BIODIVERSITY OF MACROZOOBENTHOS IN A LARGE RIVER, THE AUSTRIAN DANUBE, INCLUDING QUANTITATIVE STUDIES IN A FREE-FLOWING STRETCH BELOW VIENNA: A SHORT REVIEW

UWE HUMPESCH AND CHRISTIAN FESL

Professor U.H. Humpesch, Limnological Institute of the Austrian Academy of Sciences, Mondseestraße 9, A 5310 Mondsee, Austria Email: uwe.humpesch@oeaw.ac.at

Dr C. Fesl, Department of Limnology and Hydrobotany of the University of Vienna, Althanstraße 14, A 1090 Wien, Austria Email: christian.fesl@univie.ac.at

Introduction

The Danube is ca. 2850 km in length and is the second largest river in Europe. It rises in the Black Forest of Germany and discharges into the Black Sea (Romania and Ukraine). The catchment includes 12 other countries: Switzerland, Austria, Czech Republic, Slovakia, Hungary, Slovenia, Croatia, Bosnia/Herzegovina, Serbia & Montenegro, Albania, Bulgaria and Moldova (Fig. 1), and nearly 90 million people live in the catchment area of ca. 805 300 km². These numbers illustrate and emphasise the enormous international importance of this river.

The Austrian part of the Danube falls 156 metres in altitude over its 351 km length and, since the early 1950s, the river has been developed into a power-generating waterway, so that the continuity of the river is now interrupted by ten impounded areas. The barrages built across the river include large locks which allow shipping to pass along the international navigation (see photographs in Humpesch 1992). Only two stretches of the original free-flowing river are left, the Wachau region (above river-km 2005, west of Vienna) and the region downstream from the impoundment at Vienna (river-km 1921) (Fig. 2).

Most of the recent theories and concepts related to invertebrates, in the context of the ecology of running waters, are based on studies on small streams, whereas investigations of large rivers have played a minor role for a long time, mainly due to methodological difficulties. Our recent detailed studies on macroinvertebrates in the free-flowing section of the Danube below Vienna, provide an excellent opportunity to survey or restate scientific hypotheses on the basis of a large river – especially because the results of studies on the impounded areas of this river have been summarised by Humpesch (1992).



FIG. 1. Catchment area of the River Danube (Source: WWF).



FIG. 2. Hydroelectric power schemes on the River Danube in Austria, with dates of construction periods of the power stations (\blacksquare) and impounded stretches. m.a.A.= metres above Adrian sea level.



FIG. 3. Typical species of the macrozoobenthos of the free-flowing section of the River Danube below Vienna. (a) *Hypania invalida* (Polychaeta) with eggs (Photo: A. Kureck); (b) *Fredericella sultana* (Bryozoa) (Photo: B. Wiedemann); (c) burrowing larva of *Ephoron virgo* (Ephemeroptera) in its tube (Photo: A. Kureck); (d) *Theodoxus danubialis* (Gastropoda) (Photo: G. Falkner); (e) male and female *Dikerogammarus villosus* (Amphipoda) (Photo: A. Kureck); (f) larva of *Heptagenia sulphurea* (Ephemeroptera) (Photo: P. Maihöfer); (g) larva of *Hydropsyche* sp. (Trichoptera) (Photo: J. Waringer).

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In this review the main interest focuses on the investigation of biodiversity, i.e. the number of species and their relative proportions in the whole invertebrate community, as well as major governing environmental factors. A study of biodiversity is of fundamental importance within the field of ecology, in order to address questions such as why some species are numerous and others are rare, and what kind of influence their relative abundances have on the structure and function of the whole community.

Species composition of the Danube

The faunistic review by Moog et al. (1995, 2000) covers all of the benthic macroinvertebrates found in the Austrian part of the Danube, for which a total of 1289 species has been recorded recently. When microcrustaceans, collembolids and some dipterans are excluded, a total of 1122 species are known, of which 493 or 44 % belong to the Diptera (mostly the larvae of 'midges'). Each of the other 20 major taxonomic groups consist of 138 species of Coleoptera, 106 species of Trichoptera, and fewer species in other groups (Table 1). Some examples are shown in Fig. 3, including one of two freshwater polychaetes (Annelida) that occur in the Danube.

The macroinvertebrates were allocated to four major habitats (Table 1). These comprise the free-flowing main river channel and its associated backwaters of riverside forests, and impounded sections of the river and associated backwaters of riverside forests. This last habitat contains 713 species in all 21 major taxonomic groups, impoundments have 464 species in 17 groups, backwaters of the free-flowing sections have 430 species in 17 groups, and the free-flowing main river channel contains 310 species in 15 groups.

As stated above, of the total number of species in all four habitats, Diptera are predominant, followed by Trichoptera and Mollusca in the free-flowing main river channel, and Trichoptera, Coleoptera and Mollusca in its backwaters of the riverside forests (Table 1). Oligochaeta, Trichoptera and Mollusca predominate in the impounded areas, and Coleoptera and Trichoptera predominate in the associated backwaters of the riverside forests. Species in other groups represent less than 10 % of the total species abundance in the four habitats.

Currently, the database of Austrian Red Lists contains only mammals, birds, fishes, reptiles, amphibians, butterflies and moths (www.roteliste.at). Information is scarce for the conservation status of macrozoobenthos in the Danube: Bauernfeind & Humpesch (2001) name ten species of Ephemeroptera as endangered; similarly, Malicky (1994) lists 25 species of Trichoptera, and Frank & Reischütz (1994) declare that 45 species of Mollusca are endangered. In addition, one species of Sisyridae (Planipennia) is included in the Austrian Red List (Gepp 1994). Table 1. Summary of information on the numbers of benthic macroinvertebrate species occurring in 21 major taxonomic groups found in the Austrian part of the River Danube (Total N) and in each of four major habitats (data from Moog et al. 1995, and Moog et al. 2000).

		Free-flowing sections		Impounded sections			
Major groups	Total N	Main river	Backwaters	Impoundment	Backwaters		
Non-insects							
Porifera	2	0	1	1	2		
Hydrozoa	2	0	0	0	2		
Bryozoa	8	2	5	2	8		
Turbellaria	25	5	5	10	16		
Mollusca	68	32	46	47	61		
Polychaeta	2	1	0	2	2		
Oligochaeta	63	26	31	57	17		
Hirudinea	24	10	16	13	22		
Acarina	23	3	0	3	19		
Araneae	1	0	1	0	0		
Crustacea	23	11	10	11	15		
Insects excluding Diptera							
Ephemeroptera	40	15	8	18	33		
Plecoptera	6	0	0	2	4		
Odonata	60	1	30	7	58		
Heteroptera	30	2	26	3	22		
Megaloptera	2	0	2	1	2		
Planipennia	2	2	2	0	2		
Coleoptera	138	5	53	7	131		
Trichoptera	106	32	62	51	92		
Lepidoptera	4	0	2	0	2		
Diptera	493	163	130	229	203		
Grand totals	1122	310	430	464	713		

Recent invasions by new species of macrobenthic invertebrates

Biological invasions are large-scale phenomena of widespread importance. The presence of new species initially increases faunal diversity in the invaded area, but invaders also represent possible major threats to the established fauna, by altering the ecological structure and functioning of communities, sometimes by eradicating both common and rare vulnerable species. The Danube flows through different faunal areas and, since 1992, its catchment has been artificially connected with that of the Rhine through the Rhine–Main–Danube Canal. Therefore aquatic invaders can enter Austria by moving downriver from the west, or upriver from the east.

6

Table 2. Summary of current information on 17 invaders now found in the Austrian part of the River Danube (Tittizer 1997; Müller et al. 2002). I, impounded areas; RS/I, riverside backwaters of impounded areas; FF, free-flowing main river; RS/FF, riverside backwaters of free-flowing stretches.

Taxa	Habitat	Origin	Mode of distribution
Turbellaria			
Dugesia tigrina	I, RS/I, RS/FF	N. America	Aquaria
Annelida			
Branchiura sowerbyi	Ι	S. Asia	Aquaria; ships
Caspiobdella fadejewi	I, RS/I, RS/FF	Pontocaspian	Ships; migration
Hypania invalida	I, RS/I, FF	Pontocaspian	Ships
Gastropoda			
Ferrissia wautieri	FF, RS/FF	S.E. Europe	Ships; birds
Lithoglyphus naticoides	I, RS/I, FF, RS/FF	Pontocaspian	
Physella acuta	Ι	S.E. Europe	Ships; aquaria; birds
Potamopyrgus antipodarum	I, RS/I, FF	New Zealand	Ships; birds
Theodoxus danubialis	FF, RS/FF	Pontocaspian	Ships; birds
Viviparus acerosus	I, RS/I, RS/FF	S.E. Europe	Ships; birds
Bivalvia			*
Dreissena polymorpha	I, RS/I, FF, RS/FF	Pontocaspian	Ships; canals
Crustacea			
Chaetogammarus ischnus	I, RS/I, FF	Pontocasian	Ships; canals; migration
Corophium curvispinum	I, RS/I, FF, RS/FF	Pontocaspian	Ships; canals; migration
Dikerogammarus haemobaphes	I, RS/I, FF, RS/FF	Pontocaspian	Ships; canals; migration
Dikerogammarus villosus	I, RS/I, FF	Pontocaspian	Canals; migration
Jaera istri	I, RS/I, FF	Pontocaspian	Ships; migration
Orconectes limosus	RS/FF	N. America	Canals; exposure; migration

Currently, the presence of 17 new macroinvertebrates (Table 2) has modified the original species composition. Due to physical changes in the river (e.g. current-flow and bottom substratum) resulting from the construction of impoundments, new habitats were created, providing very favourable environmental conditions for the survival of some invaders. Typical examples of species that have actively migrated westwards into the Danube are *Dreissena polymorpha*, *Chaetogammarus ischnus*, *Corophium curvispinum*, *Dikerogammarus haemobaphes* and *D. villosus*. Species that have been carried passively into the river are *Hypania invalida* and *Jaera istri*. These are all elements of the Pontocaspian fauna with its original distribution in Russia and the Balkans. However, so far a typical invader from the west, the bivalve mollusc *Corbicula fluminea*, has not yet reached the Austrian Danube.

As these invasive species become successfully established they may pose increasing risks to native species, and sometimes to habitats and ecosystems. In this respect, elucidation of interspecific behavioural interactions among invaders and natives is urgently required. For example, in fresh waters in The Netherlands, *Dikerogammarus villosus* – an invasive Pontocaspian crustacean amphipod – is rapidly eliminating *Gammarus duebeni*, a native European amphipod, and *Gammarus tigrinus*, until now a spectacularly successful invader from North America. Laboratory experiments have shown that *D. villosus* kills and consumes both *G. duebeni* and *G. tigrinus*. This relatively large predatory invader may well reduce amphipod diversity in a range of other freshwater habitats in western Europe, including the Danube where it appears to constitute a threat to the native *Gammarus roeseli* and *G. fossarum* (Dick & Platvoet 2000; Müller et al. 2002; Pöckl et al. 2003).

A cross-section of the free-flowing section of river below Vienna

The River Danube east of Vienna has a stream size (order) of nine, but the free-flowing section which we have studied actually resembles middle reaches (stream order six) along the river continuum (Vannote et al. 1980). The value of six agrees with the zonation concept of Illies & Botosaneanu (1963), whereas the high stream order (nine) is simply a consequence of the inflow of another large river, the Inn.

In the free-flowing section, 30% of the species assemblage belong to the epipotamal zone, 20% belong to the hyporhithral zone (Illies & Botosaneanu 1963) and the remainder belong to seven other zones. Therefore this particular section of river represents a transition zone between the hyporhithral and epipotamal zones (Moog et al. 2000).

We have applied quantitative sampling and methods of analysis to a transect across the free-flowing main channel below Vienna at river-km 1889.9 (Fig. 4, p.12). Here the Danube is about 380 m wide, with depth ranging from 3.1 to 4.6 m and a mean discharge of 2170 m³ per second (Fesl et al. 1999). The riverbed is composed of rocks, stones and gravel, with occasional patches of sand and silt. The riverbed was sampled to depths of 0.26 to 11.1 cm, using a modified Petersen grab (Humpesch & Elliott 1990).

10

Important environmental variables at the river cross-section

Six major environmental variables were extracted from a principal component analysis, of which five are important in determining the species composition and relative abundance of invertebrates across the river channel (Table 3). The sixth was water temperature, ranging between $2 \degree C$ and $19.5 \degree C$, with a mean temperature of $10 \degree C$ for the study period.

At site 4 of our cross-section, close to the left bank, mean water velocity is significantly lower than at the other sites (Table 3). Temporal differences in water velocity, highest in May and July at a period of high water, result from snowmelt in the Alps.

Substratum composition also differs along the cross-section of the river. The right bank at site 1 is artificially stabilised with large boulders, and the median of the natural grain sizes is significantly higher compared with other sites of the transect. The smallest particles occur near the left bank behind a sill of sediment; in mid-channel, at site 3, particles are intermediate in size. Median grain size also varies significantly through the year. The heterogeneity of the sediment composition increases slightly from the right to the left side of the river channel, and temporal variation is low.

Sediment turnover differs between sites and temporal variations resemble those of discharge, with a lower overall sediment movement during winter and higher turnover in late spring and summer. Sediment deposited close to the left bank is characterised by a lower pore space compared with the other sampling sites, and this might be attributed to the lower water velocity and sedimentation of small particles. Through the year, the lowest pore space was found in July.

Biodiversity of the macrozoobenthos communities in relation to environmental variables at the river cross-section below Vienna

We have subjected various characteristics and attributes of the invertebrate communities to detailed analysis. The most important conclusions are summarised below.

Taxonomic composition and abundance of species

A total of 164 species were found at the four sites along the transect (Table 4), including 81 Chironomidae (mainly Orthocladiinae) and 33 Oligochaeta (mainly Naididae). Site 4 near the left riverbank has 142 species, including 68 Chironomidae (29 of these occur only at site 4) and 30 species of Oligochaeta (2 occur only at site 4). Another seven major groups consist of 50 species. Site 4 has the highest number of Trichoptera (10 out of 11 species at all sites), Ephemeroptera (9/11), Bivalvia (8/8), Gastropoda (7/8), Crustacea (6/7) and Hirudinea (2/2); two species of

Table 3. Five hydrophysical variables at four sampling sites in a cross-section of the River Danube at river-km 1889.9 (Fesl 2002). Samples were obtained monthly between September 1995 and August 1996. Locations of the sites are shown in Fig. 4.

Variable	Symbol	Site 1	Site 2	Site 3	Site 4
Mean water velocity (cm per sec)	v	182.0	206.2	197.4	139.6
Median grain size (mm; 50 % quartile)	Q2	59.5	28.9	40.7	27.9
Substratum heterogeneity	Sol	1.48	1.58	1.67	1.75
Sediment turnover	UI	1.5	3.5	2.6	2.1
Pore space (%)	PS	30.8	33.3	31.5	25.6

Bryozoa occur at three of the sites (Table 4). Altogether, site 4 has by far the greatest number of species (47) that were not found at any of the other sites.

With 142 species, site 4 has the lowest water velocity and grain size. In comparison, site 1 near the right riverbank has the largest median grain size and lowest sediment turnover (Table 3), and has fewer species (93) compared with site 4, but slightly more than at mid-channel sites 2 and 3, except for Ephemeroptera (Table 4). Seven out of 93 species occur only at site 1, 11 out of 82 species occur only at site 2, and 4 out of 71 occur only at site 3; of these 22 species with restricted distributions, 16 are chironomids and oligochaetes, and two are ephemeropterans.

Table 4. Total numbers of species (S), numbers found at each site and mean abundances in the river cross-section below Vienna; **bold numbers** in parentheses indicate species occurring at one site only, and no other site. Data for Chironomidae taken from Fesl (2002), for Oligochaeta from Fesl & Humpesch (2003) and for other groups from Fesl & Humpesch (2005). Locations of the sites are shown in Fig. 4.

Group	S	Site 1	Site 2	Site 3	Site 4
Chironomidae	81	40 (3)	37 (8)	27 (2)	68 (29)
Oligochaeta	33	28 (1)	24 (1)	25 (1)	30 (2)
Ephemeroptera	11	2 (1)	5 (1)	3	9 (5)
Trichoptera	11	7 (1)	4	4	10 (3)
Bivalvia	8	5	2	3	8 (2)
Gastropoda	8	4 (1)	1	2	7 (4)
Crustacea	7	4	6(1)	4	6(1)
Bryozoa	3	2	2	1 (1)	2
Hirudinea	2	1	1	1	2 (1)
Total numbers of species	164	93 (7)	82 (11)	70 (4)	142 (47)
Mean abundances (per m ²)	_	5314	623	1195	11 146



BIODIVERSITY OF MACROZOOBENTHOS IN A LARGE RIVER 13

FIGS 4 to 6 on facing page 12.

FIG. 4 (*Top*). Grid-map of the study area at low water level (discharge 1182 m^3 per sec) at river-km 1889.9 on the Danube, in Austria, east of Vienna. Circles indicate the possible position of ten random samples within four sites along the cross-section (sites 1, 2, 3 and 4, respectively at 30 m, 100 m, 200 m and 250 m from the right bank). Samples were obtained monthly between September 1995 and August 1996. Yellow arrow, direction of flow; red arrow, connected to a backwater area (Fesl 2002).

FIG. 5 (*Middle*). Relative abundances (log scale) of nine taxonomic groups that were determined to species level. Oli, Oligochaeta; Chir, Chironomidae; Crust, Crustacea; Trich, Trichoptera; Biva, Bivalvia; Gast, Gastropoda; Bryo, Bryozoa; Eph, Ephemeroptera; Hiru; Hirudinea.

FIG. 6 (*Bottom*). (a) Predictions of the River Continuum Concept for the relative proportions of functional feeding groups (adapted from: Oxbow River & Stream Restoration 2003). (b) Mean composition of the general functional feeding groups in the free-flowing section of the River Danube below Vienna.

In terms of total numbers of individuals per m^2 of riverbed, oligochaetes are the most numerous (*Chaetogaster diastrophus/setosus* and *Nais elinguis* were most abundant), followed by chironomids (*Cladotanytarsus* cf. *vanderwulpi* and *Cladotanytarsus* cf. *daviesi* were most abundant). These two groups account for 95 % or more of the total numbers of all individuals of all species found at each site (Fig. 5). The overall mean abundance of all species was highest at site 4 (11 146 individuals per m²), being double the mean number at site 1 and roughly 10 times the number at site 3; site 2 had on average only 623 individuals per m² (Table 4).

For the other 50 macrozoobenthic invertebrates that have been identified, Crustacea are relatively most abundant, particularly *Jaera istri* (35%) and *Corophium curvispinum* (32%), followed by a bryozoan, *Fredericella sultana* (4%), and Trichoptera, particularly *Hydropsyche contubernalis* and *Psychomya pusilla* (3%). Mean relative abundances of about 1% or less also occur in Bivalvia, Gastropoda, Ephemeroptera and Hirudinea, indicating the presence of many rare species. Total densities for all species show significant differences between sampling sites and great fluctuations through time, with peaks in November and March and lowest densities in July after floods caused by snow melting in the Alps.

A comparison of the different relative abundances of four general functional feeding groups – shredders, collectors, grazers and predators – indicates that the collectors are predominant (Fig. 6).



FIG. 7. Biplot from Redundancy Analysis (RDA) showing the first and second RDAaxes correlated with nine named community attributes (——; Eve = evenness) and six selected environmental variables (-----; ν , water velocity; *Q2*, median grain-size; *So1*, coefficient of sorting; *temp*, water temperature; *UI*, index of sediment turnover; *PS*, pore space. (Adapted from Fig. 4 in Fesl & Humpesch 2005).

Quantitative relationships between nine community attributes and six environmental factors

Redundancy Analysis (RDA) was applied to data obtained at each sampling site for each sampling date (Fig. 7). Four RDA-axes explain 99% of the relationship between nine community attributes and six environmental variables, 80% of which are explained by the first two axes. Among the relationships between hydrophysical variables and the four axes, sediment turnover shows a strong correlation with the first axis. Sediment heterogeneity is also correlated with this axis. Both grain size and pore space are negatively related to the second axis and sediment heterogeneity is positively related to the second axis.

Relationships between environmental variables and the macrozoobenthic communities at the four sampling sites indicate that increasing sediment turnover (at mid-channel sites) coincides with decreasing species richness and community persistence, but coincides with an increase in mean spatial aggregation of the species (Fig. 7). The latter is also positively related to sediment heterogeneity. A decrease in species richness also coincides with an increase in water flow. Abundance is negatively correlated with sediment turnover and pore space.

Our analysis by RDA suggests that variation in biodiversity was determined mainly by evenness (a measure of the number of species related to numbers of individuals) rather than by species richness (actual number of species present). This suggests that the cross-section of river is saturated with species, leaving no room for more new entrants. A decrease in biodiversity and number of individuals coincided with increased water velocity at some sites and, with increased movement of sediment, the spatial distribution of species decreased in combination with a decline in the overlap of areas colonised by single species.

Biodiversity as an indicator for water quality

The diverse fauna of the free-flowing section below Vienna, and the absolute abundances of species, can be used to calculate a variety of biological water quality indices. Values of six indices based on species composition are all relatively similar (Moog et al. 2000). Thus the Zelinka & Marvan Saprobic Index ranges temporally between 1.68 and 2.06, and ranges spatially between 1.75 and 2.11, indicating that conditions are mainly β -mesosaprobic. The Pantle-Buck Index indicates a water quality class of II. The Trent Biotic Index, the Extended Biotic Index and the Indice Biotique range temporally between vater quality classes I and II, and spatially between I to II–III. The Makroindex, which has no equivalent in the water quality classes, ranges between 5 and 6, where 1 would be the value for the best and 8 for the worst water quality. Biotic scores, represented by BMWP, the BMWP/ASPT and the Lincoln Quality Index, indicate a temporal variation in water quality of I to II–III, and spatial variation of I to III.

Thus water quality of the Danube is generally good, but two important conclusions may be drawn from the analyses. The Indice Biotique varied from water quality class I–II to II–III, the BMWP varied from II to III and the Lincoln Quality Index varied from I to III. These differences reflect hydrological variation rather than differences in water quality *per se* because the lower numbers of species and individuals found at some sites, categorised as a lower water quality class, are actually due to higher water velocity and greater mobility of the bottom substratum. A second conclusion is that indices based on identification to species level give more realistic results for water quality of the river than indices based solely on higher taxonomic levels.

The fauna of surface sediments (0-10 cm) and deeper hyporheic

The benthic fauna in our cross-section of the free-flowing Danube was sampled in the top 10 cm of sediment. In most large rivers and streams, this fauna may also extend further down into deeper sediments of the hyporheic zone (Fig. 8).



FIG. 8 (*Landscaped on facing page 16*). A freeze-corer developed to obtain quantitative samples of the substratum down to a depth of 1 metre (Humpesch & Niederreiter 1993). (When the core is raised up to the surface, the frozen material is divided into ten sections for analysis, representing successive depths of 10 cm). *Left:* the freeze-corer with a sample of substratum, before cobbles were laid (see text on p. 18). *Right above:* a core taken shortly after cobbles were laid (top of the core is on the left of the picture). *Right below:* a core taken 3 years after cobbles were laid (top of the core is on the left of the picture).

In deeper sediments of the hyporheic, interstitial spaces are occupied by invertebrates when space and other conditions (e.g. a flow of oxygenated water) are suitable. More especially, the early developmental stages of the surface benthos live in this zone, where there are seasonal variations in numbers, distribution and presence of particular species. In addition there are permanent members of the hyporheic fauna, which comprises many specialised forms that complete their life cycle there, especially some Crustacea, Oligochaeta and Hydracarina.

One of the most important advantages of living in the hyporheic zone is survival during adverse river conditions, such as droughts and floods. The latter may be catastrophic at times of high discharge in the Danube, and the fauna of the deeper sediments can then become a source of animals for recolonisation and replenishment of the surface benthos. Consequently the hyporheic is an ecotone linking surface water and groundwater habitats. Below, we summarise preliminary investigations on the permanent fauna of surface and deeper sediments at a site 2–3 km upstream from our main cross-section of the free-flowing river (Fig. 9).

Effect of upstream impoundment on the riverbed and its fauna

A consequence of any river regulation work is alteration of the bed-load. Where barrages are built across the Danube, bed-load transport completely stops, sedimentation occurs upstream, and erosion occurs downstream. In the case of the impoundment at Vienna, erosion set in immediately after completion of the barrage, resulting in substantial deepening of the free-flowing stretch of the Danube downstream to the Austrian border at river-km 1874. This lowered the water surface of the river and consequently lowered the groundwater table, thus disrupting the water balance of the riverside forests in the Alluvial Zone National Park 'Donau-Auen'.

Several remedial actions may be taken to overcome the problem of beddeepening, such as terracing the bottom, introduction of ground sills (concrete groynes) (see Fig. 9), flow diversion, armouring the bottom with large boulders, and the addition of coarse material to form a covering layer.


FIG. 9. Location of sampling sites between river-km 1893 and 1892. Arrow, direction of flow in the river. Dotted line, international waterway. Rectangle near the right bank shows an experimental area ($300 \text{ m} \times 70 \text{ m}$) where cobbles (size $60 \times 120 \text{ cm}$) were laid to a depth of 50 cm in September 1994. The large triangle upstream shows the position of a small island. White squares indicate the first sample (7 replicate cores, 30.9.93), taken 1 year before cobbles were laid on the experimental site. Small black triangles indicate a second sample (5 replicate cores, 19.3.96), 18 months after the addition of cobbles. White circles indicate a third sample (5 replicate cores, 31.10.97), taken 3 years after cobbles were added. (Based on Humpesch et al. 2002).

The stabilising effects of this last remedy were investigated during the period 1994–1997, when a 50 cm-deep layer of cobbles, with a relatively uniform particle size of 60×130 mm, was spread onto the riverbed over an area of 300×70 m. The effect of adding the cobbles on grain size, pore space and invertebrates was measured in samples taken over the next three years, using the freeze-corer illustrated in Fig. 8 (p. 16).

Several useful conclusions may be drawn from the results of this preliminary trial (Fig. 10). First, the median particle size for the 75 % quartile (Q3) was about 60 mm in the top 20 cm of riverbed, where the median pore space was about 25–30 %. Second, at depths below 20 cm, median grain size for Q3 generally fell to around 20–40 mm and pore spaces were reduced to about 15–20 %. Thus the smaller particles in lower sediments were more compacted together, although this compaction appears to be less pronounced in sample 1, which may have been due to active erosion of the riverbed before it was stabilised by adding cobbles. Third, coinciding with the reductions in both grain size and pore space, the total numbers of individuals in the macrozoobenthos also declined, being noticeably fewer at depths below 30–40 cm. However, median numbers between ca. 10 and 100 individuals per litre of sediment occurred in the top 30 cm of sediment, on all three sampling occasions (Fig. 10).

FIG. 10. Results from three samples taken with a freeze-corer at depths down to 1 m between river-km 1893 and 1892 (details given in Fig. 9). Vertical lines indicate maximum and minimum values; box plots show the medians (black circles) and 25 % and 75 % quartiles for each 10-cm depth down to 1 m. *Top*: total numbers of invertebrates in each depth zone for each sample. *Middle*: 75 % quartiles for particle (grain) size. *Bottom*: pore space between particles. (Based on Humpesch et al. 2002).

After cobbles were laid in the experimental area, total numbers of invertebrates were generally higher in the second sample and sometimes also in the third sample (Fig. 10) when compared with the first sample, taken before the riverbed was stabilised (for the effect of sediment turnover on invertebrate abundance see also Fig. 7, p. 14).

Approximately one-half of all the invertebrates were worms (Oligochaeta) and water mites (Hydracarina), and in the first sample a few specimens were found at depths of 90–100 cm, including also Turbellaria, Crustacea and Chironomidae.

On all occasions the total numbers of benthic invertebrates found in the top 20 cm of sediment between river-km 1893 and 1892 are some two orders of magnitude lower than the total numbers found in the top 10 cm of sediment further downstream at river-km 1889.9 (see Fig. 7 in Moog et al. 2000). Here, median grain sizes of the 50 % quartile (Q2) in the riverbed are similar to those found upstream, whereas pore spaces are rather higher (Table 3, p. 11). Hence more space is available in these particular sediments for greater numbers of invertebrates and room for a greater diversity of species.

Concluding remarks

20

The Austrian part of the Danube is alpine in character, but only two unimpeded free-flowing stretches of river remain - the Wachau region above Vienna, and the section below Vienna down to the Austrian border at river-km 1874. The latter section contains 310 species of macroinvertebrates, of which 58 species are not found in other parts of the river upstream. Also, from a total of 58 species of fish that are currently found in the Austrian Danube, the free-flowing section contains no fewer than 43 (far more than in any other section upstream (Humpesch 1992; Schiemer et al. 2005)). For some, like nase Chondrostoma nasus, the free-flowing section is a preferred spawning ground. For others, like pike Esox lucius and carp (wild form, *Cyprinus carpio*), connectivity to the riverside forests is important to provide aquatic plants for the fish to spawn on. For conservation of the rarer species of macroinvertebrates and fishes, the preservation of their natural habitat is vital; it is therefore important to preserve the unimpeded nature of the river below Vienna. Because the river is directly connected to its riverside forests and backwaters, an exchange of fauna can occur, thereby promoting a potential increase in biodiversity.

Due to the construction of a barrage across the river at Vienna, deepening of the riverbed by erosion downstream poses several problems that need to be resolved, including its effect on the surrounding groundwater table with its exceptional fauna of endemic species. More studies are needed on the ecological relationships between native and recent invasive species, and the manner in which the latter may or will affect the current structures of communities within the river fauna.

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References

- Bauernfeind, E. & Humpesch, U.H. (2001). Die Eintagsfliegen Zentraleuropas (Insecta: Ephemeroptera): Bestimmung und Ökologie [*Mayflies of Central Europe – identification and ecology*]. Verlag des Naturhistorischen Museums Wien. 239 pp.
- Dick, J.T. A. & Platvoet, D. (2000). Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. *Proceedings of the Royal Society, Series B* 267, 977-983.
- Fesl, C. (2002). Biodiversity and resource use of larval chironomids in relation to environmental factors in a large river. *Freshwater Biology* **47**, 1065-1087.
- Fesl, C. & Humpesch, U.H. (2003). Community structure and resource use of oligochaetes (Annelida) in relation to hydrophysical factors in a large river. Archiv für Hydrobiologie, Supplement Volume 147, Large Rivers 14, 307-326.
- Fesl, C. & Humpesch, U.H. (2005). Spatio-temporal variability of benthic macroinvertebrate community attributes and their relationship to environmental factors in a large river (Danube, Austria). Archiv für Hydrobiologie, Supplement Volume **158**, Large Rivers **16** (in press).
- Fesl, C., Humpesch, U.H. & Aschauer, A. (1999). The relationship between habitat structure and biodiversity of the macrozoobenthos in the free-flowing section of the Danube in Austria – east of Vienna (preliminary results). *Archiv für Hydrobiologie, Supplement Volume* **115**, *Large Rivers* **11**, 349-374.
- Frank, C. & Reischütz, P.L. (1994). Rote Liste gefährdeter Weichtiere Österreichs (Mollusca: Gastropoda und Bivalvia). In: *Rote Liste gefährdeter Tiere Österreichs* (ed. J. Gepp), pp. 283-316. Grüne Reihe des Bundesministeriums für Umwelt, Jugend und Familie.

UWE HUMPESCH AND CHRISTIAN FESL

- Gepp, J. (1994). Rote Liste der gefährdeten Netzflügler Österreichs (Neuropteroidea: Megaloptera, Raphidioptera und Planipennia). In: *Rote Liste gefährdeter Tiere Österreichs* (ed. J. Gepp), pp. 201-204. Grüne Reihe des Bundesministeriums für Umwelt, Jugend und Familie.
- Humpesch, U.H. (1992). Ecosystem study Altenwörth: impacts of a hydroelectric power-station on the River Danube in Austria. *Freshwater Forum* **2**, 33-58.
- Humpesch, U.H. & Elliott, J.M. (eds) (1990). Methods of biological sampling in a large deep river the Danube in Austria. *Wasser und Abwasser, Supplement* **2**, 83 pp.
- Humpesch, U.H. & Niederreiter, R. (1993). Freeze-core method for sampling the vertical distribution of the macrozoobenthos in the main channel of a large deep river, the River Danube at river kilometre 1889. *Archiv für Hydrobiologie, Supplement Volume* **101**, *Large Rivers* **9**, 87-90.
- Humpesch, U.H., Fesl, C. & Rüger, H. (2002). The effect of riverbed management on the habitat structure and macroinvertebrate community of a ninth order river, the Danube in Austria. *Archiv für Hydrobiologie*, *Supplement Volume* 14, *Large Rivers* 13, 29-46.
- Illies, J. & Botosaneanu, L. (1963). Problèmes et méthodes de la classification et de la zonation écologique des aux courantes, considérées surtout du pont de vue faunistique. *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie* **12**, 1-57.
- Malicky, H. (1994). Rote Liste der gefährdeten Köcherfliegen Österreichs (Trichoptera). In: *Rote Liste gefährdeter Tiere Österreichs* (ed. J. Gepp), pp. 207-214. Grüne Reihe des Bundesministeriums für Umwelt, Jugend und Familie.
- Moog, O., Humpesch, U.H. & Konar, M. (1995). The distribution of benthic invertebrates along the Austrian stretch of the River Danube and its relevance as an indicator of zoogeographical and water quality patterns part 1. Archiv für Hydrobiologie, Supplement Volume 101, Large Rivers 9, 121-213.
- Moog, O., Brunner, S., Humpesch, U.H. & Schmidt-Kloiber, A. (2000). The distribution of benthic invertebrates along the Austrian stretch of the River Danube and its relevance as an indicator of zoogeographical and water quality patterns – part 2. *Archiv für Hydrobiologie, Supplement Volume* 115, *Large Rivers* 11, 473-509.
- Müller, J.C., Schramm, S. & Seitz, A. (2002). Genetic and morphological differentiation of *Dikerogammarus* invaders and their invasion history in Central Europe. *Freshwater Biology* **47**, 2039-2048.
- Oxbow River & Stream Restoration, Inc. (2003). www.oxbowriver.com/ Web Pages/Stream Ecology Pages/Ecology Riparian/Ecology RCC.html
- Pöckl, M., Webb, B.W. & Sutcliffe, D.W. (2003). Life history and reproductive capacity of *Gammarus fossarum* and *G. roeseli* (Crustacea:

Amphipoda) under naturally fluctuating water temperatures: a simulation study. *Freshwater Biology* **48**, 53-66.

- Schiemer, F., Holcik, J., Keckeis, H. & Staras, M. (2004). Ecological status and problems of the Danube river and its fish fauna: a review. *Proceedings of the Second International Symposium on the Management* of Large Rivers for Fisheries Volume I (eds R.L. Welcomme & T. Petr), pp. 273-299. FAO Regional Office for Asia and the Pacific, Bangkok, Thailand. RAP Publication 2004/I 6 (in press).
- Tittizer, T. (1997). Ausbreitung aquatischer Neozoen (Makrozoobenthos) in den europäischen Wasserstraßen, erläutert am Beispiel des Main-Donau-Kanals. In: *Güteentwicklung der Donau – Rückblick und Perspektiven* (ed. G. Kavka). Schriftenreihe des Bundesamtes für Wasserwirtschaft **4**, 113-134.
- Vannote, R.L., Minshall, G.W., Cummings, K.W., Sedell, J.R. & Cushing, C.E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130-137.