryophaenocladius sp.	T	+	+
Cardiocladius fuscus	LR	+	+
Chaetocladius piger agg.	T	+	
Chaetocladius sp.	T	+	
Chaetocladius? sp.	T	+	
Corynoneurinae indet.	V	+	+
Cricotopus flavocinctus	LR	+	
Cricotopus sg. Isocladius	L	+	+
Cricotopus triannulatus	LR	+	+
Cricotopus trifasciatus	L	+	
Cricotopus/Orthocladius	LR	+	+
Diplocladius cultriger	V?	+	
Eukiefferiella claripennis agg.	LR	+	+
Eukiefferiella ilkleyensis	LR	+	
Eukiefferiella sp.	LR	+	+
Gymnometriocnemus sp.	T	+	+
Heterotrissocladius marcidus	PS	+	

continued

Taxon	Habitat	Palaeo	Recent
Hydrobaenus lugubris	T	+	+
Limnophyes sp.	T	+	+
Metriocnemus fuscipes	T	+	+
Metriocnemus hirticollis agg.	T	+	+
Metriocnemus terrester	T	+	+
Metriocnemus? sp.	T	+	
Nanocldius sp.	E	+	+
Orthocladius (Euorthocladius) rivulorum	LR	+	
Orthocladius (Euorthocladius) sp.	LR	+	+
Paracladius conversus	PS	+	+
Parakiefferiella bathophila	L	+	
Parametriocnemus stylatus	PS	+	
Paratrichocladius rufiventris	LR	+	+
Psectrocladius gr. sordidellus	V	+	+
Psectrocladius platypus	V	+	
Psectrocladius psilopterus	V	+	
Pseudorthocladius sp.	T	+	+
Pseudosmittia sp.	T	+	+
Rheocricotopus sp.	LR	+	+
Smittia gr. aquatilis	T	+	+
Symposiocladius lignicola	V	+	
Synorthocladius semivirens	V	+	+
CHIRONOMINI			
Beckidia zabolotzkyi	PS	+	
Chernovskiia 'macrocera'	PS	+	
Chironomini gen. 1	?	+	
Chironomus gr. plumosus	P	+	+
Chironomus gr. uliginosus	P	+	+
Cladopelma gr. laccophila	P	+	+
Cladopelma gr. lateralis	P	+	
Cryptochironomus sp.	PP	+	+
Cryptotendipes gr. holsatus	PS	+	
Demeijerea rufipes	L	+	
Demicryptochironomus vulneratus	PS	+	
Dicrotendipes gr. nervosus	L	+	+
Dicrotendipes notatus	L	+	
Einfeldia dissidens	P	+	
Endochironomus albipennis	P	+	+
Endochironomus gr. dispar	V	+	
Endochironomus tendens	P	+	
Glyptotendipes caulicola	V	+	+
Glyptotendipes gr. pallens	P	+	+
Glyptotendipes gr. signatus	V	+	
Glyptotendipes sp.	?	+	+
Harnischia sp.	P	+	+
Kiefferulus tendipediformis	P	+	
Kloosia pusilla	PS	+	+
Lipiniella arenicola	PS	+	+
Microchironomus tener	P	+	+
Microtendipes gr. chloris	PS	+	
Microtendipes rydalensis agg.	?	+	
Microtendipes tarsalis agg.	?	+	

Taxon	Habitat	Palaeo	Recent
Parachironomus arcuatus	L	+	+
Parachironomus longiforceps	L	+	+
Paracladopelma laminata agg.	PS	+	
Paracladopelma sp.	PS	+	
Paralauterborniella nigrohalteralis	?	+	
Paratendipes connectens 3 Lipina	PS	+	
Paratendipes gr. albimanus	PS	+	
Paratendipes intermedius	PS	+	
Phaenopsectra sp.	P	+	+
Polypedilum cf. *uncinatum*	?	+	
Polypedilum gr. bicrenatum	P	+	+
Polypedilum laetum agg.	L	+	+
Polypedilum nubeculosum	P	+	+
Polypedilum pedestre agg.	V	+	+
Polypedilum scalaenum	PS	+	+
Polypedilum sordens	V	+	+
Pseudochironomus prasinatus	PS	+	
Pseudochironomus sp.	PS	+	
Robackia demeijerei	PS	+	
Stenochironomus sp.	V	+	
Stictochironomus sp.	PS	+	
Tribelos intextus	P	+	
Xenochironomus xenolabis	L	+	+
Zavreliella marmorata	V	+	
TANYTARSINI			
Cladotanytarsus gr. mancus	PS	+	+
Micropsectra sp.	LR	+	+
Paratanytarsus confusus	L	+	+
Paratanytarsus tenuis	L	+	+
Rheotanytarsus sp.	LR	+	+
Stempellina sp.	PS	+	
Tanytarsus gr. brundini	PS	+	
Zavrelia pentatoma	P	+	
Total taxa		167	66

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