T. TITTIZER AND M. BANNING[1]

Biological assessment in the Danube catchment area: Indications of shifts in species composition induced by human activities

From the variety of research activities special reference is made to the development of the aquatic life community (macrozoobenthos) in the Danube reach between Kelheim (river-km 2,414) and Jochenstein (river-km 2,202). Besides the consequences of river engineering projects and today's improved water quality, the newcomer animal species that have established themselves in recent times are considered.

The training and especially the impoundment of larger watercourses for improved navigability entail fundamental changes both in the cycles of matter and in the qualitative and quantitative species composition of the biocoenosis. Many stenoecious[2] potamal species lost their livelihood, and they disappeared from the population structure of the river biocoenosis. The "ecological niches" that became vacant could be filled by euryoecious species, among them many newcomers (neozoa).

In summary we can note that the fundamental flow-induced changes in the navigable German reach of the Danube cause a shift from an originally epipotamal, lithophil fauna with prevailing passive filter-feeders and grazers towards a littoral, psammophil to pelophil fauna dominated by sediment feeders and active filter-feeders.

INTRODUCTION

The International Association for Danube Research (IAD) was established in 1956 with the aim to promote and co-ordinate the activities in the fields of hydrology, water-resources management and water pollution control in the riparian countries. The themes of highest relevance and urgency in the different specialisations are summarised in IAD Decade Programmes and serve as guidelines for research activities. For the decade 1987 to 1996 the following general themes were formulated [28]:

- Comparative limnological studies of impounded and not-impounded Danube reaches;
- Influences of power stations and impoundment weirs on the ecosystem in the River Danube;
- Interactions between tributaries and the main river;
- Improvement and unification of analytical methods;
- Joint implementation of bilateral and multilateral studies and research projects.

From the variety of research activities the following description will single out the findings about the macrozoobenthos in the Danube. In this connection special reference is made to the development of the aquatic life community in the Danube reach between Kelheim (river-km 2,414) and Jochenstein (river-km 2,202), which has been studied for some decades by the German Federal Institute of Hydrology (*BfG*), Koblenz.

Besides the consequences of river engineering projects and today's improved water quality, the newcomer animal species that have established themselves in recent times will be considered. These invasions are closely associated with the use of the River Danube by navigation. With the opening of the Main-Danube Canal (in September 1992) the Danube together with the rivers Main and Rhine provides a navigable waterway of 3,500 km length connecting the Black Sea with the North Sea.

THE STRUCTURE OF THE RIVER SYSTEM

The River Danube with its length of some 2,850 km is the second largest river in Europe next to the River Volga. It drains a precipitation area of 817,000 km². About 80 million people live in fourteen states in its catchment area (cf. Figure 1).

In a comparison with the rivers Elbe and Oder, the catchment area of the Danube is very rich in water: Although the Danube drains in Germany a smaller area than the Elbe (about 20%), it has already before the inflow of the River Inn a mean flow of about 640 m³/s and at the German-Austrian border even of 1,430 m³/s. The mean streamflow at the inflow into the Black Sea is around 6,500 m³/s. The season of high water levels in the upper reaches usually lasts from May to August, while between October and March low stages dominate. However, this general pattern may be fundamentally distorted in single years. The intensity of surges reaches its highest degree when inflowing tributaries cause sudden increases in streamflow and the riverbed narrows. For instance, at Passau, where the flows of the Danube and the Inn unite, water level variations of up to 13 m were observed. Flood marks at Passau (and at Linz and Mauthausen in Austria), which remind of the Danube flood on 15 August 1501, are the oldest of this kind in Europe [9].

[1]Bundesanstalt für Gewässerkunde (German Federal Institute of Hydrology), Kaiserin-Augusta-Anlagen 15-17, 56068 Koblenz, Germany, e-mail: tittizer@bafg.de, banning@bafg.de

[2]This paper contains a glossary of terms at the end, before the references.

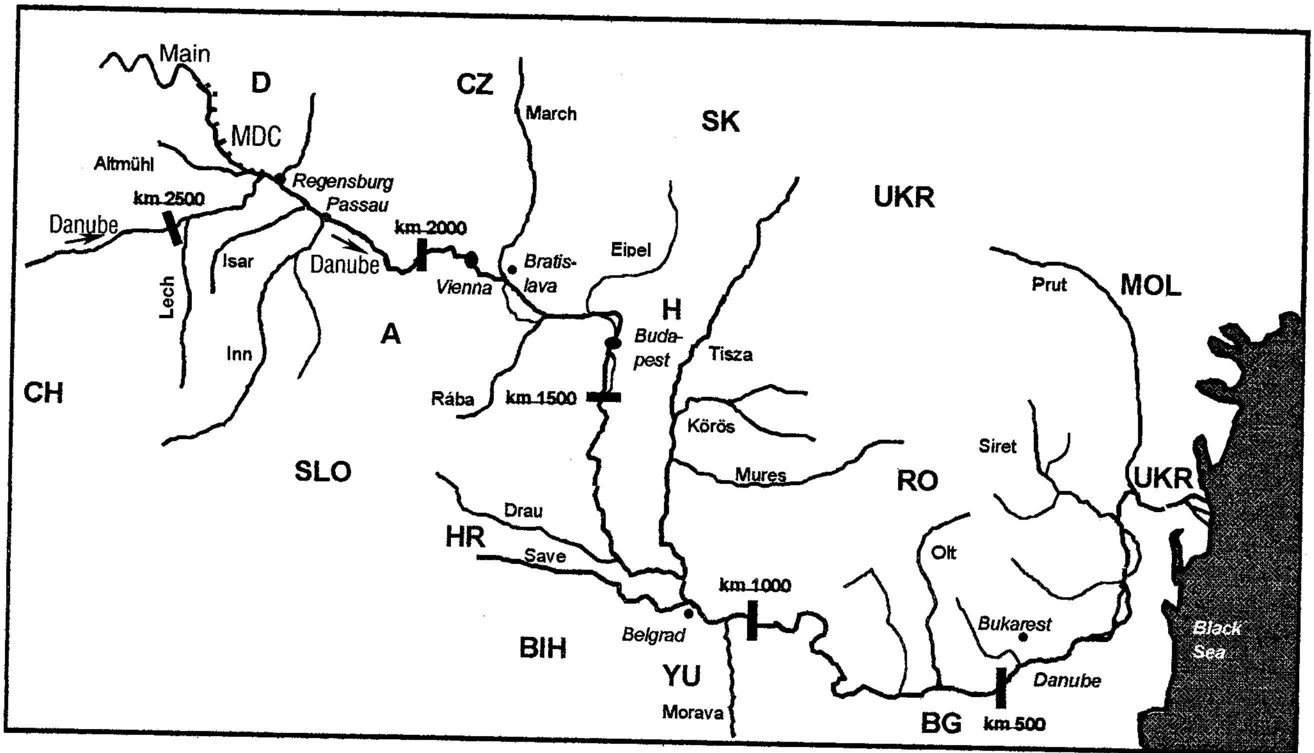


Figure 1. Catchment area of the Danube river system. Capital cities and some important rivers in the Danube river basin are indicated.
Legend: A = Austria; BG = Bulgaria; BIH = Bosnia Herzegovina; CH = Switzerland; CZ = Czech Republic; D = Germany; H = Hungary; HR = Croatia; YU = Yugoslavia; MDC = Main-Danube-Canal; MOL = Moldavia; RO = Romania; SK = Slovakia; SLO = Slovenia; UKR = Ukraine

THE IMPOUNDMENT OF THE RIVER DANUBE

Already in the Middle Ages man realised that an optimum utilisation of watercourses both as energy source and as waterway for transport can be achieved by controlled impoundment. Consequently, the impoundment of the upper Danube began in the 12th century; the first weir was erected in the year 1170. It was followed by the construction of altogether fifty-four more weirs (see Table 1). The upper course of the Danube with a bed gradient of up to 1.1 ‰ has more weirs than the middle course, where the slope is merely 0.2 to 0.5 ‰. On the navigable Danube all weirs, except the one at Kachlet, were built after WW II [32].

Impoundments always mean interventions into the sensitive control circuit between streamflow and sediment transport that characterises flowing waters. Some of the main consequences are morphological changes - essentially sedimentation and erosion processes - that may differ in dependence on streamflow conditions as well as the amount

Table 1. Overview on impoundments weirs (if possible, with the year of construction) in the River Danube and sorted per country [32].

Country	River-km	Location of impoundment weir (Year of construction)
Germany	> 2750	Neudingen (1969), Geisingen (1170)
Germany	> 2500	Fridingen (1923), Beuron, Talhof, Thiergarten, Gutenstein, Diethfurt, Scheer, Laiz, Sigmaringen, Jakobstal, Riedlingen, Rechtensstein, Obermarchtal, Munderkingen, Rottenacker, Öpfingen, Donaustetten (1926/1974), Wiblingen (1907/1960), Ulm-Böfingerhalde (1952), Oberelchingen (1961), Leipheim (1961), Günzburg (1962), Offingen (1963), Gundelfingen (1963), Faimingen (1965), Dillingen (1981), Höchststett (1982), Schwenningen (1983), Donauwörth (1984).
Germany	> 2000	Bertholdsheim (1967), Bittenbrünn (1969), Bergheim (1970), Ingolstadt (1971), Vohburg, (1993), Bad Abbach (1978), Regensburg (1977), Geisling (1985), Straubing (1995), Kachlet (1927), Jochenstein (1955).
Austria	> 2000	(Jochenstein (1955), Aschach (1964), Ottensheim-Wilhering (1974), Abwinden-Asten (1979), Wallsee-Mitterkirchen (1968), Ybbs-Persenbeug (1959), Melk (1982).
Austria	> 1500	Altenwörth (1976), Greifenstein (1985), Freudenau (1998).
Slovakia	> 1500	Gabcikovo (1986-1990).
Yugoslavia/ Romania	> 500	Djerdap/Portile de Fier I (1972), Gruia/Portile de Fier II (1984).

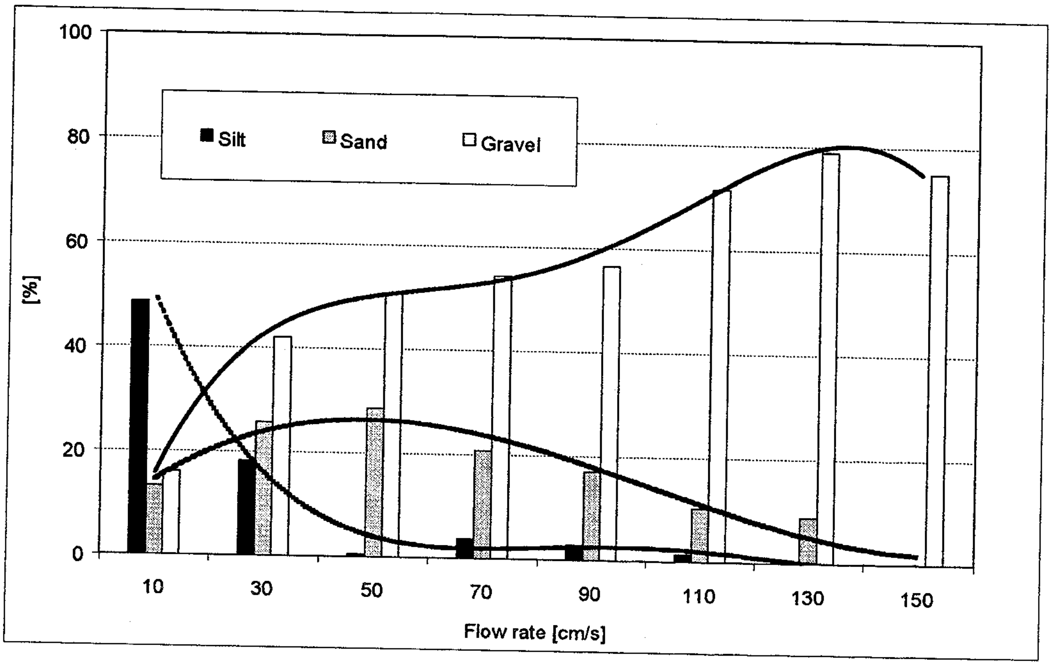


Figure 2. Distribution of bottom substrates (mean values and polynomial approximation 4. order) prevailing in the Federal waterway Danube (Germany) in dependence on the flow rate [2].

and grain-size composition of the transported solids. Other influencing parameters are the geometry and the curvature of the impounded river, as well as the shape and structure of its bottom. Generally, these morphological changes have important impacts also in other compartments (e.g. groundwater level, water quality and microbial processes, fauna and flora).

The most important ecological factors for the colonisation of the River Danube (like for any other watercourse) are beyond doubt the currents and closely associated with them the distribution of sediments in the river. Solids transport in a river is governed by certain laws. So obviously the interventions by river engineering could not remain without impacts on the morphology of the Danube.

In the free-flowing reaches of the upper Danube (Germany, Austria and partially also in the Slovak-Hungarian reach) the river bottom is predominantly covered by gravel, while further downstream in the river continuum sand deposits and loam surfaces prevail in the Rumanian and Ukrainian reaches [19]. In contrast to the free-flowing river, where sediment sorting generates a small-scale and often mosaic-like pattern [4], the German and Austrian reaches often have widespread silt deposits as a consequence of the impoundments.

The relations between the grain-size spectrum of the sediments and the mean flow velocity under conditions of mean low-flow (MLQ) can be seen in Figure 2. Thus, flow rates may be used to distinguish certain areas, where very different qualitative conditions and clearly definable biological-ecological situations develop. For instance, the flow

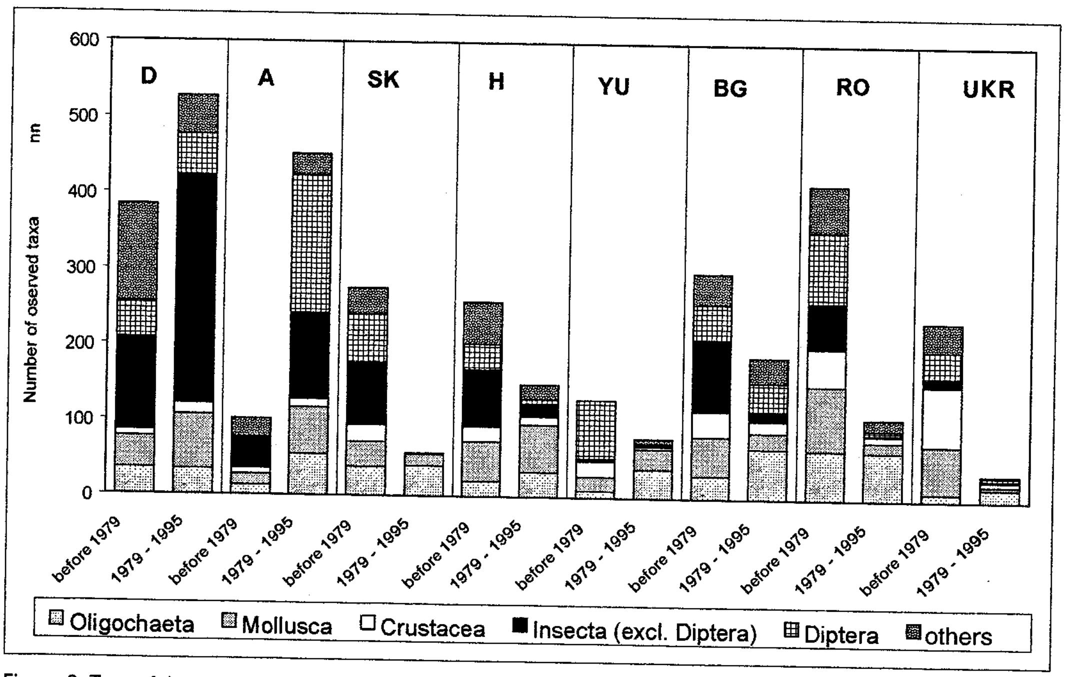


Figure 3. Taxa of the macrozoobenthos groups observed in the national reaches of the River Danube before 1979 and from 1979 to 1995 [19].

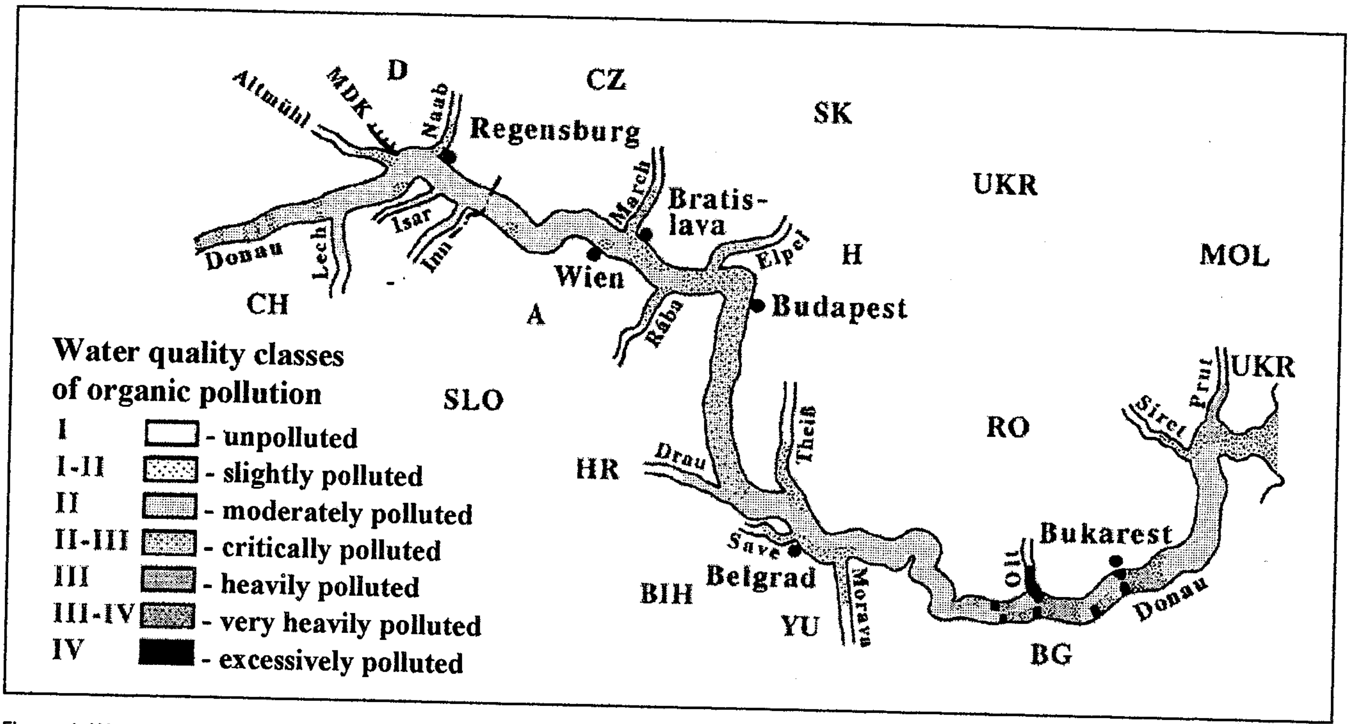


Figure 4. Water quality classes of organic pollution in the River Danube in 1995 [31].

rate of circa 20 cm/s sets a distinct limit: At this rate the dragging force of the flowing water decreases so strongly that the finest material begins to settle in the rivers or in the upper reaches of the impoundments. Upstream of these so-called silt zones in the impoundments, one finds (at flow rates of circa 40 cm/s) the usually sparsely populated "sand zone".

OVERVIEW ON THE LONG-TERM DEVELOPMENT OF THE MACROZOOBENTHOS IN THE RIVER DANUBE

A basic condition of the observation of the long-term development of a life community is the definition of a reference or initial state. Usually, this is an "anthropogenetically uninfluenced pristine state" that existed long time ago. The term "potentially natural fauna" refers in this context to organisms that can be expected to be present in the Danube, provided the wastewater load is drastically reduced and floodplains are largely reactivated.

More than thirty years have elapsed since the first major summary of the results of scientific research of the Danube was published in "Limnology of the Danube" [12]. Since then numerous research projects and publications about the organisms inhabiting this river have been produced. A new survey about the composition of the Danube macrozoobenthos can be found in [19] (Figure 3).

According to the publications from the period 1979-1995, the macrozoobenthos of the Danube comprised 936 taxa. The distinct increase in the number of species observed in Germany and Austria, however, must be called into question since most of it cannot be explained by improved wastewater treatment [19]. Especially the alarming decline of highly threatened potamal[1] species is hidden behind a purely numerical comparison [18, 27]. In fact, the overwhelming portion in the increase in the number of species is due to improved faunal knowledge on the basis of a modified and extended methodology, advances in the field of taxonomy and the immigration of not-indigenous species [2]. Similarly, the decrease in species numbers in Slovakia, Hungary and in Yugoslavia (partially also in Romania and Ukraine) is basically not explicable by deteriorating environmental conditions, but the main reason here is the presently poor intensity of research [19].

The results from the surveys in the Bulgarian (and partly also the Romanian) Danube reach give a contrasting picture. The Bulgarian reach was repeatedly surveyed in longitudinal and cross profiles after 1979. Here, the serious reduction in species diversity (Figure 3) can be assigned nearly exclusively to higher pollution in the tributaries and in the effluents from settlements along this river reach (Figure 4). Meaningful is here the decline of the insect fauna since 1979 (e.g. Ephemeroptera, Plecoptera, Odonata), which reacts very sensitively to pollution, and the simultaneous increase of the Oligochaeta, which are more tolerant against wastewater load [14, 18, 22, 25]. The decline of the sensitive mayfly species *Palingenia longicauda, Ephoron virgo, Ametropus fragilis, Brachycercus harisella and Cercobrachis minutus* and of three Plecoptera species is most likely due to increased pollution [19].

Also in the Danube reach between Kelheim and Jochenstein, which has been studied by the German Federal Institute of Hydrology since 1958, the strongest decline is assumed to affect the stenoecious potamal species, as was demonstrated in the River Rhine by [34]. Especially those species that strongly depend on summer-warm, larger watercourses were not or only in single cases able to escape to alternative habitats in times of the highest wastewater load. Some of these species have recolonised the navigable Danube probably being introduced by ships from more downstream reaches (e.g. the gastropods *Theodoxus danubialis* and *Theodoxus transversalis*). Other, often highly threatened species (such as the bivalve *Pseudanodonata complanata*, the mayfly *Ephoron virgo*, the dragonfly *Gomphus vulgatissimus* and the beetle *Macronychus quadrituberculatus*) could recolonise the Danube presumably from still existing refuges (e.g. waters in the floodplain, tributaries). However, as it is

[1]This paper contains a glossary of terms at the end, before the references.

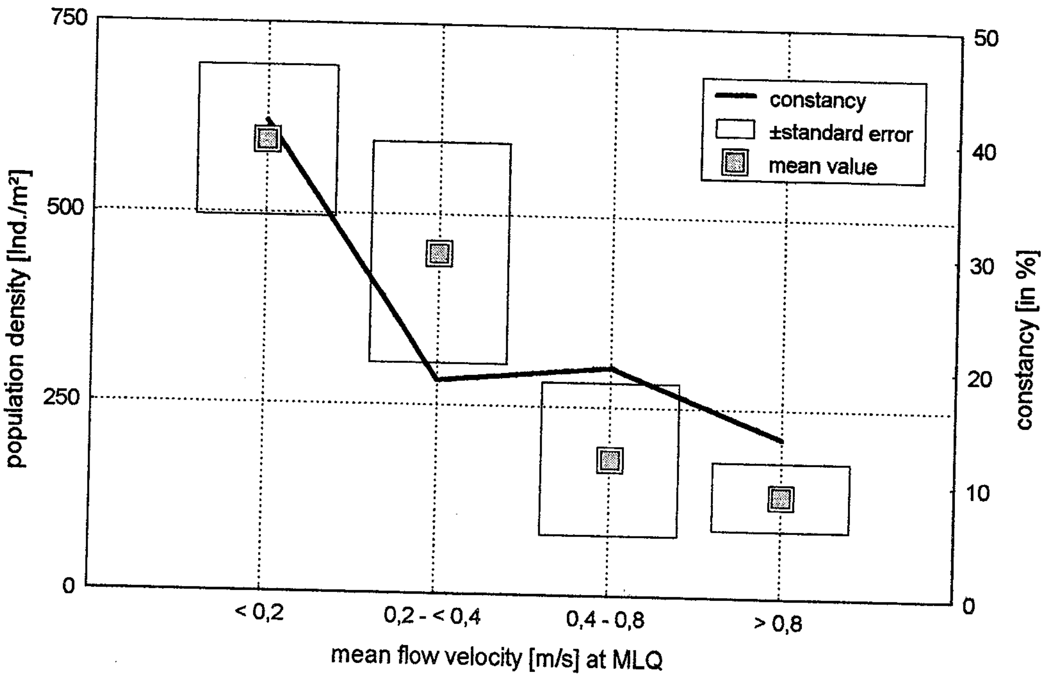


Figure 5. Mean population densities (including standard error) and constancy of *Hypania invalida* in the navigable German Danube (1987-1994) in dependence on flow velocity [2].

obviously the case in all major rivers in Central Europe, a successful re-establishment of other highly threatened or extinct potamal species often encounters to insurmountable obstacles. These result mainly from intensified river training. Just to mention a few: the Plecoptera *Isogenus nubecula* and *Perla bipunctata* which used to occur in the German Danube reach [5] as well as *Taeniopteryx nebulosa* and the Ephemeroptera *Oligoneuriella rhenana* and *Palingenia longicauda*, which is still common in the River Tisza (a major Danube tributary in Hungary) [3] and had been observed in the Bulgarian reach before 1979 [17]. In a comparison of the inventories of 1958-1985 with today's surveys (1987-1996) in the Danube, where it is a German Federal waterway, reveals a deficit of the following nine species: the "sewage fungus" *Sphaerotilus natans*, the bivalve *Unio crassus*, the mayflies *Ecdyonurus dispar*, *Ecdyonurus insignis*, *Ephemerella mucronata, Heptagenia fuscogrisea, Oligoneuriella rhenana, Rhithrogena semicolorata* group and the stonefly *Brachyptera risi*. A future recolonisation, that would be considered positive, with the exception of the "sewage fungus", remains extremely doubtful. For these species like for numerous others which are still found in the considered Danube reach (e.g. the gastropods *Borysthenia naticina, Theodoxus danubialis* and *Theodoxus transversalis*, the bivalves *Pseudanodonta complanata* and *Sphaerium rivicola*, the dragonfly *Gomphus vulgatissimus*, the mayflies *Ecdyonurus venosus* and *Heptagenia flava*, the beetles *Helochares obscurus, Macronychus tuberculatus, Normandia nitens* and *Riolus cupreus*, the caddisflies *Lasiocephala basalis, Lepidostoma hirtum* and *Oligoplectrum maculatum*) the establishment or the stability of populations capable of regeneration remain uncertain [2].

EXPANSION OF AQUATIC NEOZOA IN THE DANUBE AND FAUNAL EXCHANGE BETWEEN THE CATCHMENT BASINS OF RIVERS DANUBE AND RHINE

The training and especially the impoundment of larger watercourses for improved navigability entail fundamental changes both in the cycles of matter and in the qualitative and quantitative species composition of the biocoenosis. As described above, many stenoecious potamal species lost their livelihood, and they disappeared from the population structure of the river biocoenosis. The ecological niches that became vacant could be filled by euryoecious species, among them many newcomers (neozoa). In Germany, about 14 % of all macroinvertebrates populating navigable waterways belong to the neozoa group [29]. Such aquatic life communities changed through anthropogenic interventions and dominated by ubiquists, however, does not have the natural information content and the efficiency (in the sense of the river continuum concept [36]) that characterise a site-adapted evolutionary biocoenosis [26].

In the navigable German reach of the Danube, the spreading of numerous species of ponto-caspian origin has been observed in recent times (e.g. the crustaceans *Jaera istri, Dikerogammarus haemobaphes, D. villosus, Echinogammarus trichiatus, Obesogammarus obesus, Limnomysis benedeni, Hemimysis anomala*) and the flatworm *Dendrocoelum romananodanubiale* [10, 20, 21, 23, 30, 37, 38, 39, 40]. The essential transport mechanism proved to be the cooling-water systems of motor ships [16].

Another typical example is the dispersal of the Polychaet *Hypania invalida*. Within the group of the Annelida, Polychaeta are usually confined to marine zones. The Polychaet *Hypania invalida*, which is common in the Danube Delta and in the lower reaches, was first observed in the German Danube reach by Kothé in the summer of 1958 near Passau. Previously, the area of the "Iron Gate", nearly 1000 km upstream from the mouth, was considered as the most upstream occurrence site of *Hypania invalida* in the Danube basin [8]. In November 1987, this psammo-pelophil species was observed occasionally about 100 km further upstream near Straubing [11]. Like many other potamal species, the Polychaet has established itself in the impoundments Geisling and Straubing reaching densities of up to 8,600 individuals per square metre. It was probably through navigation that the Polychaet reached the Rhine-Main region via the Main-Danube Canal. The first evidence was found by [7] on 27 July 1995 in the Rhine at the German-Dutch border.

A correlation analysis of the population densities in the Federal waterway Danube revealed a significant negative correlation in the dependence on the mean flow velocities (Figure 5). Furthermore, a significant negative correlation with the grain size of the substrate, and a significant positive correlation with growing water depth were found [2].

As a consequence of the renewed removal of the obstacles to dispersion between the two hydrographical catchments in Europe through the construction of the Main-Danube Canal, the establishment of additional newcomer species, besides *Hypania invalida*, can be observed in many rivers in Central Europe. Most of the species of ponto-caspian origin that have established themselves in the German Danube reach have overcome the European watershed via the Main-Danube Canal and have colonised the Rhine-Main region. Figure 6 shows for example the dispersal of the "Danube isopod" *Jaera istri*. Because of the rapidity of the spread, a passive dispersal of the animals through ships must have taken place, as in the flowless Main-Danube Canal itself not a single specimen of this strictly rheophil isopod could be found so far, although each year an inventory was made along the longitudinal profile. It can be expected in future that this rheophil species will further spread in the West-European river systems.

Simultaneously, the freshwater shrimp *Athyaëphyra desmaresti* [39] and the „basket shell" *Corbicula spp.* [35], which originate from the Rhine-Main region, have already established themselves in the Danube. The bivalve *Corbicula spp.*, which is native in East Asia, has been spreading in Central Europe since the early 1980s (Figure 7). The bivalve is extremely competitive and tends to very high population densities [13]. According to our experiences with the

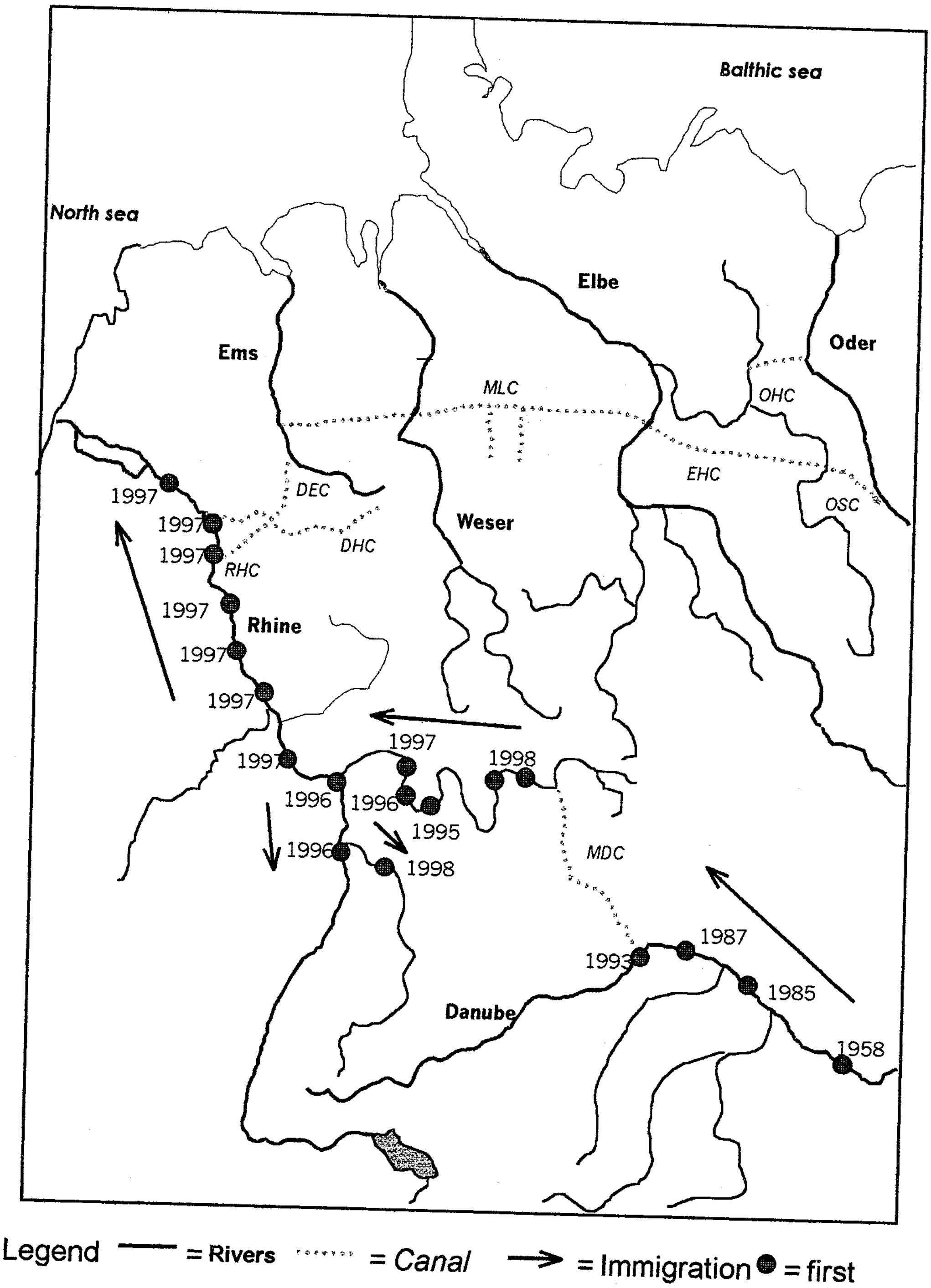


Figure 6. Dispersal of the isopod *Jaera istri* [24].

population dynamics of *Corbicula* in navigable waterways, it takes about three to four years from the first findings to larger population densities.

THE INFLUENCE OF IMPOUNDMENT ON THE MACROZOOBENTHOS IN THE RIVER DANUBE

Flow reduction as a consequence of impoundment constitutes a severe intervention into the ecosystem of flowing waters. The macrozoobenthos in the navigable German Danube reach can serve as an example to show that the flow rate as an ecological parameter influences – as [1] and others have shown - the existence or the adaptive mechanisms not only of single species. In fact, the unidirectional flow in a watercourse is a factor of crucial significance for the shaping of the ecosystem of the watercourse. Flow acts as a general factor with numerous secondary dependences such as grain-size composition of sediments and bed load transport, influences on the light climate and the trophic conditions, and it determines the direction of the transport of substances (longitudinal <-> vertical) and the place of metabolism [2].

For identifying the structures in the relations between various parameters, i.e. for their classification, they were examined by means of the method of multidimensional scaling. The analysis comprised the results of studies along the whole reach of the German navigable Danube reach in the period from 1987 to 1994 (n = 1185). The analysis of the colonisation in this reach, which is assigned to the epipotamal, thus covers the whole range of flow rates from 0.08 m/s to 1.52 m/s (at mean low flow) (see Figure 8).

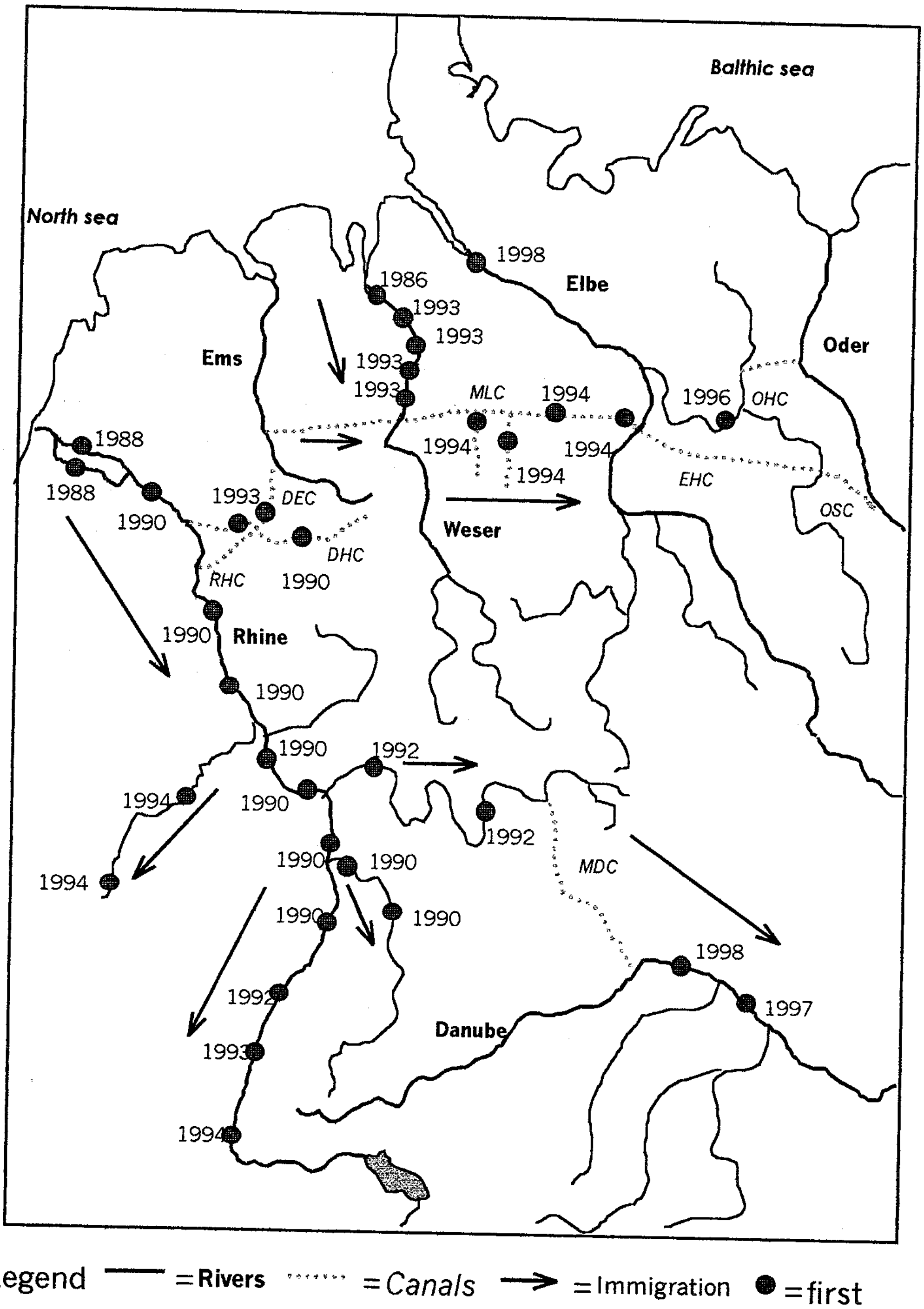


Figure 7. Dispersal of the bivalve *Corbicula spp.* in Central Europe (own and other data [24]).

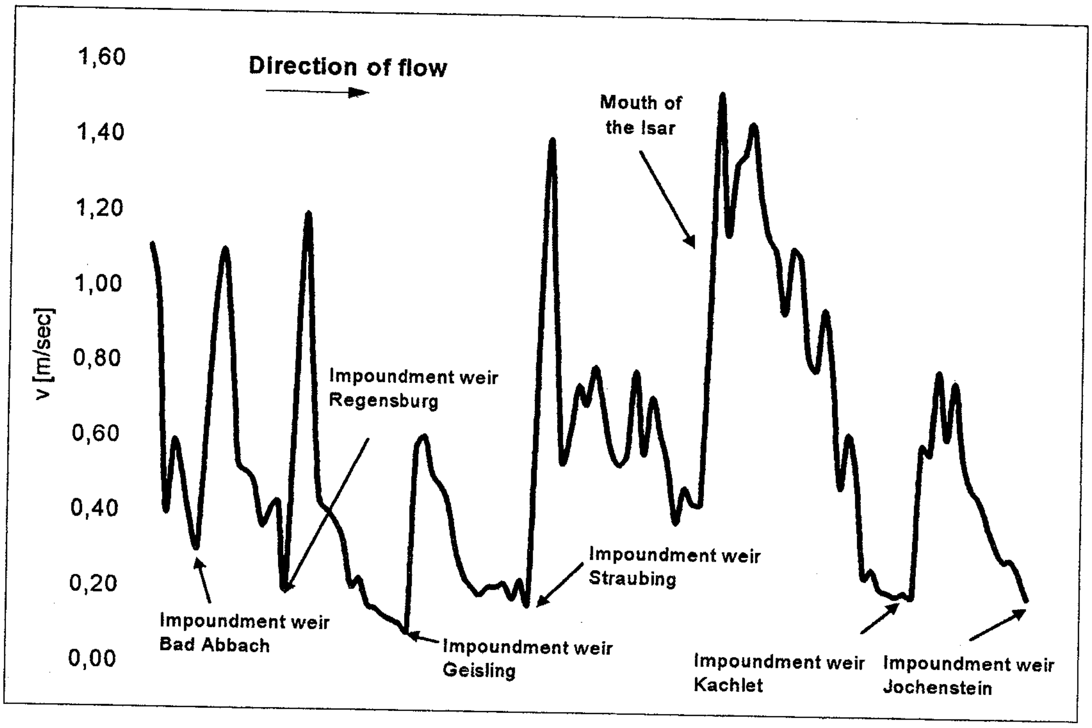
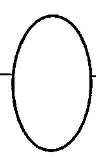


Figure 8. Mean flow velocities in the Danube with the impoundments Bad Abbach, Regensburg, Geisling, Straubing, Kachlet and Jochenstein (computed for MLQ; status of 1995) [2].

Table 2. Distribution patterns of variables in correlation to flow [2], (For explanation of the abbreviations see legend of Figure 9).

Group	Variables	Distribution		
1	WEI, PFIL, LITH, HR, EP	Binomial distribution		Optimum of flow between 0.9 and 1.1 m/s
2	SED, PEL, MP	U-distribution		Mirror image of the distribution of Group 1, pessimum of flow at 0.9 m/s
3	AFIL, PHY, LIT	Exponentially decreasing distribution		Strongly falling flanks in the flow range from 0.1 to 0.4 m/s

The aim of this procedure is to identify similarities in the mutual relations between individual variables. The analysis uses - besides the "Rheo-Index" (according to [2]) - on the one hand the abiotic variables like for example flow rate and substrata and on the other hand the biotic variables like for example the feeding types and biocoenotic regions[3]. The result of the multidimensional scaling is shown in Figure 9.

The separation into two complexes of variables in the multidimensional scaling suggests that the differentiation of the variable groups in the Dimension 1 is closely connected with the multiple effects of the flow rate. The distribution of the bottom-forming substrates silt, sand and gravel along Dimension 1 supports this thesis. In the group standing in negative configuration to Dimension 1, one finds the typical variables that characterise the river biocoenosis of the free-flowing reach of the Danube. On the opposite end of the 1st Dimension, there are the variables for the characterisation of the colonisation of the impounded Danube reaches or those of a still-water biocoenosis. The separation between the variables "coarse rock (GST)" and "shredders (ZKL)" against the variables "gravel" and "akal" in Dimension 2 leads to the assumption that the configuration along this dimension is predominantly determined by the position in the cross profile.

If one considers the variables that are closely together in multidimensional scaling in dependence on the flow rate, one recognises a nearly identical correlation pattern. Among the biological variables in relation to flow one can distinguish three types of non-linear correlations (Table 2).

The aquatic life community of a watercourse (in the navigable German Danube characterised by the variables of group 1) must - besides its adaptation to the hydraulic stress - also tolerate great variations in flow. The pejus of the distribution curves within group 1 of variables is at flow rates of 0.4 or 1.3 m/s, respectively. This spectrum marks thus the optimum range for the benthos found here. The manifold adaptations to flow of river organisms may explain the

[3]In the computation according to [14], the very high abundance of *Corophium curvispinum* was not considered. This appeared necessary since this amphipoda has a tendency to extreme outbreaks in the whole navigable German Danube reach. If *Corophium curvispinum* were included in the analysis, its dominance of nearly 67 % of the whole biocoenosis would conceal the development of the remaining organisms nearly completely.

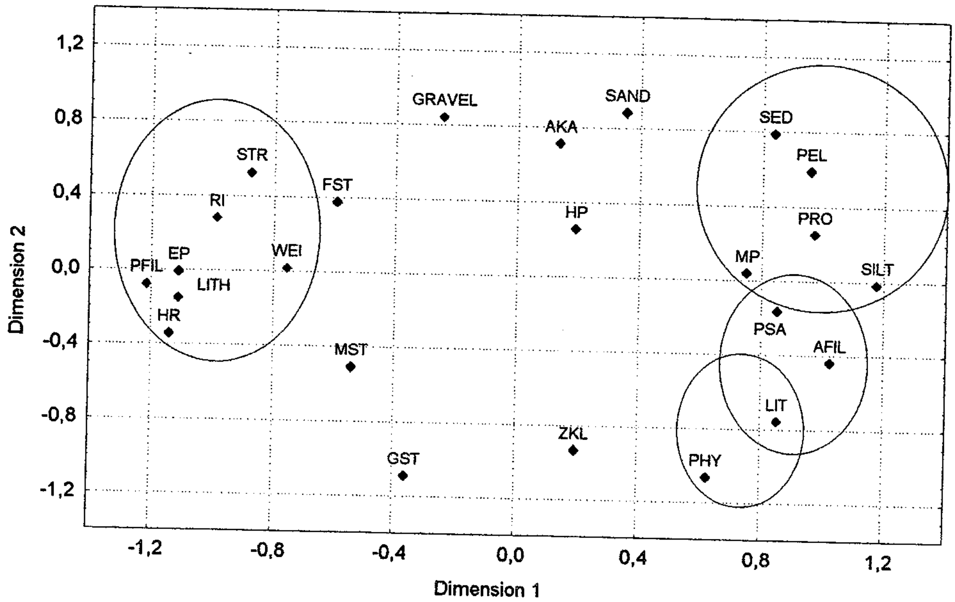


Figure 9. End configuration of the Dimensions 1 and 2 [2].
Legend: RI = Rheo-Index; STR = flow rate; percentages of the substrates: GST = coarse rock, MST = medium rock, FST = fine rock; feeding types: ZKL = shredders, WEI = grazers, AFIL = active filter-feeders, PFIL = passive filter-feeders, SED = sediment feeders; biocoenotic regions: HR = hyporhithral, EP = epipotamal, MP = metapotamal, LIT = littoral, PRO = profundal; habitat types: PEL = pelal, PSA = psammal, AKA = akal, LITH = lithal, PHY = phytal.

relatively wide amplitude of the optimum range. Especially as a defence against being drifted away, the lithophil fauna needs a relatively immobile substrate with sufficient gaps as refuge spaces for sudden short-term increases in flow velocity (e.g. during flood events). Above a threshold of about 1.3 m/s, increasing and permanent relocation of bed-load material on the gravel bed of the Danube has to be expected. This permanent relocation grinds the biofilm, that is consumed by grazing animals, off the pebbles, and the passive filter feeders lose the stable substrate as a basis to which they can attach themselves. Moreover, the availability of food in the flowing water is reduced and the metabolic activities shift into the hyporheic interstitial that is protected against the currents. This thesis is supported by the opposing correlations in the percentages of sediment feeders and the pelophil fauna (here especially numerous Oligochaeta) [2].

The link in food turnover between flowing waters and still waters are the active filter feeders. With decreasing flow intensity the transport of matter takes more and more a vertical direction and the passive filter feeders (PFIL) are replaced by active filter feeders (AFIL). As Figure 10 shows, a 1:1 ratio of PFIL/AFIL marks roughly the transition from

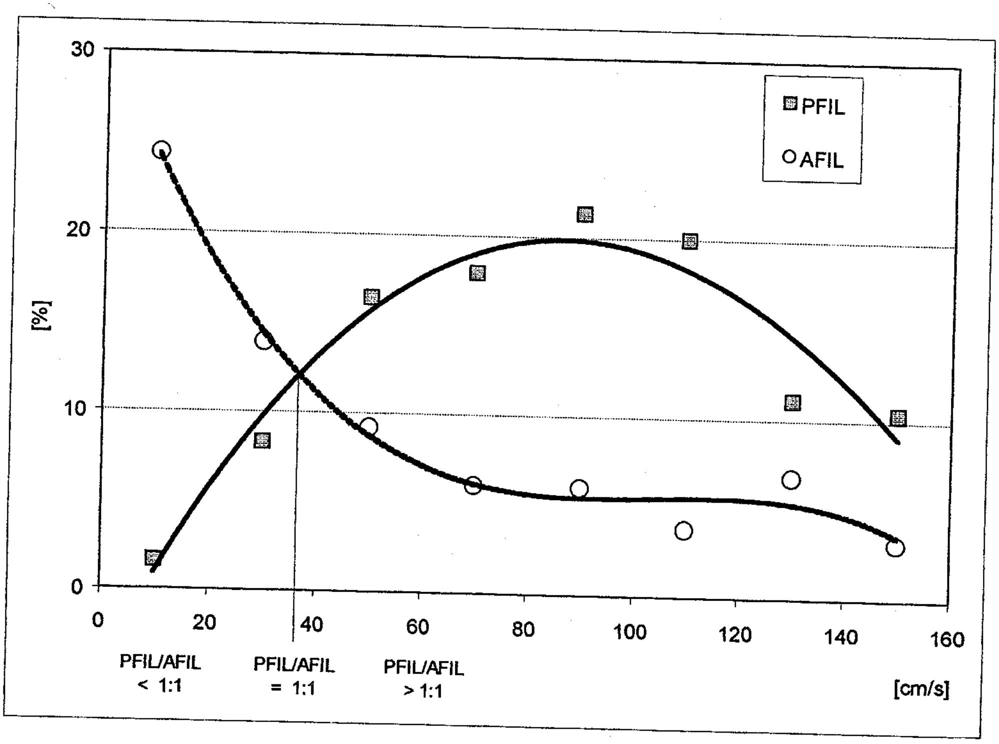


Figure 10. Variation of the percentage of passive filter feeders (PFIL) and active filter feeders (AFIL) in relation to the flow rate [cm/s] (at MLQ) (mean values and polynomial approximation 3. order) [2].

a flowing water to a still-water body with flow rates near 0.4 m/s. Several studies could identify the flow rate around 0.4 m/s as the threshold for the survival of an undisturbed "gravel fauna" [2, 15, 33].

The shift of nutrient transport from the longitudinal direction into the vertical one indicates the approximation of conditions towards the still-water situation and is also an explanation for the strong increase of the littoral component that can be observed together with an advancing reduction of flow. The enormous increase in sediment feeders below a flow rate of 0.2 m/s marks approximately the threshold for the deposition of silt (and unsedimented FPOM). The portion of sediment feeders is then closely correlated with the population density of the macrozoobenthos and indicates the exponentially improving nutrition conditions (production or accumulation and availability of food). In contrast to active filter feeders, this feeder-type depends more on the sedimentation of FPOM. The habitat of the interstitial is lost here. Moreover, due to the sedimentation the light-climatic conditions improve considerably and thus promote primary production. In the free-water zone, an increase in plankton productivity can be expected. Via the food web this leads to an increased food supply at all trophic levels of the ecosystem, what is also an explanation for the high colonisation density below a flow rate of 0.2 m/s [2].

SYNOPSIS

In summary we can note that the fundamental flow-induced changes in the navigable German reach of the Danube cause a shift from an originally epipotamal, lithophil fauna with prevailing passive filter-feeders and grazers towards a littoral, psammophil to pelophil fauna dominated by sediment feeders and active filter-feeders.

The response of the biocoenosis to the impoundment can be derived from the initially prevailing species spectrum. The species that originally made up the river biocoenosis are promoted in the sequence in which their affinity to the littoral increases. In the River Danube this phenomenon finds its expression in the strong increase in ubiquists. The basin of the navigable German Danube reach lacks other rivers that have a typical potamal fauna. Through the influence of the River Inn, the Austrian reach of the Danube can even be assigned to the rhithral [6]. Consequently, an upstream shift of species and communities in the sense of an "artificial ageing" [26] can take place here nearly exclusively through importation of species by navigation (mostly neozoa).

GLOSSARY OF TERMS

Epipotamal: upper section of a river of the plains (in Central Europe called "barbel zone").

Euryoecious: species which have a moderate to wide ecological range in regard to a special environmental parameter (opposite to stenoecious).

Lithal: substrate, dominated by stones of different size.

Lithophil fauna: organisms that prefer to live on or in a lithal substrate.

Pelal: substrate on the river bottom, dominated by mud.

Pelophil fauna: organisms that prefer to live on or in a pelal substrate.

Ponto-caspian: zoogeographic term describing the zoogeographic living area of an animal during the last ice-age. Ponto-caspian species were restricted to parts of the pontomediterraneis. In this case the area of the Black Sea and its large tributaries (e.g. the Danube River) and the Caspian area, that is the region of the Caspian Sea and its large tributaries (e.g. Volga River).

Psammal: substrate, dominated by sand.

Psammophil fauna: organisms that prefer to live on or in a psammal substrate.

Rheophil: description of organisms that prefer to stay in fast-flowing water.

Stenoecious: organisms with a very small ecological range.

REFERENCES

1. H. Ambühl, Die Bedeutung der Strömung als ökologischer Faktor, Schweiz. Z. Hydrol. 21, 133-264, 1959
2. M. Banning, Auswirkungen des Aufstaus größerer Flüsse auf das Makrozoobenthos, dargestellt am Beispiel der Donau, Essener Ökologische Schriften 9, 285 pp., 1998
3. M. Csoknya and M. Ferencz, A study of Palingenia longicauda OLIV. in the zoobenthos of the Tisza and Maros (Ephemeroptera) Tiscia 7, 47-57, 1972
4. E. Danecker, Das Makrozoobenthos in Flußstauen. Überlegungen zur Güteeinstufung, Wasser und Abwasser 31, 239-279, 1987
5. E. Dudich, Systematisches Verzeichnis der Tierwelt der Donau mit einer zusammenfassenden Erläuterung. - in: Reinhard Liepolt (Ed.), Limnologie der Donau, Schweizerbart 5, 4-69, 1967
6. N. Hary and H.P. Nachtnebel, Ökosystemstudie Donaustau Altenwörth, Veröffentlichungen des österreichischen MaB-Programms (Innsbruck) 14, 161 pp., 1989
7. A. Klink and A. Bij de Vaate, *Hypania invalida* (Grube 1860) (Polychaeta: Ampharetidae) in the Lower Rhine - new to the Dutch fauna, Lauterbornia 25, 57-60, 1996
8. P. Kothé, *Hypania invalida* (Polychaeta Sedentaria) und Jaera sarsi (Isopoda) erstmals in der deutschen Donau, Arch. Hydrobiol./ Suppl. 34 (Donauforschung 3), 88-114, 1968
9. W. Laszloffy, Die Hydrographie der Donau - in: Reinhard Liepolt (Ed.), Limnologie der Donau, Schweizerbart 1, 16-57, 1967
10. H. Leuchs and A. Schleuter, *Dikerogammarus haemobaphes* (EICHWALD 1841), eine aus der Donau stammende Kleinkrebsart (Gammaridae) im Neckar, Lauterbornia 25, 139-141, 1996
11. H. Leuchs, T. Tittizer, and M. Banning, Räumliche und zeitliche Verteilung von endemischen Arten in der Donau. – Erweiterte Zusammenfassungen der Jahrestagung der Deutschen Gesellschaft für Limnologie 1991 in Mondsee, 300-304, 1991
12. R. Liepolt (Ed.), Limnologie der Donau, 1967
13. A. Meister, Lebenszyklus, Autökologie und Populationsökologie der Körbchenmuscheln *Corbicula fluminea* und *Corbicula fluminalis* (Bivalvia, Corbiculidae) im Inselrhein, Schriftenreihe der Hessischen Landesanstalt für Umwelt, 238, 1997
14. O. Moog (Ed.), Fauna aquatica Austriaca, Lieferung Mai/95, Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft (Wien), 1995
15. E. Polzer and K. Traer, Ökologische Funktionsfähigkeit und biologische Gewässerbeschaffenheit in Fließgewässern und Flußstauen - Erarbeitung methodischer Grundlagen, Forschungsarbeiten Wasserwirtschaft Wasservorsorge (Ed. Bundesministerium für Land- und Forstwirtschaft, Wien), 324 pp, 1991
16. M. Reinhold and T. Tittizer, Zur Rolle von Schiffen als Vektoren beim Faunenaustausch Rhein/ Main/Main-Donau-Kanal/Donau, DGM 41/5, 199-204, 1997
17. B. Russev, Ecology, life history and distribution of *Palingenia longicauda* (OLIVIER) (Ephemeroptera), Tijdschrift voor Entomologie 130, 109-127, 1987
18. B. Russev, Threatened Species of Ephemeroptera (Insecta) from Bulgaria, Lauterbornia 9, 13-17, 1992.

19. B. Russev, Das Makrozoobenthos der Donau – Dynamik der Veränderungen durch anthropogenen Einfluß, Ergebnisse der Donauforschung 4, 257 – 364, 1998
20. M. Schleuter and A. Schleuter, *Jaera istri* (VEUILLE) (Janiridae, Isopoda) aus der Donau erreicht über den Main-Donau-Kanal den Main, Lauterbornia 21, 177-178, 1995
21. M. Schleuter, A. Schleuter, S. Potel, and M. Banning, *Dikerogammarus haemobaphes* (EICHWALD 1841) (Gammaridae) aus der Donau erreicht über den Main-Donau-Kanal den Main, Lauterbornia 19, 155-159, 1994
22. U. Schmedtje and M. Colling, Ökologische Typisierung der aquatischen Makrofauna. - Informationsberichte des bayerischen Landesamtes für Wasserwirtschaft 4/96, 543 pp, 1996
23. F. Schöll & M. Banning, Erstnachweis von *Jaera istri* (VEUILLE) (Janiridae, Isopoda) im Rhein. - Lauterbornia 25, 61-62, 1996
24. F. Schöll and M. Banning, Faunistische Untersuchungen (aquatische Makrofauna) an der Donau (Kelheim – Jochenstein) zur Erfassung des ökologischen Ist-Zustandes, BfG-Gutachten (unveröffentlicht) 1128, 1998
25. W. Schönborn, Fließgewässerbiologie, Gustav Fischer (Jena/Stuttgart) 1. Aufl., 1992
26. H. Schuhmacher, „Künstliche Bachalterung" - eine konzeptionelle Charakterisierung anthropogener Veränderungen von mitteleuropäischen Fließgewässern, Verh. Deutsch. Zool. Ges. 79, 318, 1986
27. B. Statzner, Fließwasserökologie aus der Sicht der Tierwelt, Schriftenreihe des Deutschen Rates für Landespflege 58, 761-763, 1989
28. T. Tittizer, Überblick über die Forschungstätigkeit im Rahmen der Internationalen Arbeitsgemeinschaft Donauforschung (IAD), Beitrag zur XVII. Konferenz der Donauländer über hydrologische Vorhersagen und hydrologisch-wasserwirtschaftliche Grundlagen (Budapest) 5.31, 885–890, 1994
29. T. Tittizer, Vorkommen und Ausbreitung aquatischer Neozoen (Makrozoobenthos) in den Bundeswasserstraßen – in: H. Gebhardt, R. Kinzelbach & S. Schmidt-Fischer (Ed.), Gebietsfremde Tierarten (ecomed), 49–85, 1996
30. T. Tittizer, Ausbreitung aquatischer Neozoen (Makrozoobenthos) in den europäischen Wasserstraßen, erläutert am Beispiel des Main-Donau-Kanals, Schriftenreihe des Bundesamtes für Wasserwirtschaft (Wien) 4, 113-134, 1997
31. T. Tittizer, Rhein, Elbe, Donau im limnologischen Vergleich, Jahrestagung der Deutschen Gesellschaft für Limnologie 1997 in Frankfurt/Main, 1997
32. T. Tittizer, Auswirkung der Stauregelung auf das Makrozoobenthos der Donau, Limnologische Berichte der 32. Konferenz der IAD (Wien), 147-160, 1998
33. T. Tittizer, H. Leuchs, and M. Banning, Einfluß der Mindestströmungs geschwindigkeit auf das Makrozoobenthos der Donau, Limnologische Berichte der 28. Tagung der IAD (Varna), 140-144, 1990
34. T. Tittizer, F. Schöll, M. Dommermuth, J. Bäthe, and M. Zimmer, Zur Bestandsentwicklung des Zoobenthos des Rheins im Verlauf der letzten neun Jahrzehnte, Wasser und Abwasser 35, 125-166, 1991
35. T. Tittizer and M. Taxacher, Erstnachweis von *Corbicula fluminea/fluminalis* (Müller 1774) (Corbiculidae, Mollusca) in der Donau, Lauterbornia 31, 103-107, 1997
36. R.L. Vannote, G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing, The River Continuum Concept, Canadian Journal of Fisheries and Aquatic Sciences 37 (1), 130-137, 1980
37. A. Weinzierl, S. Potel, and M. Banning, *Obesogammarus obesus* (SARS 1894) in der oberen Donau (Amphipoda, Gammaridae), Lauterbornia 26, 87-89, 1996
38. A. Weinzierl, and G. Seitz, *Dendrocoelum romanodanubiale* (CODREANU 1949) in der oberen Donau (Turbellaria, Tricladida), Lauterbornia 15, 23-24, 1994
39. A. Weinzierl, G. Seitz, and R. Thannemann, *Echinogammarus trichiatus* (Amphipoda) und *Atyaephyra desmaresti* (Decapoda) in der bayerischen Donau, Lauterbornia 31, 31- 32, 1997
40. K.J. Wittmann, Zur Einwanderung potamophiler Malacostraca in die obere Donau: *Limnomysis benedeni* (Mysidacea), *Corophium curvispinum* (Amphipoda) und *Atyaephyra desmaresti* (Decapoda), Lauterbornia 20, 77-85, 1995