Short Overview on the Benthic Macroinvertebrate Fauna of the Danube River

Wolfram Graf, Patrick Leitner, and Florian Pletterbauer

Abstract This article gives a rough overview on the occurrence and distribution of selected benthic invertebrates along the Danube River. The description of the benthic community within typological units of the Danube is based on the results from the Joint Danube Surveys. Species richness and abundance illustrate the structure and dominant groups of the benthic community. Furthermore the role of environmental impacts like hydromorphological changes, pollution, navigation as well as neozoa is shortly addressed and highlighted. In this context a conceptual framework of the multi-stressor complex of large rivers is introduced and discussed. Finally the biodiversity losses of selected species are reflected on a European scale.

Keywords Biodiversity, Danube, Distribution, Environmental impacts, Joint Danube Survey, Macroinvertebrates

Contents

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1 Introduction

About the macroinvertebrate fauna of the Danube, who has the knowledge and the overview? Due to the overwhelming diversity, most approaches, which aim to give a comprehensive picture, were bound to fail due to the ever-changing nature of large rivers and either naturally or anthropogenically induced faunal shifts along the time axis.

The longitudinal, lateral and vertical dimensions of large rivers have been in the focus of limnologists since the last 50 years only, and we are just at the beginning to understand the principles of ecological processes and functions. Even during that short period, large rivers have changed their character dramatically due to exposure to multiple stresses induced by human uses. The first systematic documentations of large rivers in the 1960s give us a glimpse of the organisms present at that time. Profound baseline information and monitoring efforts started much later and were confined to some national stretches of interest. All we got from earlier times – revealing more pristine conditions – are some flashlight information from outstanding naturalists, scientists and specialists on specific groups, scattered in regional publications, which has to be evaluated according to the taxonomic resolution of the time of publication.

The macroinvertebrate fauna of the Danube is highly diverse consisting of numerous systematic groups including annelids, molluscs, crustaceans and insects and comprises an incredibly high diversity. Some of these animals have a high adaptive potential to changing environmental conditions; some have been documented only once and are thought to be extinct since their discovery 250 years ago, and other Danubian elements may have never been recorded at all. Their documentation is extremely dependent on the chosen methods and seasonal aspects which is the reason why some of us still are curious and search for those legendary and long-lost organisms of large rivers which may be still out somewhere in the dark. Some have been rediscovered in tributaries, and some few have recolonised the Danubian river bottom from unknown refugia indicating a recovery of specific habitats and the overall ecological integrity.

One major basis for the evaluation of the biological inventory of the Danube is provided by the two large expeditions within the Joint Danube Survey, JDS1 and JDS2, as these include recent and methodologically reproducible results. Other sources are local information and historic records which are included in a rather subjective way. Summarising, this article tries to sketch a rough picture of the author's subjective knowledge on general distribution patterns, occurrence of typical species and faunal losses and major changes of ecological processes in the past including examples from other large rivers of Central Europe.

2 Typological Aspects and Longitudinal Zonation Patterns of the Fauna

Sources on information on macroinvertebrates can be categorised as follows: (1) - species-specific data published by specialists scattered in time and space, starting from the middle of the eighteenth century, (2) ecologically oriented academic or applied studies from the 1950s up to now, (3) data focusing on biodiversity conservation issues and (4) data from systematic documentation of benthic assemblages which was initiated by the beginning of water resources management approaches and by especially saprobiological surveys (mainly the middle of the twentieth century) leading to huge datasets focusing on abundance and dominance of higher taxonomic units and species.

While (1) builds in general the basis for species-level information, (2) is improving our knowledge on the interactions of environmental variables on organisms mainly based on case studies; (3) provides data on selected and somehow unbalanced species groups, mainly FFH species comprising of few Odonata and Mollusca within the large and heterogeneous group of macroinvertebrates; and (4) initiated a high number of various national and international monitoring efforts. With the implementation of the Water Framework Directive (WFD) in 2000, a new dimension in the conservation of freshwater ecosystems was achieved, as the overall ecological status of surface water bodies has to be assigned within the EU member states, based on bioindicative organism groups, including macroinvertebrates. Within this reference-based assessment system, a sound typology is a prerequisite and various attempts have been performed to classify the Danube River. Frequently top-down approaches based on different eco-geographic units were applied [1, 2]. Moog et al. [3] included the macroinvertebrate fauna alongside geomorphological factors like river slope, hydrology, geology and dominating substrate type in their analyses and stressed the importance of the ecoregions according to Illies ([4]; the Central Highlands, the Hungarian Lowlands, the Pontic Province, the Carpathians and the Eastern Balkan) which resulted in ten distinct Danube River sections. Nesemann [5, 6] discussed the distribution patterns of molluscs and leeches and stressed palaeoclimatic factors to be responsible for the phenomena of disjunct species distributions and faunal inhomogeneity along the Danube course. The Upper Danube can be characterised by glacial and postglacial relicts according to Nesemann who highlights recent historic events as additional parameters shaping the fauna other than geomorphology.

Like in most European large rivers, the original aquatic fauna is under extreme pressure. Damming, pollution, navigation, habitat fragmentation and the invasion of neozoa are among the main stressors leading to an insensitive, cosmopolitan and less indicative benthic assemblage [7]. Many of section-type-specific species listed in Sommerhäuser et al. [8] have not been found for decades and have hopefully survived in discrete habitats; others are expanding their areas and are invading new sections. These range oscillations in combination with a nowadays more or less homogenised fauna along the entire Danubian stretch seriously hamper a biologically based typology as well as a sound ecological assessment system.

2.1 General Distribution Patterns

Dudich [9] compiled a first reliable and comprehensive species list of nearly all systematic groups from the entire Danube based on a literature review. He annotated national occurrences and even some ecological comments on the species. During the introduction he stated his concerns about the validity of his compilation regarding obsolete literature, the changing of environmental conditions of the Danube along timescales, nomenclatorial ambiguities and obscure locality records. Although the mentioned obstacles are obvious (and still do exist), he listed 1,623 species and gave the first overview summarising the contemporary knowledge from scattered publications. Huge new data have been collated in the last 50 years, but still the overall value of Dudich [9] lies in the documentation of distribution patterns especially of Ponto-Caspian species and rheophilous species of the Upper and Middle Danube, respectively, as massive migration and irreversible faunal changes started soon after. He characterised marine groups being restricted to the delta region or to the adjacent regions (especially Gastropoda and Bivalvia and Amphipoda, Mysidacea, Cumacea, respectively) and realised some insect orders like the Plecoptera and Ephemeroptera to have their main area in the Upper and Middle Danube. Additionally the enormous densities of the Amphipoda genus *Celicorophium* in Bulgaria have attracted attention (242,136 ind./m^2 according to Russev [10]) and were discussed as essential food resources for fishes.

Twenty-eight years after Dudich [9], Moog et al. [11] published 1,142 invertebrate species from the Austrian stretch of the Danube summarising literature data including records from the floodplains which contributed considerably to the overall diversity. Their data indicate a clear north-western shift of invasive amphipods compared to Dudich's compilation. Regarding diversity 74% of the total species inventory belonged to insects.

Although the distribution of benthic macroinvertebrates along the Danube River has been investigated in earlier studies [12–14], the most coherent data were provided by the Joint Danube Surveys 1 in 2001 [2] and 2 in 2007 [15], respectively. Macroinvertebrate data were collected with comparable and standardised methods along the Danube from Ulm to the Black Sea during a defined period (August to September). General characteristics of the fauna are given in Fig. 1 (taxa richness per group) and Fig. 2 (abundance per taxa group), respectively (data referring to JDS2, typology after Literáthy et al. [2]).

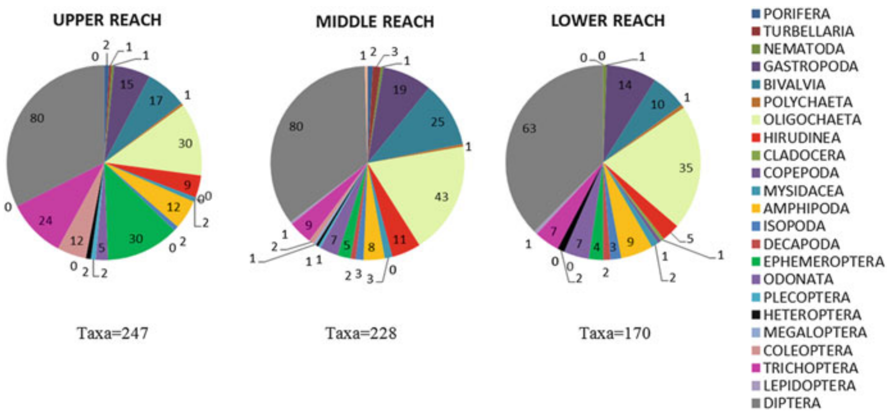

Fig. 1 Number of taxa per taxa group along the different reaches of the Danube

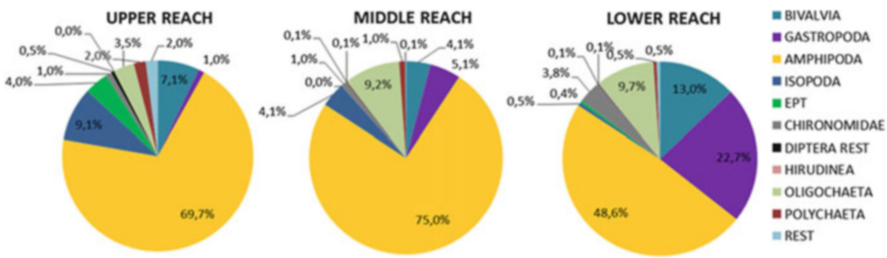

Fig. 2 Abundance of taxa per taxa group along the different reaches of the Danube

The most heterogeneous groups were Diptera (mainly Chironomidae, 174 taxa) and Oligochaeta (53 taxa) followed by Ephemeroptera (42 taxa), Trichoptera (35 taxa) and Mollusca (Bivalvia 26 taxa, Gastropoda 27 taxa, respectively). Coleoptera (17 taxa), Amphipoda (13 taxa) and Hirudinea (11 taxa) were as well noteworthy. This overall characteristic in diversity does not change along the three reaches of the Danube, although the number of insects, other than chironomids, decreases considerably downstream.

Regarding abundance (ind./m^2), Amphipoda were the dominant group in all Danube reaches and constitute up to 75%, while Isopoda (mainly *Iaera istri*) play an essential role in the upper reach and decrease downstream. Oligochaeta and Mollusca were found in increasing numbers in the lower reach.

In terms of biomass Mollusca were the most important organisms of the Danube and investigated tributaries. Due to their size Bivalvia make up more than 80% of the whole biomass, followed by Gastropoda (10–35%). Looking at the different reaches of the Danube, the increasing dominance of Mollusca from the upper to the lower reach becomes evident (Fig. 3). Although Crustacea are the most abundant group, they play only a minor role regarding biomass.

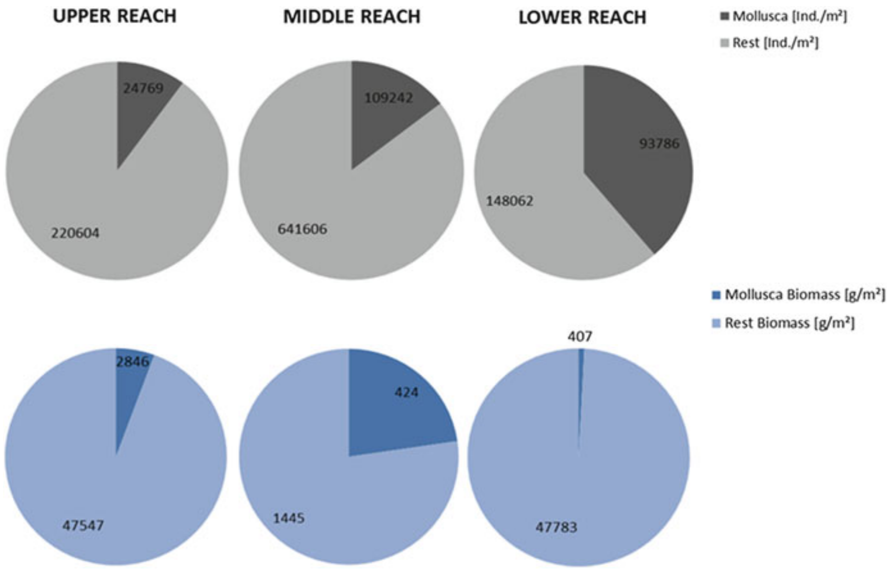

Fig. 3 Abundances and biomasses of Mollusca in comparison to the taxa rest (Airlift/Multicorer/MHS)

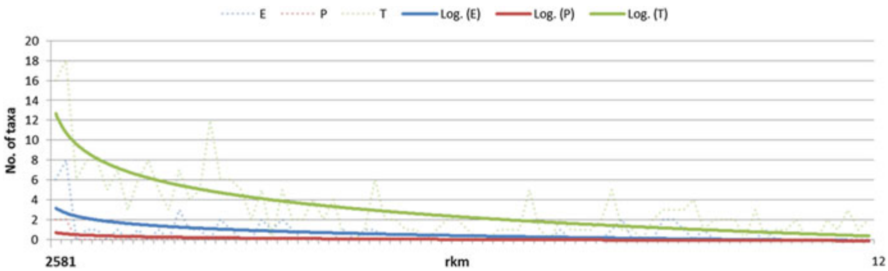

Fig. 4 Total numbers of EPT taxa recorded during JDS2 along the Danube

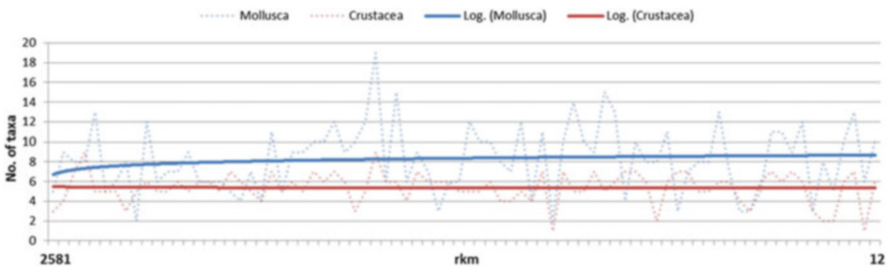

Fig. 5 Total numbers of Mollusca and Crustacea taxa recorded during JDS2 along the Danube

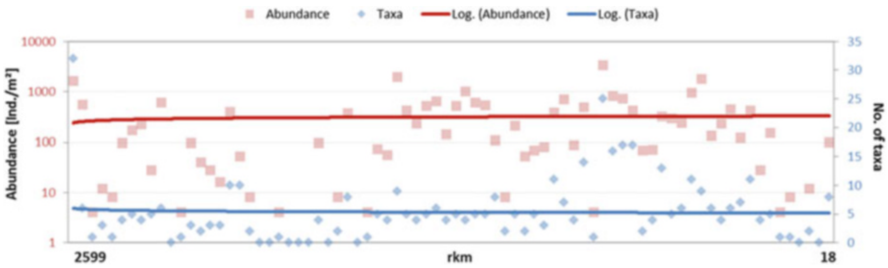

Fig. 6 Abundances and total taxa numbers of Chironomidae recorded during JDS2 along the Danube

Within insects EPT taxa (Ephemeroptera, Plecoptera and Trichoptera) are rarely found – with the exception of the upper reach. Among Trichoptera the net spinning, filtering genus *Hydropsyche* covers in considerable densities the whole stretch. Figures 4, 5 and 6 give schematically the development of diversity within EPT taxa, Crustacea, Mollusca and Chironomidae along the river course based on the results of JDS2.

Within aquatic insects exclusively, Chironomidae play a major role both in diversity and abundance.

3 Wetland Faunas

During the last decades floodplains of large rivers came in the focus of applied and basic limnological science (e.g. Amoros and Roux [16], Junk et al. [17], Schiemer [18], Ward et al. [19] and Findlay et al. [20]). Floodplains are an essential part of the aquatic ecosystem depending entirely in their spatial and temporal dimension on the pulses obtained from the river; due to regulations and damming, these hot spots of biodiversity [21] are among the most threatened ecosystems worldwide [18, 22–27]. Up to 90% of all floodplains in Europe and Northern America are heavily impacted [21]; exemplarily for land-use developments in Central Europe, floodplain areas have been reduced by 85% in Austria [28]. Within the Danube catchment floodplains have been reduced by 80% from the early nineteenth century up to now [29]. Conservation and restauration of persisting floodplains are therefore of highest priority within modern effective and sustainable aquatic ecosystem management [30–40].

Floodplains are generally seen as biodiversity hot spots as they form an ecotone from aquatic to terrestrial habitats and provide linkages between biological processes at various temporal and spatial scales [16, 17, 22, 41, 42]. Hydrological conditions and connectivity have been increasingly considered to be key drivers in creating structural and habitat diversity (Fig. 7).

Based on the distribution of habitat types within the hypothetical framework of floodplains [43, 44], Waringer et al. [45] classified 256 benthic invertebrate species

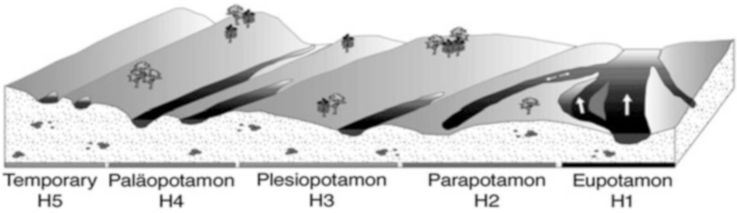

Fig. 7 Scheme of a hypothetical floodplain with habitat types according to Amoros et al. [43, 44]

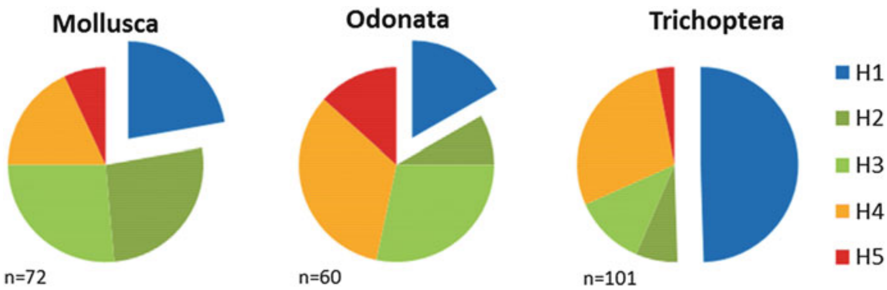

Fig. 8 Percentage of floodplain habitat type per taxa group (Mollusca, Odonata and Trichoptera); classifications according to Waringer et al. [45]

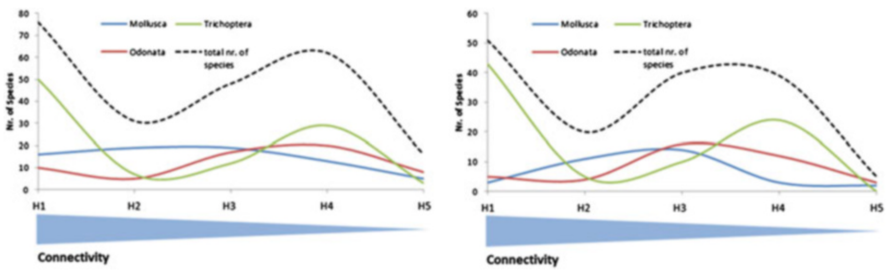

Fig. 9 *Left*: Theoretical diversity patterns of Mollusca, Trichoptera and Odonata along the connectivity gradient based on classifications taken from Waringer et al. [45]. *Right*: Species numbers of Mollusca, Trichoptera and Odonata (163 species) along the connectivity gradient documented at the floodplains near Vienna during 2001 and 2009

(Odonata, Trichoptera and Mollusca) occurring along the Austrian Danube according to their habitat-type preferences [43, 44]. Based on this data, Fig. 8 gives the percentage of species with specific habitat-type affinities which clearly indicates the dominance of floodplain species within the species pool of Mollusca, Odonata and Trichoptera along the Austrian Danube. Figure 9 left shows the potential species richness along the connectivity gradient within floodplains, peaking both at the Eupotamon and the Paläopotamon. This fits well with the conceptual biodiversity pattern along floodplains [46, 47], stressing the importance of wetlands in general. Studies on the floodplains in the vicinity of Vienna (Klosterneuburg, Lobau, Stopfenreuth, Altenwörth, Mühlwasser; investigation period 2000–2011) have confirmed these findings by high species numbers of typical floodplain organisms (in total 87 Trichoptera, 43 Odonata and 33 Mollusca species) representative for other macroinvertebrate groups (Fig. 9, right).

Under the holistic perception that floodplains are one essential part of large rivers, existing assessment systems are lacking this speciality, and new assessment approaches are currently under development to enlarge and complement WFD-compliant methods to evaluate the ecological status of large rivers and their floodplains based on macroinvertebrates [48, 49].

4 Environmental Impacts on Macroinvertebrates and Species Losses

Aquatic habitats of large rivers in Central Europe have been tremendously altered by diverse human impacts within the last centuries [50]. After river regulations for flood protection and navigation in the second half of nineteenth century and pollution due to industrialisation and human settlements, the building of hydropower plants and damming led to completely different stream characteristics regarding hydromorphological features like habitat dynamics, substrate and flow velocities. Decoupling the main river corridor from its floodplains and associated processes (like regular floods) changed nutrient cycles and influenced the characteristics of the faunal assemblages severely. Moreover large rivers are subject to invasions of nonindigenous species within the last decades which are supposed to have additional severe negative effects on the remaining native elements.

4.1 Hydromorphological Impacts

4.1.1 Channelisation

Large rivers and the connected floodplains are sensitive and complex ecosystems which are mainly determined by hydrological processes. Lateral connectivity and interactions between river and floodplain are most essential processes for ecosystem functioning [16–18, 20, 41, 42, 51–53]. During the centuries in man's desire of land reclamation and security, the alterations initiated regarding large rivers tangle processes on catchment, reach as well as local scales. The most severe ecological impacts of river straightening led to scouring processes, thus decoupling the river from its floodplains, and a tremendous reduction of aquatic area in general, especially of lentic, riparian zones.

Demek et al. give a precise summary of the well-documented development at the Danube [54]. The first systematic large-scale channelisation schemes at the Upper

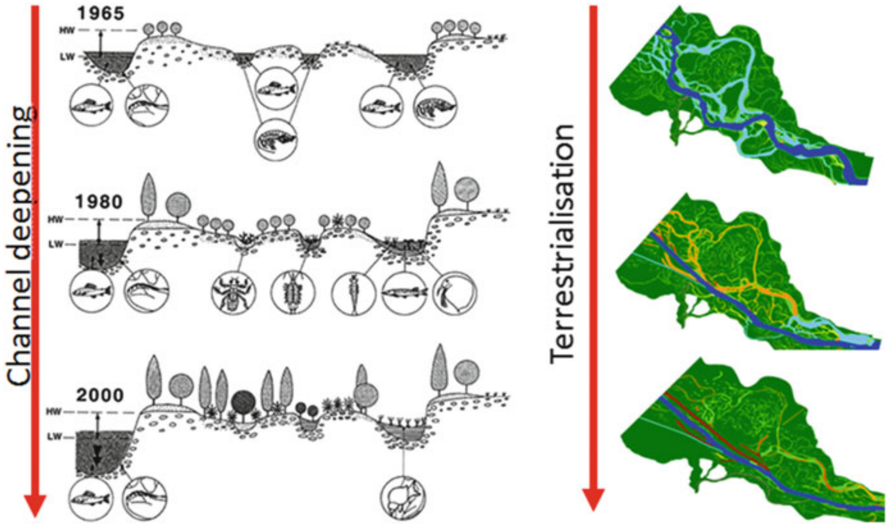

Fig. 10 Terrestrialisation processes due to River regulation and faunal reaction (*left*, Ward et al. [60]; *right*, Graf et al. [49], Danube River at Vienna)

Danube River and the Upper Rhine River were initiated as early as the end of the Napoleonic Wars (1805–1815) [55]. Hohensinner [56] and Hohensinner et al. [57–59] describe in detail the development of channelisation at the Austrian Danube since the early eighteenth century. In Fig. 10 (right) hydromorphological changes from 1715 up to now are illustrated. On the left-hand side the turnover of functional groups and the loss of biodiversity are schematically depicted.

4.1.2 Damming

In general damming leads to increasing sedimentation of fine particles due to the reduction of current velocity in longitudinal, lateral and vertical (clogging of the interstitial) dimensions [61, 62]. Faunal changes are well documented and have different extent from headrace to the weir [62–68]. In general a dramatic change of functional groups from rheophilous to stagnophilous organisms and from scraper/filter feeders to detritivorous, respectively, can be observed. Due to enhanced autotrophic production in dammed areas, the nutrient cycle is altered and filter-feeding assemblages increase below dams (e.g. Statzner [69] and Mauch [70]). Besides these local impacts damming influences the discharge regime and sediment transport considerably and changes the overall character of riverine systems (e.g. Habersack et al. [71]). The homogenised discharge dynamics and summation effects of dam chains lead to a loss of type-specific organisms which are replaced by pioneers and more opportunistic and insensitive faunal elements [72, 73] as documented by Usseglio-Polatera and Bournaud [74] and Fruget [75] at the Rhone River.

Fragmentation of habitats, especially like the succession of dams at the Upper Danube, may suppress genetic exchange of populations [76] and represent a major threat for biodiversity in general [77].

4.2 Pollution

An excellent description of various pollution pathways in Vienna during the Middle Ages is given by Kohl [78] which may be generally applied on most European cities and connected large rivers of that time. Liebmann and Reichenbach-Klinke [79] list pollution sources along the entire course of the Danube and provide a historical outline of organic pollution (e.g. the first biological water quality map of the Austrian Danube). As one example of large rivers, Tobias [80] gives an overview of the development of the oxygen and ammonium content from 1970 to 1994 at the river Main with highest pollution loads between 1972 and 1980 and a recovery afterwards which clearly correlates with the revival of the mayfly *Ephoron virgo*. Since that time water quality has substantially been enhanced during the last decades mainly because of raised environmental awareness based on continuous saprobiological surveys and subsequent improved purification processes.

Organic pollution has generally lost its primary role as stressor in aquatic systems of Central Europe and has been replaced nowadays by hydromorphological degradation. Anyhow, organic pollution had its negative effects in the past, and detailed monitoring campaigns have impressively initiated a reduction of organic pollution in the Danube (e.g. Jungwirth et al. [50], Fig. 33). In regard to water chemistry, hazardous and endocrine substances which impact biological quality elements are currently a main issue in water management. The effects of currently applied substances in agriculture as well as in industrial processes together with effluents of sewage treatment plants and their combined effects via the whole catchment areas are poorly understood (e.g. Van Der Geest et al. [81]).

4.3 Navigation

Vessel-induced waves lead to high shear stress at the river banks [82] and Liebmann and Reichenbach-Klinke already observed severe negative effects by navigation in 1967, especially caused by wave action. Juvenile fish were reported to be hurled at the riparian zone, fish were disturbed during spawning in general, and oil was polluting the substrate. Especially wave wash effects have impacts on juvenile fish as reported by Hirzinger et al. [83], Kucera-Hirzinger et al. [84] and Schludermann et al. [85]. Gabel et al. [86–88] investigated the reactions of selected macroinvertebrates and their interactions with fish under the influence of wave actions. Their findings underlie the magnitude of ecological impacts and stress, e.g. the fact that the neozoon *Dikerogammarus villosus* is more flexible than its congeners among the genus *Gammarus* thus suppressing it and other native species.

Negative effects on merolimnic organisms by mechanical damaging especially during moulting processes at the shoreline can be expected but have not been studied yet in detail; in fact the majority of insects still persisting nowadays in the Danube moult nearly exclusively at the water surface.

Furthermore ships are generally suggested to enhance the spreading of neozoa as vectors through ballast water and vessel hulls as suitable colonising substrate. The role of navigation in the process of globalisation of the fauna – the so-called McDonaldisation [89] – is hardly investigated comprehensively in all its aspects, therefore poorly understood and remains still underestimated.

4.4 Neozoa

Nonindigenous species will be discussed in detail by Paunović et al. [90] giving comprehensive and clear definitions. As neozoa are decisive and dominant elements within the benthic community of the Danube for decades, some aspects are shortly addressed here additionally.

Neozoa are per definition species which colonised a given area after the year 1492. Reliable studies on macroinvertebrates started with Linnaeus back at the end of the eighteenth century which makes the designation of certain species difficult due to lack of detailed distributional information. Zoogeographical patterns are the result of mainly climatic conditions and various either recent or historic shifts have been documented. For example, *Dreissena polymorpha* is documented from Tertiarian times in Central Europe, survived glaciation in southern areas and returned during the eighteenth century [91]. Species ranges have been and will be oscillating, but anthropogenically induced pressures like climate change and others speed up these processes and enhanced the awareness of this specific environmental problem [92].

The increasing massive occurrence of invasive alien species in connection with the increasingly documented loss of indigenous faunas of large rivers is observed on a European-wide scale (e.g. Moog et al. [93], Arbačiauskas et al. [94], Graf et al. [95], Panov et al. [96] and Füreder and Pöckl [97]). Besides biodiversity issues this phenomenon is intensively discussed in the context of ecological assessment systems and the closely linked management actions (e.g. Schöll and Haybach [98, 99], Arbačiauskas et al. [94], Panov et al. [96], Olenin et al. [100], Cardoso and Free [101] and Orendt et al. [102]).

The Danube River is – besides a northern corridor via the Volga to the Baltic Sea and a central pathway via the Dnieper to the Elbe and the Rhine – the main southern migration route of aquatic Ponto-Caspian elements [103], and the majority of neozoa in the Danube therefore clearly belong to Crustacea and Mollusca from this region, while only few others like *Atyaephyra desmaresti*, *Eriocheir sinensis* and *Corbicula fluminea* and *Sinanodonta woodiana* and *Potamopyrgus*

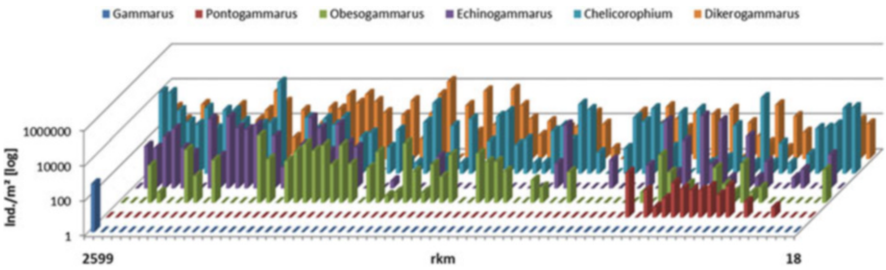

Fig. 11 Distribution of Amphipoda genera with densities along the Danube based on JDS2 data

antipodarum, respectively, are of other origins (the Mediterranean, East Asia and New Zealand; [93]). Figure 11 gives the distribution of the genera Amphipoda with densities along the Danube. Only the genus *Gammarus* is considered to be native in the Upper and Middle Danube.

Direct negative influences of invasive alien species on the original fauna have been hardly testified, but Schöll [104] found clear correlations between increasing densities of the amphipod *Dikerogammarus villosus* and the population decrease of the caddisfly genus *Hydropsyche* in the Rhine River. Moog et al. [105] describe similar interactions between *D. villosus* and *Gammarus fossarum* and *G. roeselii*, respectively, in the river Traun. According to Pöckl [106] the predator *D. villosus* shows higher fertility than the resident *G. fossarum* and *G. roeselii* and is successfully competing with them. Bącela et al. [107] also stated significant changes among the benthic associations after the new colonisation of *D. villosus* in Rhine, Oder, Danube and Meuse. Nowak [108] investigated the effect of *Dreissena bugensis* on other benthic invertebrates, but in general processes behind are still poorly understood.

The seriousness of this problem may be illustrated exemplarily by the recently documented structure of benthic assemblages of the Danube during the JDS2 expedition: Among the ten most frequent macroinvertebrate species sampled, nine are assigned as neozoa [95], above all occurring in very high densities and frequency (see Fig. 12).

In terms of abundance neozoa dominate clearly the benthic communities and reach up to 50% of all documented taxa in the Upper and Middle Danube (Fig. 13).

Neozoa are characterised by Statzner et al. [109] as ecologically flexible, as having high fertility rates, and as nonsensitive thereby being more robust which enables them to colonise disturbed environments. In fact, large river ecosystems are multiply stressed and among the most threatened ecosystems worldwide. Invasive elements may just fill up empty niches after the loss of indigenous elements. Analysing the enhanced invasions in Austria since the 1980s, Moog and Wieser [110] and Korte and Sommerhäuser [111] mention the increasing water temperatures as one essential trigger, which was also mentioned earlier by Rahel and Olden [112].

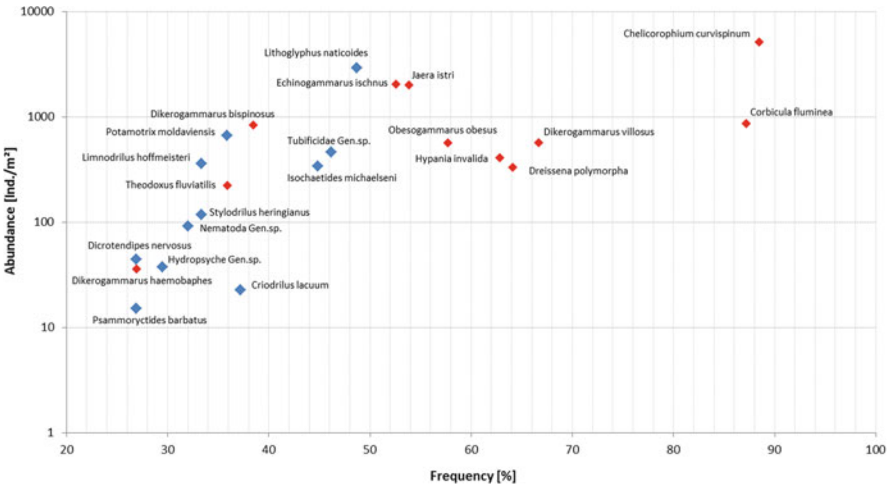

Fig. 12 Most dominant taxa (frequency >25%) and their average abundances (when present) in the Danube during JDS2; neozoa marked red

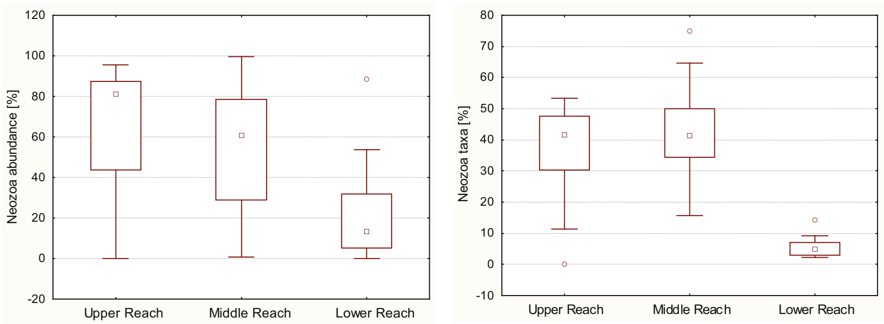

Fig. 13 Box-and-whisker plots of neozoa abundance and neozoa taxa numbers

From an ecological point, the most dominant neozoa have severe impacts on the entire functioning of aquatic ecosystems as they (1) reach high densities (e.g. 500,000 ind./m^2 of *Chelicocorophium curvispinum* in the Morava [113] dominate the benthic community and colonise niches of indigenous faunas), (2) act partly as bioengineers changing the habitat characteristics entirely (*Chelicocorophium* spp. alter the microhabitat structures by building tubes; *Corbicula* spp. provide a specific habitat for other species, respectively, as the diameter of adult shells resembles microlithal conditions; [114]) and (3) intervene significantly in the nutrient cycle, e.g. *Corbicula* spp. This Asian clam – an active filter feeder – shows mass occurrence and can reach a biomass of more than 7 kg/m^2 ([93]; Danube at Linz, Austria); Rey [115] stated even a biomass of 30.8 kg/m^2 in Lake Constance.

Nakano and Strayer [116] recently gave a worldwide overview on biology, impacts and ecosystem engineering of biofouling animals. They stress the fact that biofoulers are economically important and estimate a yearly global cost of 277 million US$ to be caused by them. Documentation of faunal changes (e.g. Paunovic et al. [117, 118], Borza [119, 120], Borza and Boda [121] and Borza et al. [122]) is therefore essential as it seems that shifts and range oscillations have not ended yet (e.g. Fischer [123] and Fischer et al. [124]). Large datasets as compiled by the Joint Danube Surveys are extremely useful and necessary in monitoring of the ecosystem functioning and potential changes in ecosystem services. Restoration of hydromorphological conditions hopefully will contribute to achieve improvements in ecological integrity, but as stated by Füreder and Pöckl [97], a substantial recovery is probably impossible.

5 Large River Species and Losses

Large rivers in Europe have undergone many anthropogenic modifications and have lost a high share of their indigenous fauna, especially sensitive insects like Ephemeroptera, Plecoptera and Trichoptera (EPT taxa). Other than in commercially important species like fish, we have few indications of the occurrence of macroinvertebrates on species level of large rivers during the centuries. Many of these species once covered a large area in Europe (summarised exemplarily for Plecoptera by Zwick [77]); nowadays nearly all of them are listed in Red Data books of most countries as threatened or even extinct. Den Hartog et al. [125] documented a disappearance of 85% of these species in the Lower Rhine, Mey [126] describes a similar phenomenon regarding Trichoptera, and Fittkau and Reiss [7] highlighted this fact in general.

The Danube River seems to be no exception. Among Trichoptera only the river-type specific *Hydropsyche contubernalis* and *H. bulgaromanorum* were found along all reaches accompanied by local populations of *Setodes punctatus* during JDS2. Other and more frequently documented species of that group are known to be more or less insensitive and typical for slow current velocity. Ephemeroptera were mainly represented by few species of the genus *Caenis* and *Heptagenia* only which occurred sporadically. Plecoptera could not be found downstream of the site Oberloiben, while Raušer [127] reported a rich indigenous stonefly community for the Danube and listed the following well-documented species according to literature: *Brachyptera trifasciata*, *B. braueri*, *Oemopteryx loewii*, *Taeniopteryx araneoides*, *T. nebulosa*, *Perlodes dispar*, *Isogenus nubecula*, *Isoperla obscura*, *Isoperla difformis*, *Marthamea vitripennis*, *Xanthoperla apicalis* and *Isoptena serricornis*.

The few historical information indicates that these species once indeed occurred in very large numbers. Calderini [128] described the disturbance of local people by masses of *Brachyptera trifasciata* in Italy, and Ausserer [129] mentioned this species to be "specialmente in primavera molto comune in tutta la fauna".

Kühtreiber [130] remarked "all silts and sand banks are teeming with them", giving us possibly a hint on the substrate type preferred by this species. Bridges in Prague were so crowded with the nowadays nearly vanished *Brachyptera braueri* that the public called it the "Prague fly". *Isogenus nubecula* was described in Brauer and Löw [131] as "very common" in the vicinity of Vienna. Mass emergence of the species *Oemopteryx loewii* was reported as early as 1775 by Schäffer [132] from Regensburg, of which nowadays only few females are left in museums. The last reliable finding is reported by Russev [133] from the Bulgarian Danube in 1955. Although cumulative effects of multiple stressor interactions are responsible for this losses, the last records of conspicuous species are well coinciding with the period of dam building at the Upper Danube.

Most of those potamal species had wide distributions in Europe once. Zwick [77] cites records of *Isogenus nubecula* from England, France (Paris), the Netherlands, the Danube at Ulm and Vienna, Dresden and Bulgaria, and similar large areas have been covered once by *Marthamea vitripennis* [134] and *Xanthoperla apicalis* [135].

Today's populations are isolated and persisted exclusively in small and severely fragmented refuges as in the case of *Isogenus nubecula* in the river system Lafnitz/Raba in Austria/Hungary and the Tisza in Hungary [136, 137]. Other examples which demonstrate similar fates of large river species are given in, for example, Fittkau and Reiss [7], Zwick [77, 134] and Fochetti and Tierno de Figueroa [138]. A few of these species seem to have survived in discrete refuges and have been rediscovered only recently. *X. apicalis* of which some vouchers from 1884 (Danube at Vienna) exist in the Museum of Natural History in Vienna was recently collected in the middle of the 16th district of Vienna [139]. This long-lost species is apparently recolonising some large rivers in Central Europe (e.g. Braasch [140]).

Among Ephemeroptera *Ephoron virgo* is another example of a potamotypic species with mass emergence which was so conspicuous that Schäffer [141] reported it already in 1757. After some decades of disappearance, its revival was reported yearly by local newspapers along the Upper Danube as its numerous corpses can lead to operations of snowplough trucks to prevent accidents. Production of these potamotypic mayflies was incredibly high, and Tobias [80] cites old reports, whereas locals attracted specimens with fire and lamps and gathered them at the shore. At the river Saône in France, 100 tons of corpses were yearly collected and used as food for swines, fishes or birds and as fertilisers or even sold to pharmaceutical industries (Lampert [142], in Tobias [80]).

Another Ephemeroptera, the large species *Palingenia longicauda* (4 cm in body length), was formerly found from the Netherlands to Ukraine [143]. Nowadays *P. longicauda* covers 2% of its former range [144] which led to listing it as one of the few aquatic insects in Appendix II of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention). It is doubted to have colonised the Upper Danube [145] but was regularly recorded from the Bulgarian stretch and some tributaries. Incredibly high densities reached between up to 3,350 specimens/m^2 and biomasses up to 660 g/m^2 [146], contributing essential to food resources for, for example, fishes. According to Russev [143, 146] *P. longicauda* is a habitat specialist which burrows tubes in clayey substrates, the argillal. Since

1974 records from the Danube River are missing maybe caused by reduced habitat availability among other stressors as stated by Russev [147] in 1992. Recently some specimens were found by G. Chiriac at Braila in 2011 (personal communication) which doubtlessly confirmed its return or persistence in refuges of the Lower Danube stretch. Soldán et al. [148] report one population at the Danube Delta, and another well-known and famous site is the River Tisza where spectacular mass emergences can still be observed [149].

Both mentioned Ephemeroptera species are burrowers living in U-shaped tubes and are therefore eco-engineering their environment. They filter out fine organic particles; thus, their reduced occurrence influences the nutrient turnover of the ecosystem. Stief et al. [150] found that microbial communities of burrows are different to that of the sediment and conclude that the presence of *E. virgo* contributes significantly to the ecological connection between the water column and the sediment and to the biogeochemical processing of organic matter in the riverbed. This specific food niche now is occupied nearly entirely by the invasive filter feeders *Chelicocorophium* (Crustacea) and *Corbicula* (Mollusca), besides the trichopteran genus *Hydropsyche*. Additionally to their effects on the aquatic ecosystem – e.g. Gheracopol et al. [151] stated that the diet of a starlet consisted 69% of *P. longicauda* – their mass emergence transferred a huge biomass to the terrestrial, nourishing a long list of organisms like spiders, birds, bats, etc. This stresses the importance of macroinvertebrates as available resource for consumers in general and in 1967 Russev [152] stated a yearly production of 19.235 tons of benthic biomass in the Danube Delta.

Like the mentioned species above, some stenoecious trichopteran species of large rivers as *Platyphylax frauenfeldi* belong to the most endangered aquatic species on a European scale with only one known vital population at the River Drava in Hungary [153, 154]. Another species, *Parasetodes respersellus*, has undergone dramatic population losses since the 1960s in Central Europe. Recently it was rediscovered in the Tisza River [155]. It once inhabited the Lower Danube in Romania where it was found prior to 1962 for the last time [156]. These species may nowadays act as umbrella species for an intact community and their occurrence may indicate vital processes and essential river-specific abiotic-biotic interactions. However, in Trichoptera only one case of extinction has been documented (*Hydropsyche tobiasi*, [154]) though human-induced considerable regressions or even extinctions in several national states are regularly reported (e.g. Botosaneanu [157]).

In fact many typical and nowadays extinct or endangered species of large rivers show mass emergences and short but synchronic flight periods (*Ephoron virgo*, *Palingenia longicauda*, *Xanthoperla apicalis*, *Isoperla obscura*). This phenomenon seems to be essential for mating and reproduction success; as minimum population size is not known, slight reductions of swarming stages may lead to severe bottlenecks leading to abrupt species losses within the whole catchment.

As pointed out earlier, the benthic assemblages are nowadays clearly dominated by nonindigenous, invasive or cosmopolitan elements which probably have strong negative effects and misbalance the ecological functioning of the whole system.

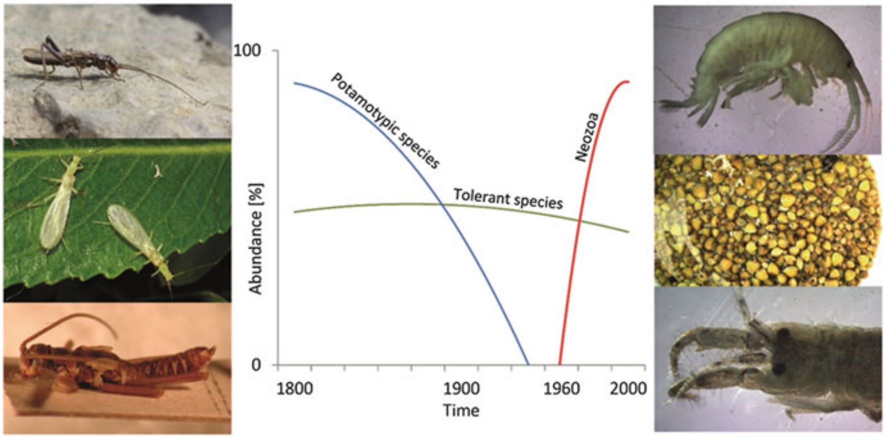

Fig. 14 Conceptual development of the fauna of large rivers in Central Europe from 1800 to 2000. Photos: *left*, indigenous species of the Danube, *Brachyptera trifasciata*, *Xanthoperla apicalis*, *Taeniopteryx araneoides* (pinned specimen, Museum Budapest, Photo: D. Murányi); *right*, invasive species, *Corbicula fluminea*, *Dikerogammarus villosus*, *Chelicocorophium curvispinum* (Graf and Pletterbauer, unpublished)

Figure 14 illustrates the above-mentioned processes documented in large rivers in Central Europe conceptually.

Molluscs are another typical and prominent element of large rivers and still colonise the Danube with many species. Two species, namely, *Unio pictorum* and *U. tumidus*, are the most common large mussels of the Danube which form the highest biomasses of benthic invertebrates in the main channel. The third species, *U. crassus*, which can only be rarely found in the Danube has undergone a strong decline throughout Europe in the recent decades; e.g. in Germany this species receded by about 90% of its former distribution area [158]. Consequently *U. crassus* is an endangered species which is mentioned in Annex II and IV of the European Fauna-Flora-Habitat Directive (e.g. Csar and Gumpinger [159]). Following Nesemann [5, 6] *U. crassus* occurs with several subspecies in the Danube basin (tributaries and Mosoni-Duna); only one living specimen from the main channel was recorded for the Austrian stretch [160]. Csányi et al. [161] report on the first record of *U. crassus* in the Lower Romanian Danube between Calarasi and Braila. *Anodonta anatina* is present in the Middle Danube, while the Asian species *Sinanodonta woodiana* increases steadily in density from the Middle Danube to the Delta but has invaded successfully backwaters all over the Danube floodplains. The Asian clam *Corbicula fluminea* covers the whole river stretch in high densities, while *C. fluminalis* is still rare and is present at few sites only. The zebra mussel *Dreissena polymorpha* is abundant on the Upper and Middle Danube; the newly invader *D. bugensis* has already spread to Vienna and above [123, 124].

Regarding snails, two *Viviparus* species (*Viviparus acerosus* and *V. viviparus*) are still common along the banks. Within Neritidae, *Theodoxus fluviatilis* has the widest distribution along the Danube; it is considered to be a neozoon. The Danube

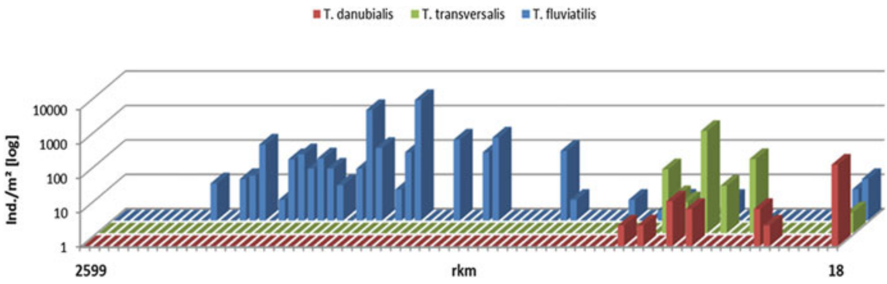

Fig. 15 Distribution of three species of the genus *Theodoxus* along the Danube recorded during JDS2

basin-specific *T. danubialis* is mainly restricted to the Lower Danube, while the formerly widespread *T. transversalis* is living now in a very restricted section at the Lower Danube (Fig. 15).

6 Conclusion

Large rivers have been altered for centuries (e.g. Tockner et al. [162, 163]), and Hering et al. [164] summarise the multiple interactions between various stressors of aquatic ecosystems worldwide. The Danube is regrettably no exception, but drivers and pressures fit well in a Pan-European scale. Rates of habitat modification of large rivers are currently so high that virtually all natural habitats and protected areas are destined to become ecological "islands" in surrounding "oceans" of altered habitats. This process of fragmentation and isolation in landscapes under human influence – main concepts in the island biogeography theory – is predicted to lead directly and indirectly to accelerated species extinctions at both the local and the global scales, thus reducing the world's biodiversity at all levels [165, 166]. In the context of the so-called McDonaldisation of the biosphere [89], the dispersal of many species is inhibited, while others – mostly more flexible species in ecological terms – become common and overtake the niches of indigenous species. Replacement of vulnerable taxa by rapidly spreading taxa that thrive in human-altered environments will ultimately produce a spatially more homogenised biosphere with much lower diversity. Regarding aquatic ecosystems and in particular large rivers, similar processes have already been observed by Fittkau and Reiss [7], Zwick [77, 134] and Fochetti and Tierno de Figueroa [138]. The multi-stressor complex appealing on large rivers, especially in Central Europe, is conceptually given in Fig. 16.

Potamal communities at the edge of their ecological capability might collapse when temperature increases due to climate change that adds to the deadly anthropogenic cocktail [167]. But with few exceptions there is no evidence of an actual decrease in species richness of rather flexible riverine and wetland assemblages in

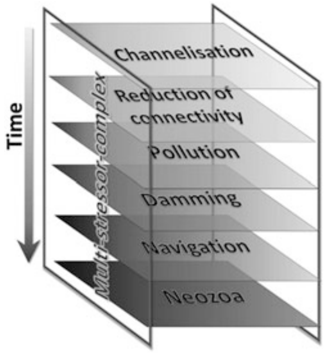

Fig. 16 Conceptual framework of a multi-stressor complex of large rivers (Graf and Pletterbauer, unpublished)

lowlands of Central Europe, simply because most of these communities have been already dramatically shaped by anthropogenic pressures of various kinds; those surviving organisms are tolerant cosmopolitans which cover a large area of ecoregions.

On the other hand, there are signals of a recolonisation regarding some riverine species which indicates improvements in the overall habitat quality and the ecological status. Awareness of the vulnerability and sensitivity of the large river ecosystem has risen and various restoration plans are put in praxis along the Danube. Linear systems like rivers are depending on processes within the entire catchment, and local efforts – despite their undoubted merits – can only marginally soften large-scale impairments. International cooperation is therefore required to monitor and improve the ecological status of the Danube and to conserve its fauna.

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