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Deliverable 5-C: Report on legacy and tipping points in large rivers

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Content

Non-technical summary

Large rivers have always been in the focus of human attention. Ancient and modern civilisations have arisen, prospered and dwindled on their banks, leaving us with the myths and legends that their waters provoked. Large rivers are of major economic relevance as providers of substantial services like, most notably drinking water, food, energy and transport. Large rivers have been altered since centuries and have undergone dramatic human-induced changes. Thus, large rivers are among the most stressed ecosystems worldwide.

In large rivers the stability as well as the disturbance amplitude trigger integral ecosystem functions and determine where and when which habitats are available within a temporal context. Thus, the basis for a sufficient understanding on the effects of stressors and their role in faunal changes strongly depends on the understanding of the ecosystem processes and their interlinkages which determine ecosystem functioning. This deliverable addresses the historical development of stressors in large European rivers and their legacy on the faunal elements, which have been typical in those rivers. Nowadays rare potamontypic Plecoptera, aquatic insects, have been chosen to act as umbrella-species reflecting ecosystem health.

The analyses showed a common development of the major stressors damming, navigation and neozoa in large rivers during the second half of the 20th century, which can be observed for other economical and societal factors too. The major regulation with corresponding channelization effects have been already finished at the beginning of the 20th century. However, those channelization effects have been emphasised by measures related to damming and to the improvement of large river navigability.

We found a considerable shrink in the distribution area of selected indicator species, namely of the aquatic insect order Plecoptera, the stoneflies. The analyses identified few refugia in Central France (Loire, Allier), Austria/Hungary (Raba, Lafnitz) and Hungary/Romania (Tisza) where a combination of several species still can be found after 1990. These systems show some communalities like natural discharge and sediment regimes. Even though neozoans have invaded them, unbroken dynamic processes seem to lessen their negative effect on indigenous faunas. Losses are identified in many river systems, especially in Scandinavia and Spain. Even though the analyses are related to uncertainties due to data gaps, the general trend seems plausible.

Especially invasive species in consequence of inland navigation tremendously changed the faunal composition of aquatic insect assemblages. Biological reference communities are lost for most large rivers since long times and cannot be described empirically. To establish ecological integer ecosystems as demanded by the Water Framework Directive, the few river systems, which still sustain typical large river species, must serve as reference to restore hydrologically and sedimentologically dynamic habitats.

Introduction

Large rivers renege borders – neither political nor eco- or bioregional borders. Hence, they constitute transnational and –regional ecosystems. However, large rivers are among the most stressed ecosystems worldwide. Relevant stressors comprise channelization, damming, eutrophication, alteration of sediment transport, and neozoa, which are also found in smaller riverine ecosystems, and furthermore drainage and decoupling of floodplains as well as navigation, which are special to large river systems. As part of Work Package 5, task 5.2 deals with large rivers and their stressors on the European scale.

Objective

The task consists of two parts: (i) Legacy and tipping points, and (ii) Development of an assessment system for large European rivers. This deliverable is dedicated to the first part of the task which addresses the historical development of stressors on large European rivers and their legacy. Data from a wide range of European rivers will be summarised with emphasis on the Danube, the largest river in Central Europe, to give a qualitative as well as quantitative evaluation on the stressors and theirs effects on biological quality elements over time. The analyses will be related to different stressors and pressures like overfishing, pollution, channelization, dam construction, navigation, and invasive species. Finally, the stressors will be related to documented changes in the aquatic communities and ecosystem services which provides additional understanding of the legacy of large European rivers.

The findings will then feed into the second part of the task, which aims at the development of an assessment system for large European rivers as the currently existing assessment schemes have been mainly developed for small and medium-sized wadeable rivers, and lack full applicability for large rivers. The knowledge gained from both parts will help to assess the potential of recovery and provide guidance for prioritising restoration measures for large European rivers in the future.

Background

Independent of sectors, the development of socio-economy shows a uniform pattern on the global scale over time. Even tough, the global human uses last back for several hundreds of years, the intensity of human uses with according consequences for ecosystems tremendously speeded up since the 1950s (Steffen et al., 2015). The trend and acceleration of the anthropogenic developments like population growth, use of fossil fuels, global commerce, and industrial chemical processes combined and amplified with highly important implications for riverine ecosystems as well as large rivers. This relevance for riverine ecosystems is directly mirrored by the increasing number of dams and increase of water use (Fig. 1). Accordingly, Fig. 1 also shows that the level of use steadily increased slowly till ~1950, followed by an exponential increase since then.

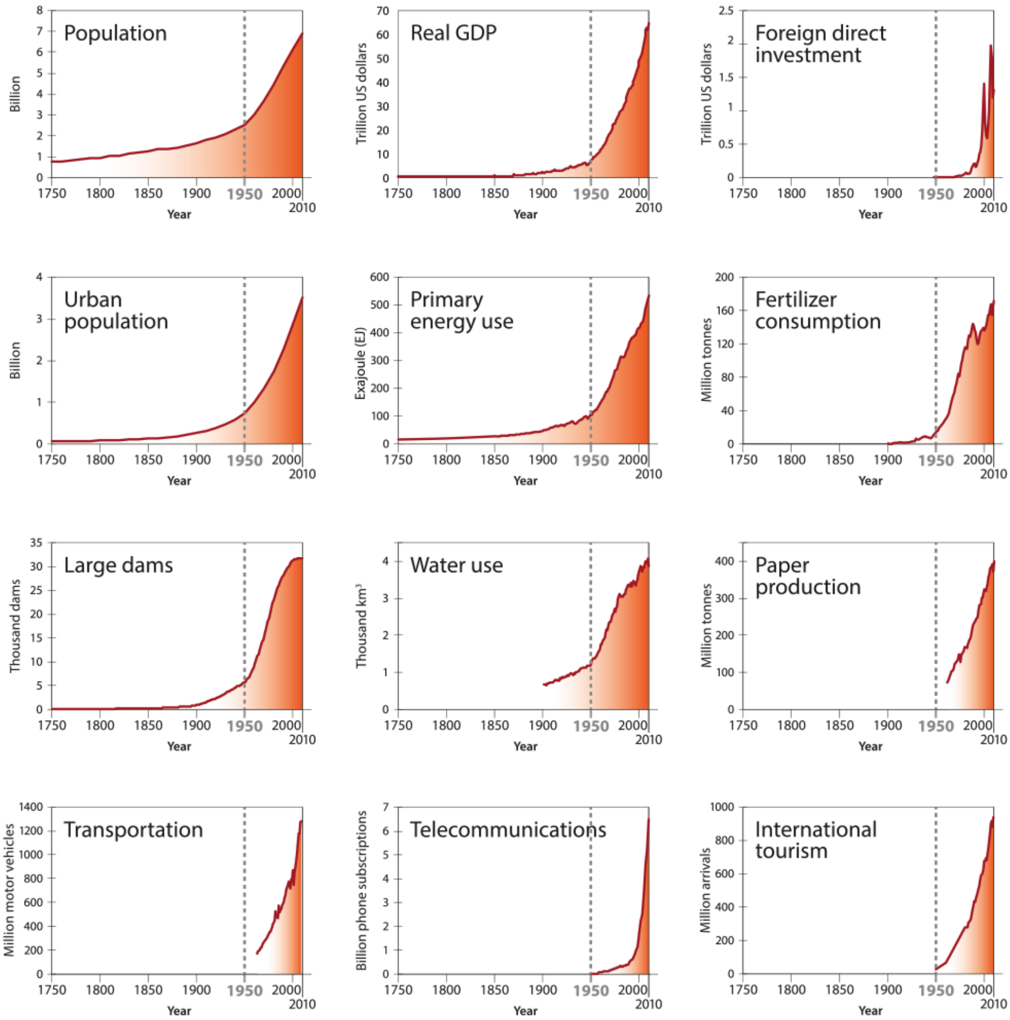

Fig. 1: Socio-economic trends for twelve indicators from 1750 to 2010 from Steffen et al. (2015) including the river-relevant indicators 'Large Dams' and 'Water Use'

Large rivers have always been in the focus of human attention. Ancient and modern civilisations have arisen, prospered and dwindled on their banks, leaving us with the myths and legends that their waters provoked. Large rivers are of major economic relevance as providers of substantial services like, most notably drinking water, food, energy and transport (Demek et al., 2008; Kohl, 2010), well represented by a large number of European capitals situated next to large rivers.

Beside those benefits for human civilisation, large rivers are inherently linked to risks and uncertainties, especially due to flood risk. Therefore, mankind sought to control large rivers to gain better flood protection and to secure the provision of beneficial services. The waves of alterations on large rivers were strongly related to the technical abilities, like the invention of steam-engines, and the interest of socio-economy, like provision of goods to capitals.

Nearly all large rivers in Europe have undergone dramatic changes since decades, or even centuries. However, the documentation of these changes is still scattered and often related to sectoral perspectives and interests. In this report, the occurrence and development of various stressors through time should be described in a broader context. Starting with a synthesised description of the history of drivers and pressures and followed by some detailed but representative examples of stressor developments in the 20th century. This more comprehensive view on the stressor development will be then linked up to tipping points of biological communities, i.e. on distribution patterns of large river Plecoptera species in Europe over time supplemented by the information on fish stocks in the Danube River. These analyses will be based on existing sources (i.e. reviewed literature). However, historical data often comprises inconsistencies and gaps. Thus, the identification of changes is mostly related to qualitative differences; where possible, quantifications were taken into account.

Large river functioning

Rivers can be classified by length, by discharge or by catchment area into size-classes (e.g. Tockner et al., 2009). The intercalibration exercise of the European Commission recognises rivers as large by a catchment size threshold exceeding 10,000 km^2. On a global scale discharge volume or river length are mostly used to build river size rankings and to identify the largest ones.

However, does such a classification or ranking reflect the ecosystem ‘large river’ properly? And in turn: Which processes and functions determine the characteristics of a large river ecosystem? And accordingly, are faunal elements, which are characteristic of large rivers, restricted in their occurrence to river systems with a defined catchment size? These questions are not directly related to the historical development of stressors but they have to be considered in the development of a functioning assessment system. Faunal elements as well as processes and functions characterising large rivers, are definitely not linked to size-indicators thresholds like length or catchment area as mentioned above.

Large rivers feature a multitude of habitats, which are linked to different processes, and thus, a diverse fauna under pristine conditions. Accordingly, some of those habitats and processes can be found in medium-sized rivers too. The knowledge on the temporal change of stressors and faunal elements should inform about the relevant ecosystem processes being impacted. In turn, it is possible to look for reference ecosystems where both the faunal elements and thus the intact ecosystem processes still occur. In summary, this implies the necessity to consider smaller river systems too.

Different ecological theories and concepts tried to synthesise the knowledge on processes and functions of riverine ecosystems and help to highlight characteristics, which can be expected in large rivers. The river continuum concept (Vannote et al., 1980) postulated a production to respiration ratio smaller than one and a dominance of collectors for large river sections. Junk et al. (1989) highlighted the importance of flood pulses in river-floodplain systems, whereas floodplain size generally increases with river size as well as flood duration and predictability which in turn emphasises the importance of floodplains in large rivers. Ward (1989) conceptualised on the processes of riverine ecosystems by the four-dimensional nature of lotic ecosystems where beside the spatial, the temporal dimension was taken into account too. The dynamic and comprehensive nature of a large river ecosystem and the fundamental role of processes acting on habitats like sedimentology is highlighted by e.g. Moss (2008). Others underlined the importance of scales and their hierarchy (e.g. Frissell et al., 1986; Poff, 1997) and yet others focussed on the patterns and amplitude of processes (e.g. Lake, 2000; Poff & Ward, 1990; Townsend, 1989; Townsend et al., 1997). In common, those concepts underpin the relevance of diverse habitats and dynamics of the inherent processes or try to unify those aspects (Thorp et al., 2006).

However, processes initiating habitat quality and availability are inevitably linked to typology of large rivers whereas braided sections form distinctive different templets than meandering courses. From a biological aspect these types are well reflected by the prevailing organisms under near natural conditions and have to be considered in assessment approaches.

Geology, climate, and basin land cover have been often reported as primary drivers of stream and river ecosystems (Bhowmik et al., 1984; Resh et al., 1988). Under undisturbed conditions, river processes and dynamics vary over time, responding to seasonal, annual, and long-term changes in the three drivers. Water and sediment discharge regimes within the basin stream network provide the major mechanisms for the drivers to affect changes in the river dynamics. Within a basin, as rivers increase in size in the downstream direction, predictable gradients occur in the forces that shape the river, control the substrate, and provide organic material (Webster & Patten, 1979; Vannote et al., 1980).

In summary, in large rivers the stability as well as the disturbance amplitude trigger integral ecosystem functions, which determine where and when habitats are available. Thus, the basis for a sufficient understanding on the effects of stressors and their role in faunal changes strongly depends on the understanding of the ecosystem processes and their interlinkages which determine ecosystem functioning. However, the complex linkages between these ecosystem processes, directly affecting the habitat of biota and therefore the biological state, are not sufficiently quantified respectively proven especially in large rivers.

The history of drivers and pressures in European large rivers

The EU FP7-project REFORM 'Restoring rivers FOR effective catchment Management' (Grant No 282656) addressed hydro-morphological river modifications and their restoration (i.e. rehabilitation, mitigation). Within the D3.4 larger rivers were discussed as satellite topic. This chapter, based on Van Geest et al. (2015), syntheses the findings on the historical trajectory of driving forces, river regulation and rehabilitation of large European rivers. This syntheses includes a summary for the timeline of occurrence of drivers and pressures based on six case-study rivers.

Nowadays, almost all large rivers in Europe are heavily regulated, channelized and dammed, which often started centuries ago. Consequently channels incised, floodplains aggradated and hydroperiods have been modified to support hydropower generation, navigation and freshwater supply, and to protect the hinterland from flooding (Tockner et al., 2009). Due to this multiple stressor complex, the identification of the primal causes for degradation is complicated. As a consequence, former extensive aquatic/terrestrial transition zones lack most of their basic ecological functions.

Many large rivers in Europe are affected by the same drivers and associated pressures. However, little is known, on the chrono-sequence (timeline) in the occurrence of these drivers and pressures. Accordingly, this synthesis addresses the following questions:

- Are there any differences in the timeline of occurrence of drivers and associated pressures between rivers?
- What are commonalities, and what are differences?
- Are these differences related to climate regions in Europe?

A description of the evolving stressors over time may give insight into the causes for major transition points for species composition in large river ecosystems.

The case study rivers

In Van Geest et al. (2015), six case studies have been described that are spread across Europe. These case studies are representative of various European conditions with regard to climate, hydro-morphology and catchment size (Table 1). The case studies are situated in six countries. All these rivers can be characterised as large rivers (catchment area larger than 10,000 km^2), although they differ in climatic zone, river length, catchment size, discharge, slope and river style. Large rivers can be considered as unique ecosystems and results are difficult to generalize. Still these case studies together give a good impression on the present regulation and rehabilitation of large rivers in Europe.

Table 1: General characteristics of the six case studies described in this chapter (based on Van Geest et al., 2015)

	Trent	Delta Rhine	Po	Ebro	Vistula	Danube (Delta)
Country	GB	NL	IT	E	P	RO
Climate	Atl	Atl	Alp/Cont	Med	Cont	Cont
Length (km)	275	1,250	650	930	1,048	2,857
Catchment (km^2)	10,466	185,260	74,000	85,530	194,700	801,463
Discharge (m^3/s)	28.5	2,200	1,540	462	1,046	6,500

Qualitative historical timeline of occurrence of drivers and pressures

Detailed information regarding the extent of drivers and pressures (i.e. exact determination of time and intensity of occurrence) are scarce. Thus, we will mostly discuss the time line in a qualitative manner.

Differences between rivers

Between the case studies, there are large differences in timing of these pressures. Along the river Po, deforestation already occurred during Roman Age, while for the other rivers this started in the Middle Age. Although data are scarce, this resulted in a strong increase of sediment load into rivers, which probably have resulted in large changes in hydro-morphological functioning of these rivers.

Large scale embankment of the river Rhine already started in the 14th century, while for the other rivers the majority of the embankments have been constructed much later, in the 19th (Trent, Vistula) or 20th century (Po, Ebro, Vistula). As a result, large parts of the active floodplains were permanently cut off from river flooding and have been converted to agriculture land, resulting in a large loss of wetlands along rivers.

Before the 19th century, small adjustments were already made to facilitate navigation in rivers. From the start of the Industrial Revolution (at the end of the 19th century) however, the conditions for navigation were strongly improved by channelization, bank protection and dredging of the main river channel. Commonly, this has resulted in a huge loss of highly dynamic pioneer habitats along rivers. The construction of large dams was mainly concentrated in the second half of the 20th century, thereby changing water levels, sediment budgets and impeding longitudinal connectivity for migrating fish.

Table 2: Timing of most dominant pressures for hydro-morphology in the catchments of the rivers Trent, Po, Ebro, Delta Rhine, Vistula and Danube (Delta). When no information is given, then this pressure is not considered as an important pressure.

River	Deforestation catchment	Construction embankments	Channelisation, bank protection, dredging	Large dams	Water dams
Trent	Middle Age?	19th - today	19th - today	19th - today	
Delta Rhine	Middle Age	14th - today	19th - today		
Po	Roman time	20th	19th - today	20th	19th - today
Ebro	Middle Age - 1950	> 1950	> 1950	> 1950	> 1950
Vistula	Middle Age?	1850 - today	14th - 18th		
Danube (Delta)	Middle Age?	20th	1880 - 1990	> 1950	

In the text below, the timeline of each of different drivers (and associated pressures) are discussed in more detail.

Flood protection and agriculture

The primary drivers were flood protection and agriculture for early regulation of all rivers (Table 1 & Table 2). For many rivers, these forms of river regulation started already centuries ago. For the river Po, the human-induced changes became already important during the Roman age. In this period, the dramatic increase in agricultural development and deforestation strongly increased the sediment load of the river and caused an extension of the Po delta along the Adriatic coastline. Deforestation also had a strong influence on the hydro-morphology of other rivers (e.g. Ebro).

Additionally, large parts of (formerly active) floodplains were embanked in all case studies, both for flood protection and agricultural use of the land. These results are in line with many other rivers in northern temperate regions. For North-America and Europe, it has been estimated that approximately 90% of the original floodplain of rivers has been permanently cut off from river flooding by the construction of embankments (Tockner & Stanford, 2002) resulting in a huge loss of low-dynamic habitats in floodplains, such as wetlands and hardwood forest.

The river regulations at around 1800 resulted in a river landscape in which the floodplain area was strongly reduced, but with the possibility for the main channel to migrate freely in the remaining active floodplain, resulting in a dynamic landscape with regular rejuvenation.

Navigation

Especially from the start of the industrial revolution (at about 1850), there was a strong need to improve conditions for navigation. Channelization of rivers for shipping activities has a negative impact on the occurrence of highly dynamic habitats as a result of the stabilisation of the river bed (by groynes, bank protection) and by deepening of the main channel. From this moment onwards, the position of the main channel became fixed and the area of shallow water in the main channel declined strongly.

Navigation plays an important role in many rivers in Europe, and accordingly, also for the case studies in this report. Of our case studies, only the river Vistula in Poland has not been regulated for navigation purposes, and – hence – large parts of the main channel of the river have not been channelized. Beside the hydro-morphological consequences of waterway constructions, navigation directly affects aquatic organisms by vessel-induced waves.

Construction of dams

In the decades after the World War II, many dams were constructed in the rivers. These dams were used for the generation of hydropower, as well as for water supply and irrigation. This has resulted in a decreased longitudinal and lateral connectivity, thereby impeding conditions for migratory fish and other species. Additionally, the construction of the dams resulted in altered hydrological regimes in rivers and reduced the sediment supply to downstream sections, as well to river deltas. Of the case studies, especially the rivers Trent, Po, Ebro and Lower Danube have been severely impacted by the construction of dams.

Pressure effects on hydromorphological processes and ecology

For the majority of the case studies, only limited information was available regarding the observed impacts of pressures on hydro-morphology and ecology. It seems that the sequence of drivers (and associated pressures, see above) have initiated major transition points for ecological processes and biota along large rivers. In the following, the main results are discussed in respect to the time line for the occurrence of these drivers and pressures.

Effects of deforestation

Many catchments of rivers have been strongly affected by deforestation. This has already started many centuries ago, and occurred during the Roman age (river Po) to medieval times (for many other rivers). As a result of deforestation, there was a strong increase in runoff of sediments into the river, which has a strong impact on the hydro-morphological processes and - hence – on river style. Although this must have had a large impact on river systems, there is a large lack of knowledge on the effects on hydro-morphological processes, as well on ecological processes and species composition. Moreover, gradual changes in climate (e.g. increased precipitation) may have caused similar changes to river systems, by changing vegetation composition and runoff patterns of river catchments.

Effects of embankments

The construction of embankments has resulted in a strong reduction of the active floodplains along rivers. Along the Delta Rhine, the river was already completely embanked at about 1400, but for other case studies this started from the 19th century (Table 2). Almost all rivers in Europe are embanked, and hence there are only a few examples left of extensive, intact floodplains. The case study of the Danube Delta may serve as an example for such systems. In extensive floodplains, there are clear gradients in hydrologic residence time i.e. water age and hydraulic resistance, resulting in gradients of sedimentation and nutrients along the lateral dimension of floodplains. Along embanked rivers, however, such gradients are strongly shortened, because of the reduced width of the active floodplain.

Effects of pressures related to navigation

In Europe, large parts of river floodplains were already embanked and floodplains were partly used for agricultural purposes. However, the main channel river was still able to change its course, resulting in a more or less continuous formation of new habitats, such as islands, point bars and abandoned channels. The main channel was still shallow, and in the river-bed there was a gradient from coarse sands in the erosive zones to silt in the depositional areas. Thus, although these rivers did not represent pristine conditions, they were still dynamic processes and according habitats with extensive land use that was largely adapted to the natural morphological patterns and processes (Middelkoop et al, 2005). Paleolimnological research along the Delta Rhine indicates that parts of the river banks may have been covered by macrophytes, while dead trees provided snag habitats which were important for a large number of macroinvertebrate species (e.g. Simulidae; Klink, 1989).

For many rivers, at that time there have already been minor adjustments to the river bed to facilitate navigation. From the start of the Industrial Revolution however, there was a strong need to improve conditions for navigation. Consequently, groynes were constructed, river banks of the main channel were protected with rip-rap and the main channel was deepened. Additionally, dead wood (snag habitat) was removed. As a result, the rejuvenation of the landscape stopped due to the fixed position of the main channel. This has had strong impact on hydro-morphological processes, habitats and thus species composition.

Because of the fixed main channel, the continuous formation of new habitats ceased while succession continued, and thus the overall landscape age increases. This has resulted in a dramatic change in riverine landscape composition in favour of species typical for less dynamic habitats, as was shown and discussed in several studies (Petts & Amoros, 1996; Johnson, 1997; Hughes, 2001; Marston et al., 1995; Tockner & Stanford, 2002). Those changes are strongly related to a legacy effect, as it takes quite some time before their effects get visible. An observed high biodiversity is often a relict of former conditions that will develop towards a lower diversity and a shift in landscape position (Geerling, 2008; Bravard et al., 1986; Tockner and Stanford, 2002). In such a setting, floodplain age distribution can develop as shown in Fig. 2.

In addition to rejuvenation, succession will also cease as land use in the floodplains (partially) changes towards agriculture, as is the case along many regulated rivers. Some ecotopes are converted to pastures or fields, while other will remain in a more natural state. The latter will become relic ecotopes that stay in ecological succession, e.g. relic disconnected side channels. Such a landscape has ‘gaps’ in its age distribution; i.e. it is a temporal discontinuous landscape

(Geerling, 2008; Fig. 3). Although data is scarce, it can be assumed that this has resulted in a strong decline of many riverine species. Nowadays, a large number of riverine species characteristic for young, dynamic habitats are extinct or have strongly declined in number.

Construction of dams

In many rivers, large dams have been constructed, especially after the World War II. There are many comprehensive reviews of the hydro-morphological effects and ecological impacts downstream of dams (e.g. García de Jálon et al., 2013 and references in this report). Overall, the ecological impact of dams often result in three types of environmental alterations (Rood, 2005): (1) changes in the released flow regime (quantity and quality); (2) reduced passage of alluvial materials, in particular suspended solids, and (3) fragmentation of the river corridor, resulting in interruptions in downstream and upstream passage of biota (e.g. fish species).

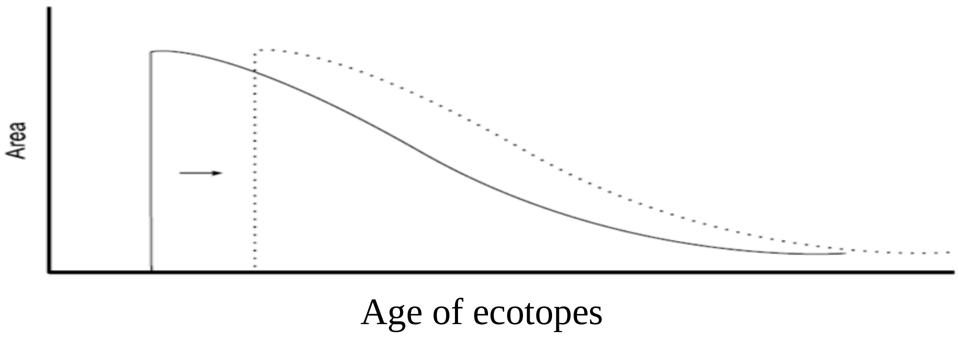

Fig. 2 Conceptual graph of a hypothetical area versus age of natural ecotopes of river with habitat rejuvenation (solid line) versus a regulated river without rejuvenation (dotted line). Along regulated rivers, existing ecotopes continue their succession, while pioneer sites are disappearing (after Geerling, 2008).

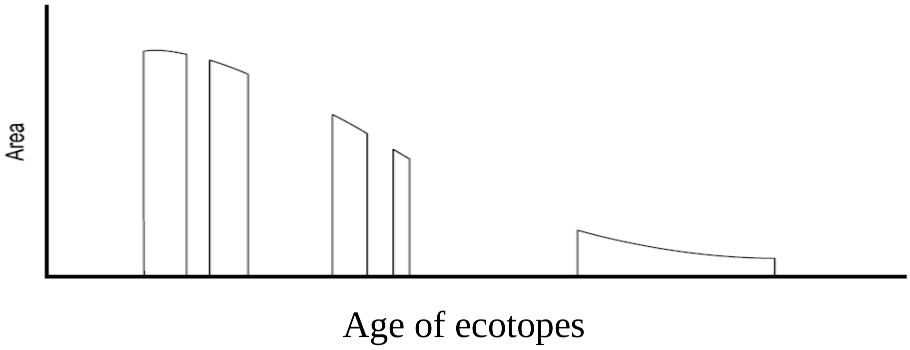

Fig. 3 Conceptual graph of a hypothetical area versus age of natural ecotopes in regulated river floodplains without rejuvenation and with land use changes to agriculture (after Geerling, 2008).

Conclusions on the stressor history in the case studies

Humans have a long history for affecting the hydro-morphological and ecological functioning of rivers. Along the river Po, deforestation started already during Roman Age, while for the other rivers this occurred in the Middle Age. In subsequent centuries, the rivers were embanked (Rhine: 14th century; other rivers 19th and 20th century) and the position of the main channel was fixed with groynes, bank protection and dredging (19th/20th century). After 1950, many dams were constructed.

Although data are scarce, several major transition points can be expected during these developments. The first transition point probably took place during deforestation of the catchment, which strongly affected hydro-morphological functioning of rivers. Another major transition point for river ecosystems is the large scale embankment of lowland rivers, which resulted in a large loss of wetland habitats and hardwood forest. However, at that time there was still the possibility for the main channel to migrate freely in the remaining active floodplain, resulting in a dynamic landscape with regular rejuvenation. Nowadays, these habitats have disappeared due to the fixation of the main channel with groynes, bank protection and dredging. As a result of all these modifications, the former extensive aquatic/terrestrial zones along large rivers in Europe lack most of their basic ecological functions, and the habitats for their characteristic species composition have strongly deteriorated.

Selected quantitative stressor timelines in large European rivers

The summary of the REFORM case studies in the preceding chapter gives a good overview of the general temporal development of human-induced changes in large European rivers. Due to the fact that major parts of the Europe consist of cultural landscape, large rivers in Central Europe have been tremendously altered by diverse human impacts over the last centuries (Jungwirth et al., 2014; Petts et al., 1989). After the Industrial Revolution starting from the end of the 19th century, the pronounced channelization of rivers, the construction hydropower plants and damming led to a completely different hydro-morphology of the rivers with a strong decrease in typical dynamic processes. Different stressors interfere with each other and create a multi-stressor complex (Fig. 4). This chapter focuses on selected stressor developments in the 20th century.

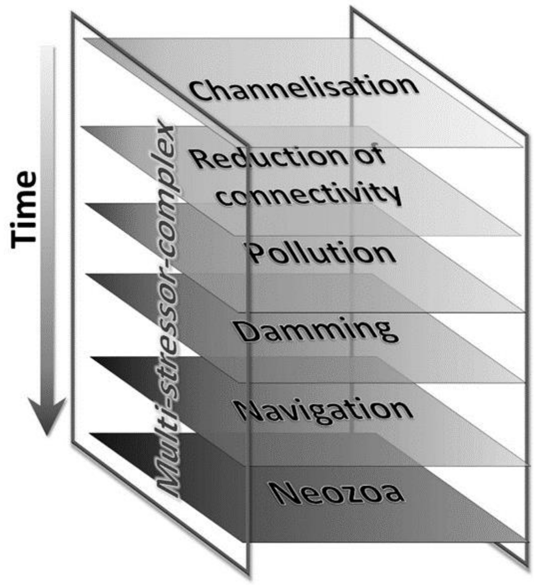

Fig. 4: Conceptual description of multi-stressor development and overlay over time

Information on the temporal development of stressors was derived by reviewing a magnitude of sources. Beside scientific literature and books, we included data from statistical services (http://ec.europa.eu/eurostat/, http://www.statistik.at/), internet resources, e.g. webpages of hydropower companies, localities, and grey literature, which provided information on the historical development of human-induced changes of large European rivers.

Hydromorphological changes

Hydromorphology, as defined by the Water Framework Directive (WFD), represents the physical characteristics of the shape, boundaries and content of a water body. Hence, the term hydromorphological changes summarises several effects on riverine ecosystems which in turn impact different ecosystem processes. In the following the development and effects of channelization and damming are discussed in more detail.

Channelization

Large rivers and – connected with them – floodplains are sensitive and complex ecosystems which are strongly determined by hydrological processes. Lateral connectivity and interactions between river and floodplain are essential processes for the ecosystem-functioning (Amoros & Roux, 1988; Gergel et al., 2002; Junk et al., 1989; Schiemer and Zalewski, 1992; Ward, 1989).

A precise summary of the well documented development and progressing channelization at the Danube is given by Demek et al. (2008). The first systematic large-scale channelization schemes at the Upper Danube River and the Upper Rhine River were initiated as early as the end of the Napoleonic Wars (1805 – 1815; Pasetti, 1862). Hohensinner (2008) and Hohensinner et al. (2004, 2005, 2008a, b) describe in detail the development of channelization at the Austrian Danube since the early 18th century. In Fig. 5 (right) the hydromorphological changes from 1715 up to now are illustrated. Based on the digitisation of different habitat types sensu Amoros et al. (1987) the hydromorphological change over time can be described by the change of the habitats (Fig. 6). All habitats have been reduced in size. However, after all channelization works more or less only main channel habitats (Eupotamon A) persisted. On the left hand side of Fig. 5, this succeeding reduction of habitat types is schematically related with the turn-over of different functional groups and the loss of biodiversity.

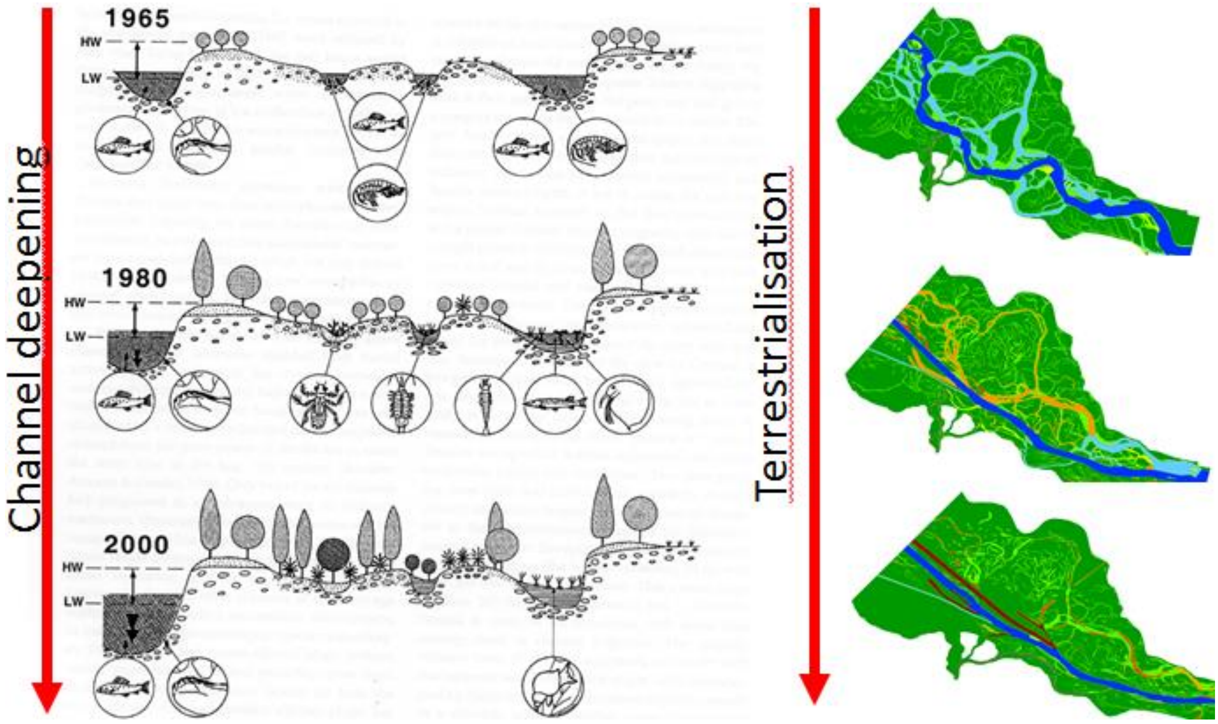

Fig. 5 Terrestrialisation processes due to river regulation and faunal reaction (left: Ward et al. 2002; right: Graf et al. 2013, Danube river at Vienna)

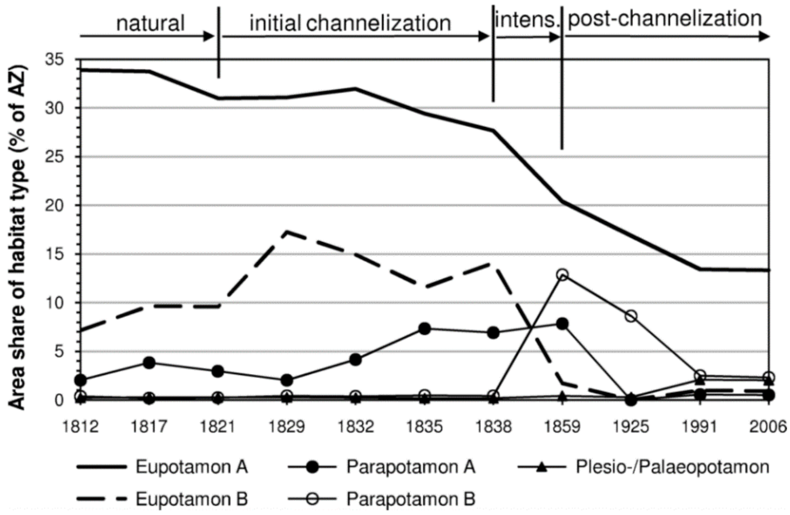

Fig. 6: Temporal change of habitat types from 1812 to 2006 on a Danube River stretch in Austria (Hohensinner et al., 2011), AZ=active zone, intens. = intensive channelization

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 (Moog, 1986; Banning, 1998). Faunal changes are well documented and have different extend from headrace to the weir (Herzig et al., 1987; Moog & Jungwirth, 1992). In general a dramatic change of functional groups from rheophilous to stagnophilous organisms and from scraper/filter feeders to detritivorous species 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, 1981; Mauch, 1981). 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., 2013). The homogenized 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 (Resh et al., 1988).

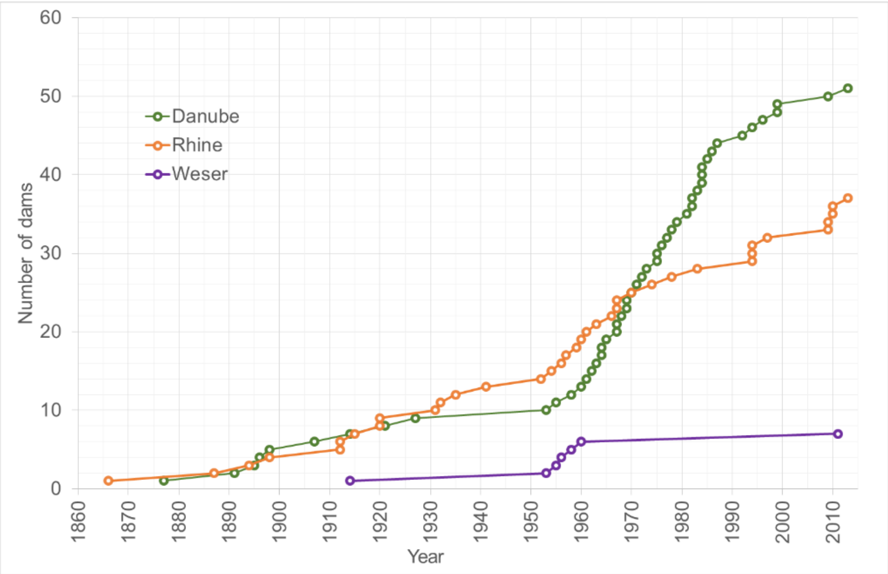

Fig. 7: Number of dams along Danube, Rhine and Weser since 1860

River bed incision is a direct consequence of channelization and sediment retention due to damming. The reduced flow velocities upstream of a dam lead to sediment deposition. Downstream of the dam, the river tries to compensate for this deficit in bed load material and the river bottom is more intensely scoured followed by a drop of the water table. This water table drop also leads to a reduced lateral connectivity between the main river and the floodplains. This degradation process can be observed on several river stretches across Europe. Fig. 8 shows the progressing incision of the Danube River between Vienna and Bratislava between 1950 and 2003. In 1991, the construction of the hydropower plant Freudenau was finished followed by a distinctive drop of the water table.

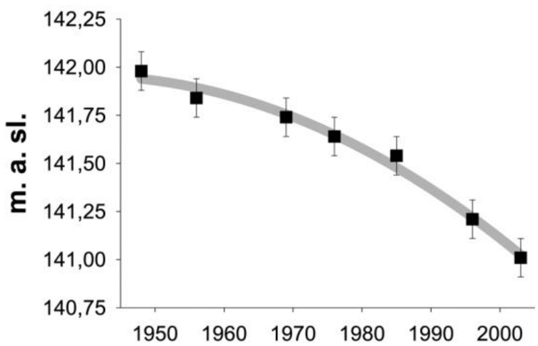

Fig. 8. The low water table of the Danube from 1950 to 2003 (gauge at Wildungsmauer, river-km 1894.7); m.a.sl. - metres above sea level. (Reckendorfer et al., 2005)

Pollution

Water quality pollution is a major stressor of rivers on a European scale. The water of rivers represented not only one of the most important large distance transportation system for societies in earlier days, but also the most important mean of waste transport. Both are fundamental reasons why large settlements and cities preferably developed next to rivers and in a lot of cases next to large rivers.

An excellent description of various pollution pathways in Vienna during the Middle Ages is given by Kohl (2010), which may be generally applied on most European cities and connected large rivers of that time. Liebmann & Reichenbach-Klinke (1967) 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 (1996) 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 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., 2014). In regard of water chemistry, hazardous and endocrine substances, which impact biological quality elements, are a currently emerging issue in water management. The effects of today's 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.

Navigation & Neozoa

The following chapter is dedicated to two special components of human-used large river systems whose occurrences and intensities are interlinked. Navigation on rivers is accompanied by several impacts on the ecosystem, which directly and indirectly affect the aquatic fauna. Likewise, the distribution of neozoa is also triggered by navigation. Accordingly, both stressors are commonly discussed.

Navigation

Most of the dams shown in Fig. 7 were built for power generation but on the River Weser the dams were actually built to provide constant water depth for vessels. Also on the Danube, the construction of dams led to an improved navigability of shallow passages as well as sections with turbulent currents. Accompanying, navigation channels were constructed to improve the waterways with according effects on river morphology.

In 1954 the Conférence Européenne des Ministres de Transports (CEMT) established an international classification system dividing the European waterways into five classes, depending on their dimensions based on the dimensions of five vessel types. Accordingly, a waterway’s class was determined by the largest standard vessel it can accommodate at which the width was the main determining factor. The first convoy of push barges travelled along the Rhine in 1957 with a subsequent success for inland water transport. The CEMT responded in 1961 by adding Class VI to its classification, which became inadequate too soon. In a new, uniform classification drawn up by the CEMT and the UN’s Economic Commission for Europe (ECE), known as CEMT1992 (Fig. 9), on the one hand East European waterways were taken into account and on the other hand larger size classes were included.

	Type de voies navigables Type of Inland waterways	Classe de voies navigables Classes of navigables waterways	Automoteurs et chalands Motor vessels and barges					Convois poussés Pushed convoys					Hauteur minimale sous les ponts
			Type de bateaux: caractéristiques générales Type of vessel: générales characteristics					Type de convoi- Caractéristiques générales Type of convoy- Générales characteristics					Minimum height under bridges
			Dénomination Designation	Longueur Length	Largeur Beam	Tirant déau Draught	Tonnage Tonnage		Longueur Length	Largeur Beam	Tirant déau Draught	Tonnage Tonnage	
				m	m	m	t		m	m	m	t	m
D'INTERET REGIONAL	OF REGIONAL IMPORTANCE	I	Péniche Barge	38.50	5.05	1.80-2.20	250-400						4.00
		II	Kast-Caminois Campine-Barge	50-55	6.60	2.50	4.00-650						4.00-5.00
		III	Gustav Koenings	67-80	8.20	2.50	650-1000						4.00-5.00
D'INTERET INTERNATIONAL	OF INTERNATIONAL IMPORTANCE	IV	Johan Welker	80-85	9.50	2.50	1000-1500		85	9.50	2.50-2.80	1250-1450	5.25/or 7.00
		Va	Grand bateaux Rhenands/Large Rhine Vessels	95-110	11.40	2.50-2.80	1500-3000		95-110	11.40	2.50-4.50	1600-3000	5.25/or 7.00/or 9.10
		Vb							172-185	11.40	2.50-4.50	3200-6000	
		VIa							95-110	22.80	2.50-4.50	3200-6000	7.10/or 9.10
		VIb		140	15.00	3.90			185-195	22.80	2.50-4.50	6400-12000	7.10/or 9.10
		VIc							270-280 193-200	22.80 33.00-34.20	2.50-4.50 2.50-4.50	9600-18000	9.10
		VII							285 195	33.00 34.20	2.50-4.50	14500-27000	9.10

Fig. 9: CEMT classification of waterways from 1992 (source: http://www.pianc.org/)

After the success of push barges, container ships are increasingly in use on inland waterways since the late 1970s as inland navigation vessels are perfect for transporting containers with their rectangular holds.

Table 3: Properties of container transport on the Rhine in the year 1996, 2001, and 2006; TEU = Twenty-foot Equivalent Unit, which characterises the capacity of vessels (source: http://www.watererfgoed.nl/)

property	1996	2001	2006
average carrying capacity (survey data)	185 TEU	273 TEU	310 TEU
average number of containers (survey)	122 TEU	165 TEU	188 TEU
average load factor	66%	61%	61%
proportion of containers loaded	73%	67%	70%
- upriver	59%	49%	56%
- downriver	88%	86%	87%
average weight of all loaded containers*	12.4 t/TEU	12.7 t/TEU	11.4 t/TEU
- upriver*	12.1 t/TEU	11.6 t/TEU	10.6 t/TEU
- downriver*	13.7 t/TEU	13.8 t/TEU	12.4 t/TEU
proportion of 20-foot containers	55%	31%	32%
proportion of 40-foot containers	45%	68%	66%
proportion of 45-foot containers	0%	1%	2%
proportion of high cube containers	7%	18%	31%
proportion of pallet wide containers	0%	0%	3%

* incl. weight of empty container; percentages refer to proportion of TEU

The temporal comparison of different features of container transport on the Rhine, shown in Table 3, reveals that the capacity of container ships is growing steadily. The proportion of 40-foot containers rose from 45% to 66%, and the proportion of high cubes from 7% to 31% within the ten years from 1996 to 2006.

In summary, this underlines the increasing size of vessels which are used for inland navigation and therefore the increasing navigation intensity. The amount of transported goods doubled on the Austrian Danube with a sharp increase after the collapse of the Eastern Bloc at the beginning of the 1990s (Fig. 10). Only the amount of inland transport stagnated.

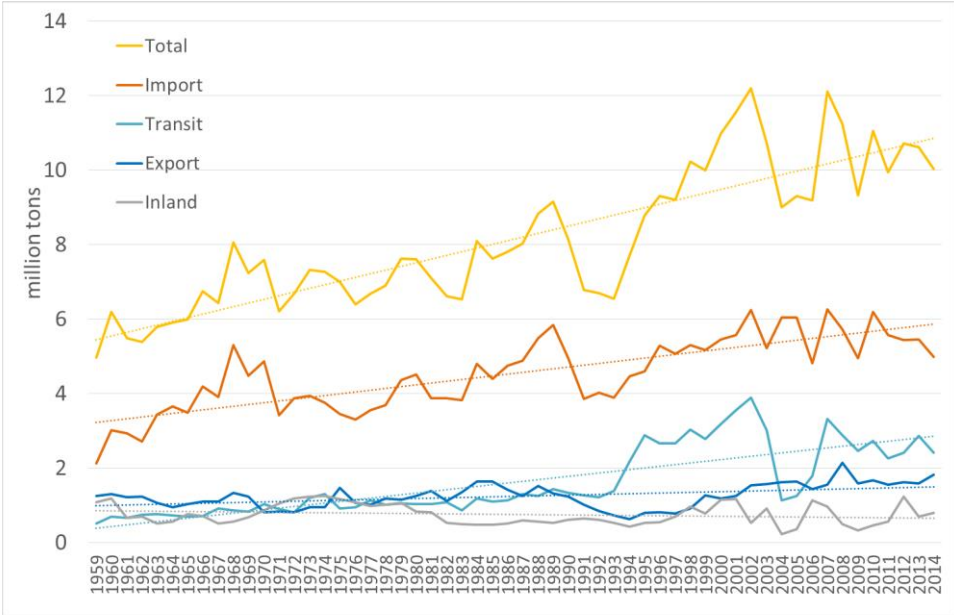

Fig. 10: Transported goods in million tons on the Danube River in Austria from 1959 to 2014

This trend is totally underpinned by Fig. 11, which reveals a continuous and sharp increase of average vessel size between 1970 and 2010, with almost tripling the average vessel size.

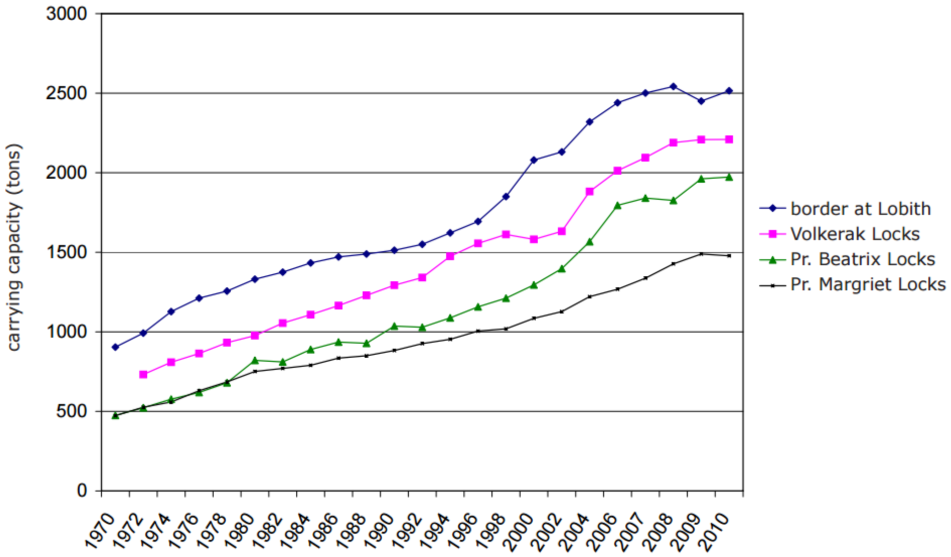

Fig. 11: Temporal development of average vessel size (indicated by carrying capacity) from 1970 to 2010 on the Scheldt-Rhine Canal (Volkerak Locks), the Lek Canal (Pr. Beatrix Locks & Pr. Margriet Locks), and the Rhine (Lobith) (source: http://www.watererfgoed.nl/)

Beside the morphological changes as accompaniment of navigation on rivers, vessel induced waves lead to high shear stress at the river banks (Liedermann et al., 2014). Liebmann & Reichenbach-Klinke (1967) already observed severe negative effects by navigation, 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 etc. was polluting the substrate. Especially wave wash effects have impacts on juvenile fish as reported by Hirzinger (2002), Kucera-Hirzinger

(2009) and Schludermann et al. (2014). Gabel et al. (2008; 2011a, 2011b) investigated the reactions of selected macroinvertebrates and their interactions with fish under the influence of wave actions.

Negative effects on merolimnic organisms by mechanical damaging, especially during moulting processes at the shoreline can be expected but have not 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.

Neozoa

Neozoa are per definition species, which colonise a given area after the year 1492. Reliable studies on macroinvertebrates started with Linnaeus back at the end of the 18th century, which made the designation of certain species difficult due to lack of detailed distributional information. Current and historical zoogeographical patterns are mainly the result of climatic conditions. Accordingly, various shifts, either recent or historic, have been documented. For example *Dreissena polymorpha* is documented from tertiarian times in Central Europe, survived glaciation in southern areas and returned during the 18th century (Grossinger 1794). Species ranges have been and will be oscillating, but anthropogenic induced pressures, like navigation or climate change, speed up these processes.

The increasing 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., 2007; Graf et al., 2008). Besides biodiversity issues, this phenomenon is intensively discussed in the context of ecological assessment systems and the closely linked management actions (Orendt et al., 2009).

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 (Bij de Vaate et al., 2002) and the majority of neozoa in the Danube therefore clearly belong to Crustacea and Mollusca from this region. Fig. 12 describes the distribution of the genera Amphipoda with densities along the Danube River. Only the genus Gammarus is considered to be native in the Upper and Middle Danube. Accordingly, the whole Danube River is nowadays home of the different genera of Amphipoda.

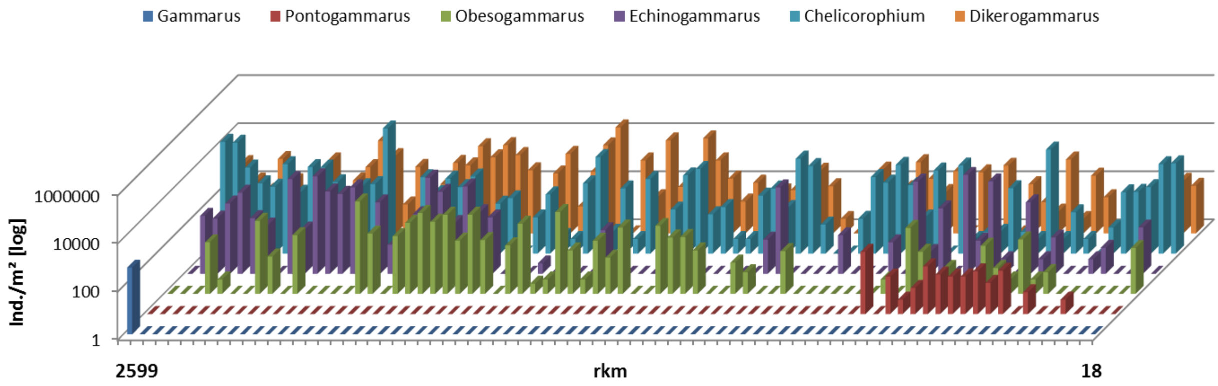

Fig. 12: Distribution of Amphipoda-genera with densities along the Danube based on JDS 2 data

Direct negative influences of invasive alien species on the original fauna have been hardly testified, but Schöll (2006) 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. (2013) described similar interactions between *D. villosus* and *Gammarus fossarum* and *G. roeseli* respectively in the river Traun. According to Pöckl (2006) the predator *D. villosus* showed higher fertility than the resident *G. fossarum* and *G. roeselii* and is successfully competing with them. Bącela et al. (2008) also stated significant changes among the benthic associations after the new colonisation of *D. villosus* in Rhine, Oder, Danube and Meuse. Nowak (2012) investigated the effect of *Dreissena bugensis* on other benthic invertebrates, but the processes behind species competition are still poorly understood.

The seriousness of this problem may be illustrated exemplarily by the recently documented structure of benthic assemblages of the Danube River during the JDS 2 (ICPDR 2008) expeditions which sampled along the whole river: Among the ten most frequent macroinvertebrate species sampled, nine are assigned as neozoa (Graf et al., 2008), above all occurring in very high densities and frequency (Fig. 13).

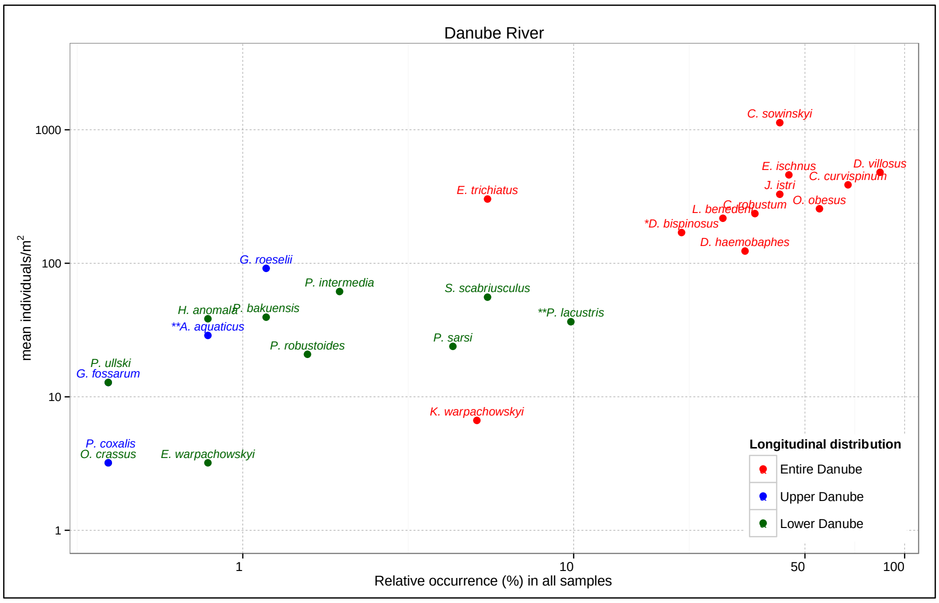

*Fig. 13: Occurrence, frequency and abundance of Peracarida in the Danube River. *: Absent in the Lower Danube; **: Occurrence also in the Middle Danube, downstream of Belgrade. In terms of abundance neozoa dominate clearly the benthic communities and reached up to 50% of all documented taxa in the Upper and Middle Danube*

Neozoa are characterised by Statzner et al. (2008) as ecological flexible, having high fertility rates and as non-sensitive, thereby being more robust, which enables them to colonise impacted environments. In fact, large river ecosystems are multiple-stressed and invasive species may just fill up empty niches after the loss of indigenous elements or outcompete the impaired populations. Analysing the enhanced invasions in Austria since the 1980s, Moog (2010) and Korte & Sommerhäuser (2012) mention the increasing water temperatures as one essential trigger, which was revealed earlier by Rahel & Olden (2008) too. Another important driver, which represents a pressure to other faunal elements too, is navigation. Beside the direct transport of individual through ballast water or on the outside of the vessel, the hydromorphological changes which are implemented on waterways favour the establishment of neozoa.

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./ m² of *Chelicocorophium curvispinum* in the Morava (Graf et al., 2005), dominate the benthic community and colonise niches of indigenous faunas, (2) act partly as bio-engineers changing the habitat characteristics entirely (*Chelicocorophium* spp. alters the microhabitat structures by building tubes, *Corbicula* spp. provides a specific habitat for other species respectively as the diameter of adult shells resembles microlithal conditions), 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/m² (Moog et al., 2007; Danube at Linz, Austria).

Linking shipping intensity (indicated by the amount of transported goods) and the number of neozoa foung along the Austrian Danube shows a clear coinciding pattern. Again, the socio-political event of the fall of the Eastern Bloc is remarkably recognisable (Fig. 14).

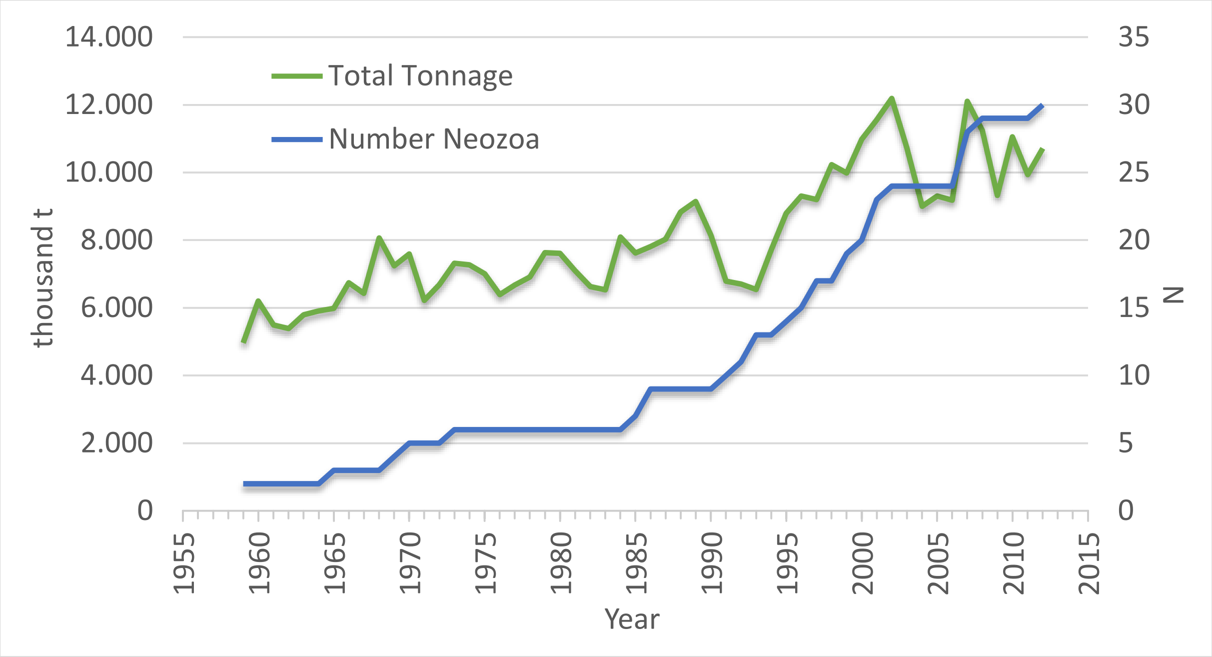

Fig. 14: Development of total tonnage freight and number of neozoa in the Austrian section of the Danube River from 1959 to 2013 (data sources: Statistik Austria, Moog et al., 2013)

Large river fauna

Beside their hydro-morphological characteristics, large rivers also feature and especially featured typical faunal elements and species. However, referring to historical communities and species, which a river once featured, is possible for economically relevant fish species like sturgeons but difficult for other biological elements like Plecoptera (Tittizer et al., 1991).

The analyses of faunal changes address two aspects: (1) disappearance of typical Plecoptera species in large European rivers and the change of distribution patterns over time, and (2) the changes and shifts in fish assemblages of large rivers over time based on the example of the Danube River.

Changes in the Plecoptera fauna of large European rivers

Many of the species occurring in large rivers typically covered large areas in Europe (summarised exemplarily for Plecoptera by Zwick, 1992 and Graf et al., 2008). Accordingly, we can assume that the Plecoptera fauna of large rivers has been uniformly shaped with slight replacement of sibling species at zoogeographical borders. These ‘legends of large rivers’ still persist in discrete refugia. Hence, they are able to indicate sites with ecologically integer processes, potentially serving as reference to identify those ecosystem processes which are necessary to sustain faunal elements typical for large rivers (e.g. Bojková, 2009; Bojková et al., 2011; 2012a; 2012b; 2013; Graf & Kovács, 2002; Kovács et al., 2004; Ruffoni & Le Doaré, 2009; Greulich, 2014; Chovet & Lecureuil, 2009; Wantzen & Richard, 2014) scattered across Europe.

Definition of species of interest

The species records based on spatial explicit occurrences is highly important to link species occurrences with stressors through space and time. Principally, two major criteria were applied to identify Plecoptera species of interest for the purposes of this report. Firstly, the species have a high conservation status mirrored by the Red List classification, i.e. critically endangered or extinct. Secondly, the species were once wide-spread and potamotypic (large river) species. This criterion was checked by information from http://www.freshwaterecology.info (Graf et al., 2008).

The International Union for Conservation of Nature (IUCN) Red List of Threatened Species (further called ‘Red List’) is the most comprehensive inventory of the conservation status of biological species. The conservation status is identified on the basis of assessments on regular intervals and provides information on range, population size, habitat and ecology, use and trade, as well as threats of species. Based on these criteria, the Red Lists classify species into different threatening categories (Fig. 15). Basically, the feasibility of this approach differs between taxonomic groups, especially on the global scale. Hence, Regional Red Lists report the threatening status of species within a certain country or management unit. Therefore giving the possibility to (1) implement the approach for species which are not of global concern, and (2) to directly feed into management actions. The creation of a Regional Red List has to follow a clear and repeatable protocol.

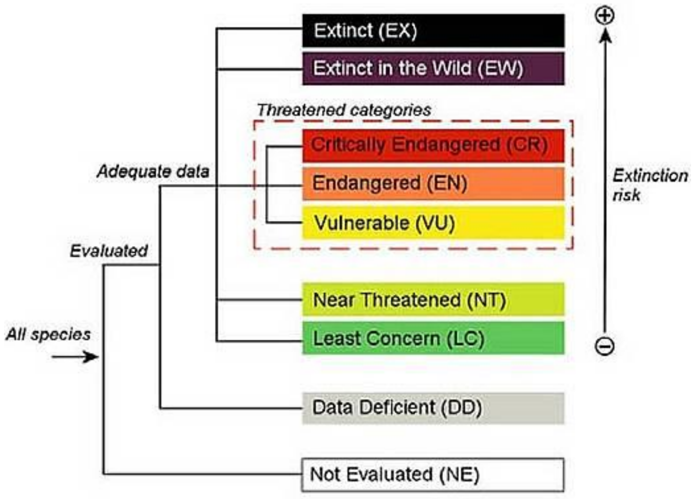

Fig. 15: IUCN Red List categories, EX=extinct, EW=extinct in the wild, CR=critically endangered, EN=endangered, VU=vulnerable, NT=near threatened, LC=least concern; not shown: DD=data deficient, NE=not evaluated (source: www.iucn.org)

As an initial step we collected and screened several Regional Red Lists to identify, underline and highlight the conservation status and extinction risk of Plecoptera typically occurring in large European rivers.

A Red List for Plecoptera was available for the following regions: Switzerland (Lubini et al. 2012), Germany (Reusch & Weinzierl, 2001; Saxony Voigt & Küttner, 2015; Brandenburg (Braasch & Berger, 2003), Bavaria (Weinzierl, 2003), Hesse (Wolf & Widdig, 2013), Sachsen-Anhalt (Böhme, 2004)), Czech Republic (Bojková & Soldán, 2013), Poland (Fialkowski & Sowa, 2002) Norway (Kjærstad et al., 2010), Serbia (Petrović et al., 2014), Spain (Verdú & Galante, 2006), Croatia (Popijac, 2008), Slovenia (Sivec, 2002), Great Britain (Craig, 2015). Additionally comments on the status of species was included from the following sources: Boumans (2011), Bojková et al. (2012a), Bojková et al. (2012b), Popijac & Sivec (2009);

Based on the criteria the following species were defined as the species of interest:

Chloroperlidae
- *Xanthoperla apicalis* (Newman, 1836)

Perlidae
- *Agnetina elegantula* (Klapálek, 1905)
- *Marthamea vitripennis* (Burmeister, 1839)

Perlodidae
- *Besdolus ventralis* (Pictet, 1841)
- *Isogenus nubecula* (Newman, 1833)
- *Isoperla obscura* (Zetterstedt, 1840)
- *Isoperla pawlowskii* (Wojtas, 1961)
- *Perlodes dispar* (Rambur, 1842)

Taeniopterygidae
- *Brachyptera braueri* (Klapálek, 1900)

Brachyptera trifasciata (Pictet, 1832)

Sources for species records of Plecoptera

Initially, stonefly data were extracted from the so-called DAEP database (Schmidt-Kloiber et al., 2016; Graf et al., 2016). The 'Distribution Atlas of European Plecoptera' (DAEP) database is an initiative which have been started within the EU-funded project BioFresh (Contract No. 226874, www.freshwaterbiodiversity.eu). DAEP aims at compiling as many (adult) stonefly data from Europe as possible to increase the knowledge about distributions over space and time of this highly sensitive organism group. Even after the end of the BioFresh project in the year 2014, the work on the database was continued, mostly focusing on filling the distribution gaps and an extensive quality control.

The database currently holds about 100,000 occurrence records of stoneflies from all over Europe. Occurrence data in the dataset were provided by 20 data holders. All data will be made available through the Freshwater Biodiversity Data Portal (www.freshwaterplatform.eu) as soon as data compilation and quality control is finished.

Based on the information from DAEP, we extended the species records by screening taxonomical papers and records described in other literature sources (e.g. Bojková, 2009; Bojková et al., 2011, 2012a; 2012b; 2013; Graf & Kovács, 2002; Kovács et al., 2004; Ruffoni & Le Doaré, 2009). The combination of the data led to a total of 1742 species records across Europe (Fig. 16).

Spatial and temporal units of analyses

The analyses to investigate changes in the distribution of Plecoptera cover a spatial and a temporal level. The temporal level is principally given by the date of the occurrence record. For further analyses, the dataset was split into two parts comparing the periods before and after 1990. The year 1990 was chosen because at this time the human-induced changes such as river straightening or damming (e.g. the construction of the last hydropower plant on the Danube in Austria started in 1992) as well as the impact of those changes on the ecosystems have been in full operation.

The spatial level was handled by two approaches: firstly, the species records were analysed on the bases of their location, i.e. coordinates. In the second approach, we delineated in total 92 large river catchments across Europe based on the CCM v2.1 (Vogt et al., 2007). In some cases, these catchments summarise areas without a large river (e.g. southern Scandinavia). Based on the catchments, the records were intersected with those spatial units. After the intersection, only the information, if a species occurred or not was kept. By this procedure we accounted for inhomogeneous sampling efforts especially for accumulated records within small areas (e.g. Raba catchment). Furthermore, we assumed that if a species occurred in the period after 1990 that this species must have been present in the period prior to 1990, too.

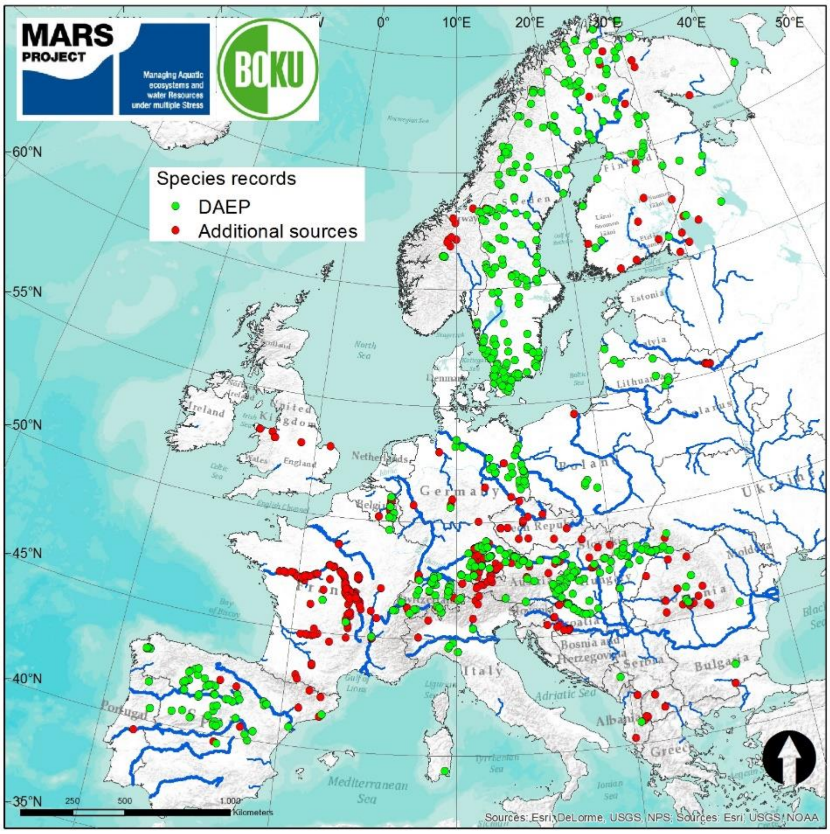

Fig. 16: Location of the species records for the ten Plecoptera species of interest (N=1742)

Results & Discussion

Large rivers in Europe have undergone many anthropogenic modifications and have lost a high share of their indigenous fauna, especially sensitive insects like Plecopterans. Nowadays, a majority of them is found on Red Lists of different countries as threatened or even extinct, which represent a high threatening status (see Fig. 15). Many of the once abundant and characteristic species of large rivers have drastically declined in their abundance or are even extinct in Central Europe, since their habitats have either completely disappeared or are too fragmented for natural recruitment in large abundances.

The spatial distribution of the records (Fig. 18) and large river catchments with species records of the Plecoptera species of interest before and after 1990 (Fig. 19) showed a reduced distribution across Europe. Species records especially reduced in the northern and western part of Europe. Interestingly, the total number of records does not differ that much (943 before/799 after 1990). Comparing the number of records per catchment (Fig. 17), it gets obvious that especially the number of catchments with 20 to 50 records decreased. Species-specific maps showing the record locations as well as the large river catchments with records for both periods can be found in the appendix (Fig. 29 to Fig. 38).

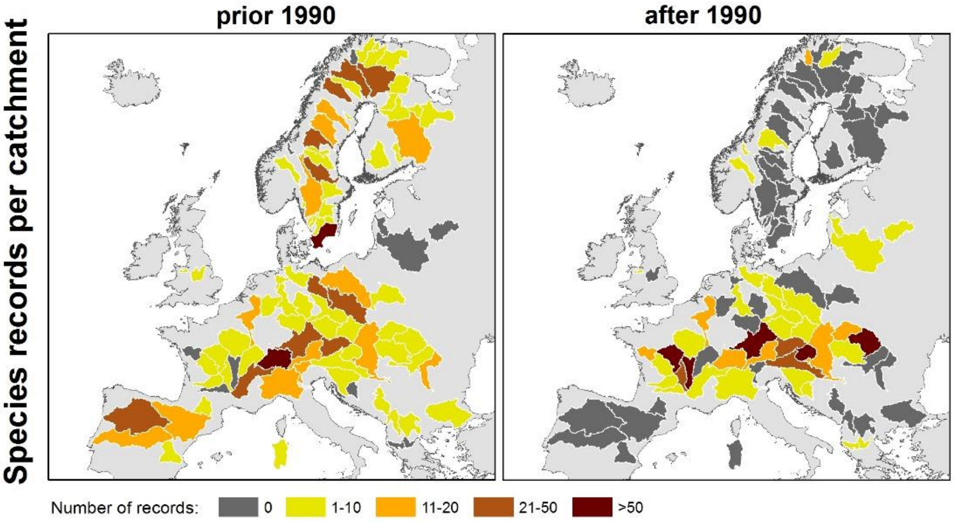

Fig. 17: Number of species records per catchment before 1990 (left) and after 1990 (right)

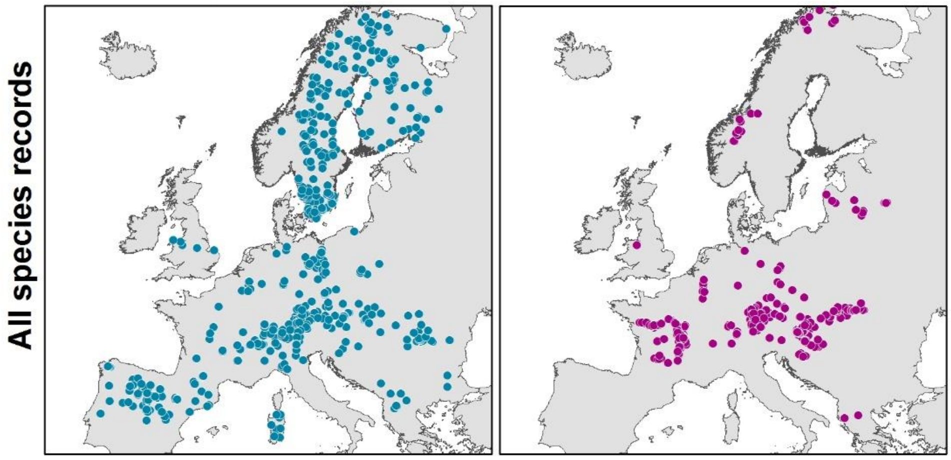

Fig. 18: Distribution of record points of all ten Plecoptera species of interest before 1990 (left) and after 1990 (right)

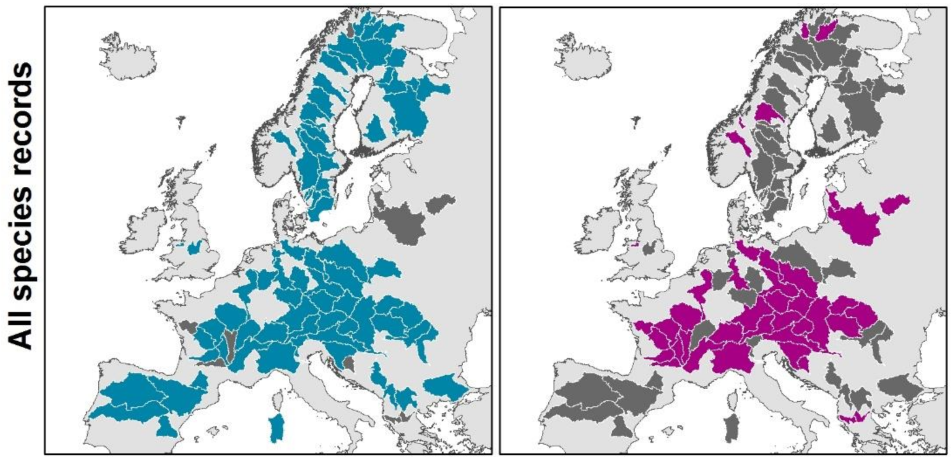

Fig. 19: Distribution of large river catchments with records of all ten Plecoptera species of interest before 1990 (left) and after 1990 (right)

Based on the intersection between large river catchments and record locations it was possible to identify the number of catchments with species records before and after 1990 (Fig. 20). Each species (with exception of *A. elegantula*) showed a reduced number of catchments with records for the period after 1990. The strongest decrease in the number of catchments with records occurred for *I. obscura*. In total, less than the half number of catchments were found with a species record after 1990. *A. elegantula*, *B. ventralis*, and *I. pawlowskii* revealed for both periods a relatively small number of records.

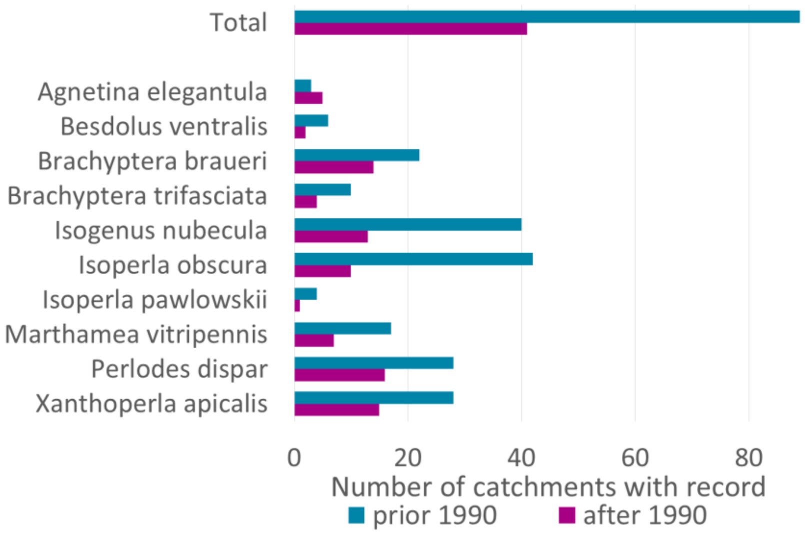

Fig. 20: Number of large river catchments with occurrence records of the ten Plecoptera species of interest and in total of all species before 1990 (turquoise) and after 1990 (purple)

Summing up the occurrence of the ten single species per period and catchment underlines the shrinkage in the distribution of those large river specialists (Fig. 21). Before 1990 eleven large river catchments featured more than five of the Plecoptera species of interest. After 1990 only two areas remained with five or more of those species, namely the Raba catchment and the middle section of the Danube River including the rivers Vah, Hron and Ipel. In turn, no records were identified for a large number of areas formerly featuring large river Plecoptera. Furthermore, some catchment areas kept a stable number of species from the period before to the period after 1990. These catchments include the following river basins: Loire incl. Allier, Drava, Inn, Nemunas and the upper part of the Tisza Basin.

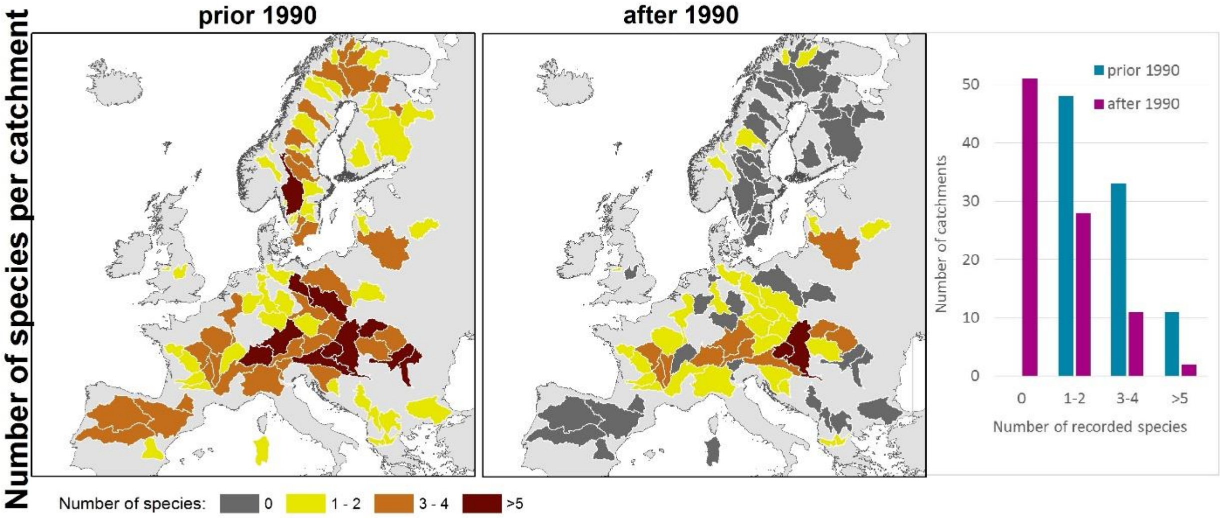

Fig. 21: Number of recorded species per catchment before 1990 (left) and after 1990 (middle) as well as summarising the number of catchments per record number category (right)

The coordinates of the record points were used to compare the distribution ranges of each species as well as the distribution centres (indicated by the median) between the two periods (Fig. 23). Interestingly, *A. elegantula*, which showed a larger number of catchments with records after 1990, revealed a shrinkage in latitude as well as a shift in both latitude and longitude. The records of *B. ventralis* shifted eastwards for the period after 1990. The range of distributions shrank in latitude and longitude for *B. braueri*. *B. trifasciata* shifted eastwards after 1990. Even though the number of catchments clearly decreased for *I. nubecula*, the species showed no shrinkage in longitudes. In turn the latitudes indicated a distinct shrinkage. *I. obscura*, which showed the largest decrease in the number of catchments with records, revealed no shrinkage neither for latitude nor for longitude. However, the median of latitude clearly shifted southwards. The records of *M. vitripennis* clearly shrank for both latitude and longitude. The latitudes of *P. dispar* records shrank and shifted southwards for the period after 1990 with comparable ranges of longitudes for both periods. *X. apicalis* showed the largest shrinkage in latitude as well as a westward shift of longitudes.

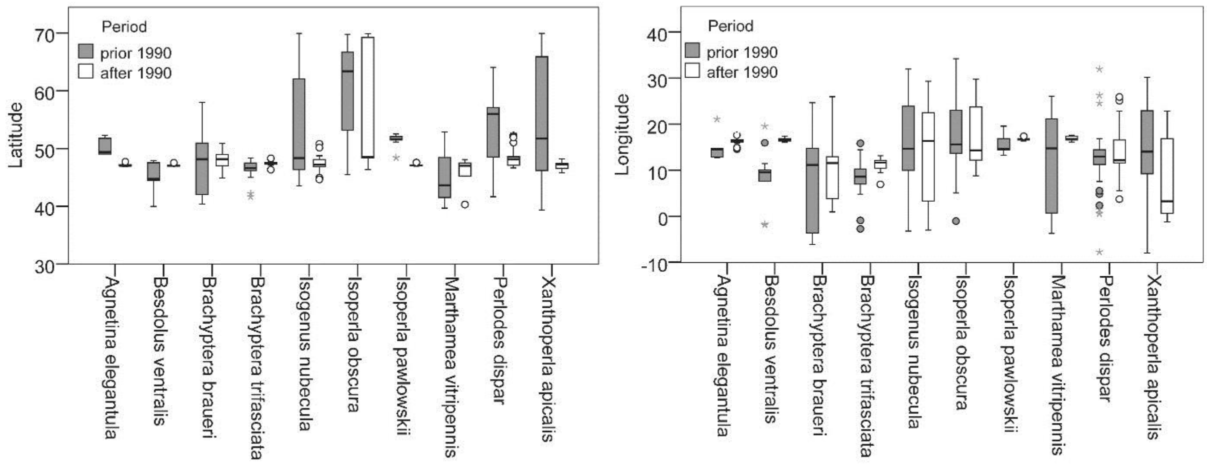

Fig. 22: Shift in latitude (left) and longitude (right) for species records of the ten Plecoptera species before 1990 (grey boxes) and after 1990 (white boxes)

There are some examples from literature on typical faunal elements of large rivers in Europe, which indicate that these species once occurred in very large numbers – in such large numbers that the presence of the species was not only recognised by taxonomical specialists or ecologists but by ordinary people too. Bridges in Prague were so crowded with the nowadays nearly vanished *B. braueri* that the public called it the “Prague fly”. Calderini (1868) described the disturbance of local people by masses *of B. trifasciata* in Italy, and Ausserer (1869) mentioned this species to be “specialmente in primavera molto comune in tutta la fauna“, i.e. the species have been very common for the fauna during spring. Kühtreiber (1934) remarked “all silts and sand banks are teeming with them”, giving in turn a hint on the preferred substrate type by this species. *I. nubecula* was described in Brauer & Löw (1857) as “very common” for the Danube in the vicinity of Vienna. Mass emergence of the species *Oemopteryx loewii* was reported as early as 1775 by Schäffer from Regensburg, of which nowadays only few females are left in museums. The last reliable finding is reported by Russev (1962) from the Bulgarian Danube in 1955. In the Danube, Plecopterans could not be found downstream of site Oberloiben (Joint Danube Survey 2; ICPDR, 2008) while Raušer (1957) reported a rich indigenous stonefly community for the Danube and listed the following well documented species: *B. trifasciata*, *B. braueri*, *O. loewii*, *Taeniopteryx araneoides*, *T. nebulosa*, *P. dispar*, *I. nubecula*, *I. obscura*, *I. difformis*, *M. vitripennis*, *X. apicalis* and *Isoptena serricornis*. Other examples which demonstrate similar fates of large river species are given in e.g. Fittkau & Reiss (1983), Zwick (1984; 1992) and Fochetti & Tierno de Figueroa (2006).

Although cumulative effects of multiple stressor interactions are responsible for these losses, the last records of conspicuous species are well coinciding with the period of dam-building at the upper Danube. Zwick (1992) cites records of *I. nubecula* from England, France (Paris), the Netherlands, for the Danube at Ulm and Vienna, Dresden, and Bulgaria, and similar large areas have been covered once by *M. vitripennis* (Zwick 1984) and *X. apicalis* (Zwick 1999). Today’s populations are isolated and persisted exclusively in small and severely fragmented refuges as in the case of *I. nubecula* in the river system Lafnitz/Raba in Austria/Hungary and the Tisza in Hungary (Graf & Kovács, 2002; Kovács et al., 2002).

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 (Graf, 2010). This long lost species is apparently recolonizing some large rivers in Central Europe (e.g. Braasch, 2003).

Few refugia of typical large river assemblages in Central Europe still exist, which can serve as reference sites. However, the records on theses reference assemblages are published in hidden taxonomic journals which are thus overseen by water authorities (e.g. Graf & Kovacs, 2002). The recent records of the species enable the identification and investigation of ecosystem processes, which support the occurrence of these species. One example for such an integer system is the River Lafnitz, a tributary of the Raba river, which has a length of 114 km and a catchment size of 1994 km², which is not seen as a 'large river' by the WFD. The Lafnitz still provides near-natural hydro-morphological conditions without impacts of navigation or big dams. Even though, the Lafnitz River cannot be considered as large river, it provides characteristic large river habitats.

Fish assemblages of the Danube

Fish assemblages of large rivers have been subject to human influence since millennia. In contrast to many other aquatic taxonomic groups biodiversity change was also initiated by direct human exploitation. For instance, on the Lower Danube fishery dates back to the Mesolithic and Neolithic period. In the Middle Danube fish remains from human settlements have been proven for the Late Copper Age about 4500 years before present (Bartosiewicz & Bonsall, 2004). Large predator species and sturgeons were main targets. Thus, exploitation and in recent centuries overexploitation was clearly an important driver of fish assemblage changes in large rivers beside the indirect effects of human induced habitat change and climate variability.

Materials

Fish assemblage changes of the Danube have been compiled for this report based on printed species inventories and scientific literature mainly of the 19th and 20th centuries as well as based on recent publications especially on fish catch statistics. For the Austrian Danube and Danube sturgeons also archival sources have been utilized. The systematic screening of commercial catch data as collected and reported by FAO since the 1950s (FAO Capture, Aquaculture and Global production databases 1950 – 2014) did not yield results relevant for species conservation or assessment as especially for the Danube countries and riverine freshwater fish species no differentiation between individual species was made.

Results & Discussion

Based on the different documents and sources finally used several trends of fish assemblage development can be described for the Danube:

Long-term, regionally progressing decline of specific species and final threat of these species in the entire river.

The main example for this development are the four diadromous Danube sturgeon species (*Huso huso*, *Acipenser stellatus*, *A. gueldenstaedti*, *A. nudiventris*). Beluga sturgeons (*Huso huso*) might have migrated in the past as far upstream as Regensburg (e.g. Schmall & Friedrich, 2014). It is however unclear, if the Bavarian Danube was ever an important spawning place. In the Austrian Danube, regular migration of sturgeons are proven from the 12th up until the 16th century. After the 16th century, the number of migrating individuals seems to have declined. An increasing fishing pressure in the Hungarian Danube might be a plausible explanation (see Balon, 1968). As records of the Viennese fish markets on sturgeon delivery from Hungary indicate, the abundance of sturgeons in the Hungarian Danube declined dramatically in the late 19th century (Haidvogl et al., 2013; 2014; Jungwirth et al., 2014). Although to the best of our knowledge this was so far not yet proven and/or published this decline of yields seems to have been the result of an increasing catch in the Lower Danube. At the end of the 19th century, average yearly catch of sturgeons in the Lower Danube amounted to about 700 tons. In the 20th century, human induced habitat alterations added to (over-)exploitation. In the 1960s, beluga, Russian and stellate sturgeon, as well as few ship sturgeons where caught regularly in Yugoslavia. Catches of about 16 tons per year reported in Busnita (1967), in 1961, e.g. 12 tons were caught, in 1962, 21 tons. From the 1970s onwards, the Iron Gate hydropower dams stopped spawning migrations beyond the Lower Danube. In the Lower Danube and in the delta populations dramatically declined until the end of the 20th century due to continued partly illegal fishing and habitat alterations aiming mainly at supporting navigation.

Fig. 23 depicts (average) catches of sturgeons in the Lower Danube and the Danube Delta since the late 19th century (Schiemer et al., 2003; internal data M. Staras, DDNI).

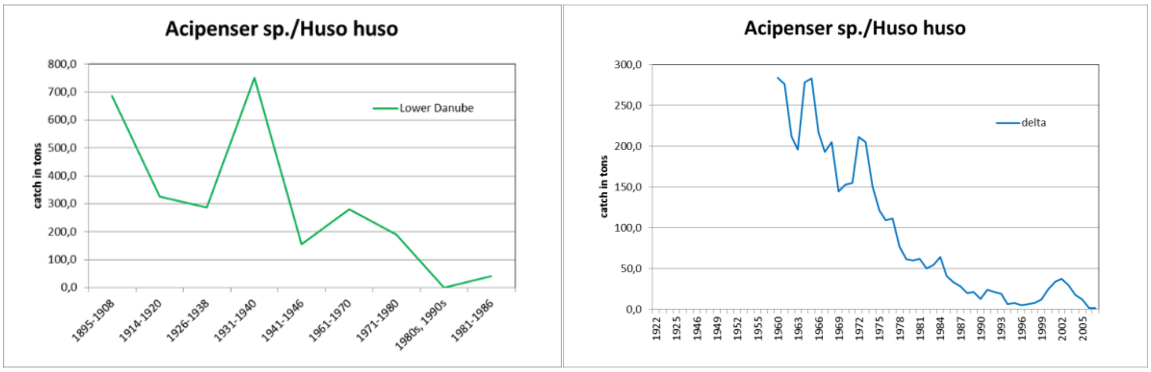

Fig. 23: Catches of sturgeons in the Lower Danube and in the Danube Delta according to Schiemer et al. (2003; right) and internal data of M. Staras (left)

Sturgeons and diadromous species in general are a valuable example to demonstrate the long-term effects and patterns of fish population decline in large rivers due to overfishing. A decline of sturgeon catch and average fish lengths from the 7th/9th to the 12/13th century in archaeological sites along tributaries of the Southern Baltic Sea demonstrates that the Danube was by no means a singular case (Hoffmann, 1996).

Extinct species with a narrow geographical niche

According to Kottelat & Freyhof (2007) 13 fish species have gone extinct in Europe since 1700. Notably, four are from the Danube catchment although definite species identification is in some cases difficult due to the lack of museums specimen available for morphological and genetic analysis. This concerns specifically *Alburnus danubicus* (Danube shemaya) which was recorded for the Lower Danube in Romania and Bulgaria and coastal lakes. Only two written descriptions from Antipa (1909) and Drensky (1943) exist as basis for species determination (see Kottelat & Freyhof, 2007). *Romanogobio antipai* (Danube delta gudgeon) occurred in the Lower Danube in Romania and Ukraine from the confluence with Arges downstream to the delta. *Salmo schiefermuelleri* (Mayforelle) was reported e.g. by Heckel (1851) and Heckel & Kner (1858) for subalpine lakes of the Austrian Danube catchment (e.g. Attersee, Traunsee, Fuschlsee) and occurred probably also in lakes of the Swiss Rhine drainage. *Gasterosteus crenobiontus* (Techirghiol stickleback) inhabited the freshwater springs of the hypersaline Romanian Lake Techirghiol. It is assumed that it has gone extinct due to the hybridization with *G. aculeatus* after the originally separated habitats of these two species were transformed and became connected due to irrigation.

Identifying the extinction of an individual species especially on regional scale strongly depends on sufficient sampling effort. For instance, in Austria the European mudminnow (*Umbra krameri*) was considered to be extinct after 1975. This species inhabits small, shallow and vegetated waterbodies of the Middle and Lower Danube and is native in the Upper Danube as far upstream as Vienna. Suitable habitats strongly decreased in the 20th century due to flood plain drainage and disconnection. Nevertheless, in Austria a remaining population was rediscovered by Wanzenböck in 1992 in a floodplain waterbody of the present national park downstream of Vienna (Wanzenböck, 1995; Wanzenböck & Spindler, 1995).

Decline of phytophilic spawners due to large scale disconnection of floodplains in the Middle and Lower Danube (and large tributaries)

As described by Staras (e.g. 1999) hydrology was an important factor of fish productivity in the Danube delta. Productivity increased with the number of days and height of flooding as reported by Anitpa (1912): In 1904/05 (1 April 1904-31 March 1905) no flood occurred and a total of 920 tons of fish were caught. In 1907/08 the water level reached 5.4 m and the inundation lasted for 128 days; a total of 6,448 tons fish were caught. Drainage measures halved the floodplains originally amounting to 466,000 ha in the late 1950s and continued in the 1960s. This also altered the hydrological regime. As a result fish productivity declined. Total fish catch declined from 10-20.000 tons per year before and during the 1960s to 5,000 - 6,000 tons after 1984. This development affected species differently. Especially for pike-perch (*Sander lucioperca*) and pike (*Esox lucious*) as phytophilic spawners catches dropped in the late 1960s from 2,500 tons to about 500 tons in the 1970s and less after (for pike) and from up to 300 tons in the 1960s to 100 tons and less afterwards (for pike-perch; see Fig. 22). Catfish (*Silurus glanis*), a nest guarder, was effected similarly in the delta.

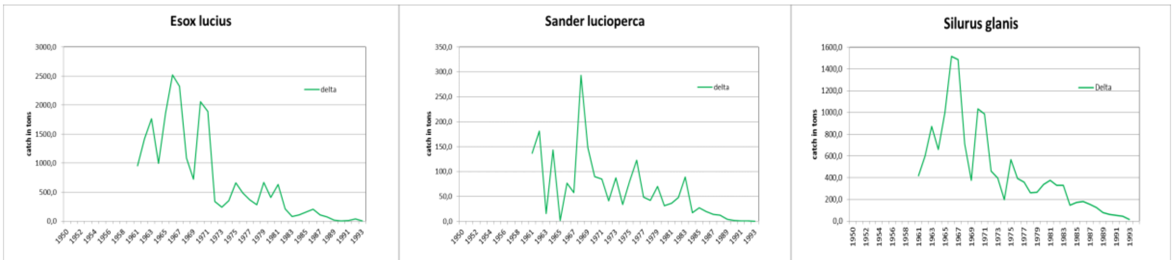

Fig. 24: Catches of pike (left), pike-perch (middle) and catfish (right) in the Lower Danube and Danube delta from 1960 – 1993 (data from Staras, DDNI)

A similar link between hydrological conditions and fish catch has been reported for the Tisza at Szeged already in the 19th century (1834 to 1900). Also here fish ecological conditions were fundamentally altered due to channelization of the river between 1846 and the 1880s aiming among others to colonize the extensive floodplains for grain production as new railway lines offered the opportunity to export them into other parts of the Austro-Hungarian monarchy. As a consequence, 1.6 Mio ha floodplains were lost and only 0.2 Mio ha remained. Fish catch declined drastically although unfortunately no statistics have been published but only a verbal assessment of the situation (Repassy, 1906).

(Intended) introduction of non-native fish

Non-native fish species had been introduced to the Danube since more than 100 years for commercial fishery purposes (eel) or recreational fishery (rainbow trout or brown bullhead), for water management (grass carp, silver carp) or they occur due to invasive behavior (Neogobiidae, see below). Altogether, 14 species were purposefully introduced along the entire Danube during the 20th century (Schiemer et al., 2003). According to Schiemer et al. (2003), two of them have to be considered as naturalized: false harlequin (*Pseudorasbora parva*) and pumpkinseed (*Lepomis gibbosus*). If Prussian carp (*Carassius gibelio*) is perceived as non-native a third species is acclimatized. However, the status of this species in the Danube catchment seems still unclear (see also Kottelat & Feyhof, 2007). It appeared in the Lower Danube in the first quarter of the 20th century but was rare until 1970. Soon after, it invaded the middle and the upper sections of the river. In the Romanian Danube delta the Prussian carp already contributed between 40 and 60 % of the yearly catch from 1970 – 2011. The grass carp (*Ctenopharyngodon idella*) was introduced in fish farms in 1962 to increase productivity and to control aquatic vegetation in ponds. It has reproductive populations in the lower Danube, as is also the case for silver carp (*Hypothalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*) (Schiemer et al. 2003).

Recent occurrence of invasive fish species

Invasive fish of the Danube relates in particular to the human induced, unintended dispersal of species which are native in the Lower Danube and spread into the Middle and Upper Danube and in recent years also to tributaries such as the Austrian Morava and Thaya (Lusk et al., 2010). Dispersal happened mainly with the release of ballast water from ships as the first appearances of these species were observed in and close to the large freight harbors (Wiesner, 2005). For fish of the (former) Neogobiidae family, no records upstream of the Iron Gate were made before 1970. In 1994 they were observed for the first time in the upper Danube (Austria; Wiesner, 2005). At present, *Neogobius melanostomus* (round goby) and *Ponticola kessleri* (former *N. kessleri*) became dominating in the rip-rap all along the Danube between Kelheim up to the Iron Gate. In the 2nd Joint Danube Survey (JDS), round goby was the third most common species after bleak (*Alburnus alburnus*) and Prussian carp and *P. kessleri* was the fifth most common after roach (*Rutilus rutilus*). In JDS 3 apart from bleak, round goby clearly dominated the fish community with a relative proportion of 46 % and 26 %, respectively, whereas the round goby was in particular frequent in the Danube upstream the Iron Gate where it is non-native (Bammer et al., 2015).

Fishery catch statistics and patterns of fish assemblage and populations decline

It is often difficult to make direct use of fishery catch data as long-time series are missing and/or fishing effort is insufficiently reported. However, data from the Danube delta investigated by fish biologists from the DDNI (e.g. Navodaru et al., 2001) and data analysed by Serbian fish biologists (esp. Jaric et al., 2016) demonstrate the interest of catch data to reveal patterns of human pressure on freshwater fish assemblages as this has been proven already for marine fish and fishery (e.g. Pauly and Palomares, 2005; Essington et al., 2006). In the Danube Delta, the catch of catfish, pike and pike-perch declined in the beginning of the 1970s. After, yields especially of Prussian carp and common bream (*Abramis brama*) increased putting more intense fishing pressure on these species (Fig. 25). Although a decline of individual species in commercial fishery has to be interpreted with caution as cultural aspects can be involved, too, this example seems to reflect a real species decline rather than a change of preferences for other species. For the Serbian Danube commercial catch are available since the late 1960 reporting among others yields for catfish, pike-perch, carp (*Cyprinus carpio*), Prussian carp and common bream. As Jaric et al. (2016) point out fish catch statistics were particularly affected by misreporting in the period of 1990 -2005 and thus omitted in their analysis. In the two periods finally kept (1969-1989; 2006-2010) total catch in tons did not decline as much as in the Danube Delta and in fact even increased in recent years. But more detailed analyses of e.g. average fish lengths and weights as well as mean trophic level of caught fish showed that fishery has unsustainable effects as within the studied period fish tended to become smaller, to reproduce younger and to have a shorter lifespan.

Fig. 25: Increase of catches of Prussian carp and common bream after the decrease of pike and pike-perch harvest in the Lower Danube and Danube delta

Synthesis

The ecological condition of large rivers depend on drivers and pressure and resulting stressors that can occur at multiple spatial scales (Frissell et al., 1986; Ward et al., 2002; Wiens, 2002). However, the ecological condition of a large river is not only dependent on the local condition of the river system but also on stressors operating at larger spatial scales as the catchments of large rivers cover large areas (Allan et al., 1997; Roth et al., 1996). Accordingly, the stressor may evolve over longer temporal scales. Accordingly, investigating the changes which occurred over long periods may give valuable insights and deepen the understanding of assemblage shifts which in turn represent the quintessential basis for bio-assessment (Birk et al., 2012).

Large rivers have been altered since centuries. Hering et al. (2015) summarise the multiple interaction between various stressors of aquatic ecosystems worldwide. The rates of habitat modification in large rivers have been 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 island biogeographic theory – is predicted to lead directly and indirectly to accelerated species extinctions at both the local and the global scale, thus reducing the world's biodiversity at all levels (McArthur & Wilson, 1967; Lawton & May, 1995).

Potamal communities at the edge of their ecological capability might collapse when temperature increase due to climate change adds to the deadly anthropogenic cocktail (Travis, 2003). But with few exceptions there is no evidence of an actual decrease in species richness of rather flexible riverine and wetland assemblages in lowlands of Central Europe, simply because most of these communities have been already dramatically shaped by various anthropogenic pressures in the decades before; those surviving organisms are tolerant cosmopolitans which cover a large area of ecoregions.

There are few signals of a re-colonisation regarding some riverine species which indicate improvements in the overall ecological integrity, mainly water quality. Awareness of the vulnerability and sensitivity of the large river ecosystems has risen and various restoration plans are put in praxis like along the Danube. River systems incorporate processes within the entire catchment and local efforts - despite their undoubted merits - can only marginally soften large scale impairments such as disruption of migration pathways or continuous channelization.

Biological reference communities are lost for most large rivers since long times and cannot be described empirically (e.g. Ehlert et al., 2002). Large rivers in Europe have lost a high share of their indigenous fauna, especially sensitive insects like Ephemeroptera, Plecoptera and Trichoptera (EPT-taxa), which is underlined for Plecoptera by the presented results. The findings of this study improve the knowledge on the historical change of riverine macroinvertebrates and give important evidence on the faunal shifts which occurred in large European rivers. In contrast to fish, which have been of economic interest and at least fisheries statistics give hints on historical assemblages, there are few studies dealing with historical occurrences of macroinvertebrate species in rivers.

We found a considerable shrink in the area of selected indicator species, namely of the aquatic insect order Plecoptera, especially for the co-occurrence of the selected species; the main refugia are few aquatic systems in Central France (Loire, Allier), Austria/Hungary (Raba, Lafnitz) and Hungary/Romania (Tisza) as well as in remote areas of Eastern Europe (Lithuania, Belarus), where a combination of species still can be found after 1990. Theses river systems are still inhabited by a high and typical fauna and seem to be least disturbed systems. Losses are identified in many rivers, especially in Scandinavia and Spain as well as other southern European regions.

In fact, many typical and nowadays extinct or endangered species of large rivers showed mass emergences and short but synchronic flight periods (e.g. *X. apicalis*, *I. 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.

Large river systems with reduced occurrence of these species are multiple stressed by channelization, damming, navigation and neozoa. The relationships between these stressors and the major ecosystem responses are synthesised in Table 4. The combination of these stressors may lead in most cases to additive or synergistic effects. However, this interaction is not quantifiable from the available historical data for several reasons.

Table 4: Summary of relationships between pressures, impacts and their biotic and abiotic responses

Pressure	Impact	Abiotic response	Biotic response
Damming	Longitudinal Connectivity	Discontinuity	Migration
Damming	Hydrological/ sedimentological regime	Disturbance regime change / homogenisation	?
Damming	Sediment retention	River bed incision	
Damming	Flow reduction	Sediment retention / Siltation	Loss rheobiont species
Channelization	Lateral connectivity	Loss of wetlands	Species loss
Channelization	Increase of hydraulic stress	Loss of instream lentic habitats Loss of retention	Loss of stagnophiluous species – less shredders
Channelization	Rip rap	Homogenisation – loss of small-sized substrate Change land-water surface interface	Loss of fine sediment habitat
Navigation	Vessel-induced waves	Pulse release – lateral hydraulic stress	Physical disturbance of surface dwelling taxa – merolimnic species
Navigation	Morphological degradation navigation channel	Gravel extraction	Loss of habitat – extreme conditions
Navigation	Neozoa	Habitat engineering	Loss of habitat – less grazers Competition

In most cases the historical biological data is simply too scattered in time and space to gain a homogenous information and to compare different rivers or river sections over time. The initial intent behind the work of this study has been to describe the development of stressors as well as faunal changes over time for several time slices within the 20th century. However, the collection of historical information is constrained by a two-sided challenge: detailed but small-scaled information vs. coarse but large-scaled information. To collate an appropriate database would take tremendous efforts, which are absolutely not feasible within this deliverable.

Looking in more detail on the species records, inconsistencies are obvious: The first period in the analyses till 1990 covers a much longer time frame (more than 100 years) compared to the period after 1990 (25 years). In contrast, the intensity of ecological sampling extremely increased in the 21st century induced by the WFD and its monitoring obligations. Furthermore, several ecologists even started campaigns to sample some of these species again without success. This information is written down in reports and articles but it is hardly possible to integrate it in a spatial explicit manner as in most cases this absence is described for large areas like whole countries or river systems. Large datasets with repeated samplings as compiled by the Joint Danube Surveys are extremely useful and necessary in monitoring of the ecosystem functioning and potential changes in ecosystem services.

Moreover, the stressor timelines underlined the parallel evolvement of the major stressors damming and navigation accompanied by channelization and neozoa in the second half of the 20th century, which impedes the untangling of detailed cause-effect relationships or the interaction types of stressors, respectively. Moreover, the quantifiable stressors do not represent the direct impact on the ecosystem process. They represent proxies, which can have similar effects on the ecosystem processes; in most cases an effect on the disturbance regime and in turn on the naturally dynamic habitat processes. Looking on river systems, which still feature some of the Plecoptereaen species of interest, it gets obvious that those systems show neither damming nor navigation impacts. Accordingly, dynamic processes in hydrology and sedimentology seem key to support large river typical Plecoptera (see Fig. 26).

Fig. 26: The Loire (left and middle) and Allier river (right), source: A. Ruffino

In relation to riverine ecosystem dynamics and especially for large rivers with adjacent floodplains habitat age gives the possibility to highlight the degree of dynamics in the system. In a pristine, least disturbed river-floodplain system, habitats along a hydrological gradient – from the lotic main channel to lentic floodplain lakes - can be found (Amoros et al., 1987). Channelization, damming and navigation reduce either the area where the dynamic processes can take place such as reducing lateral connectivity or they directly suppress them, e.g. by affecting the hydrological regime. The changes of such habitat types are depicted in Fig. 23 for the Danube at Vienna (a channelized, dammed and navigated river section) from the beginning of the 19th century up to 2011 (Graf et al., 2013). If the hydrological dynamics in the floodplain are completely eliminated the remaining lentic habitats are exposed to siltation and will diminish over time.

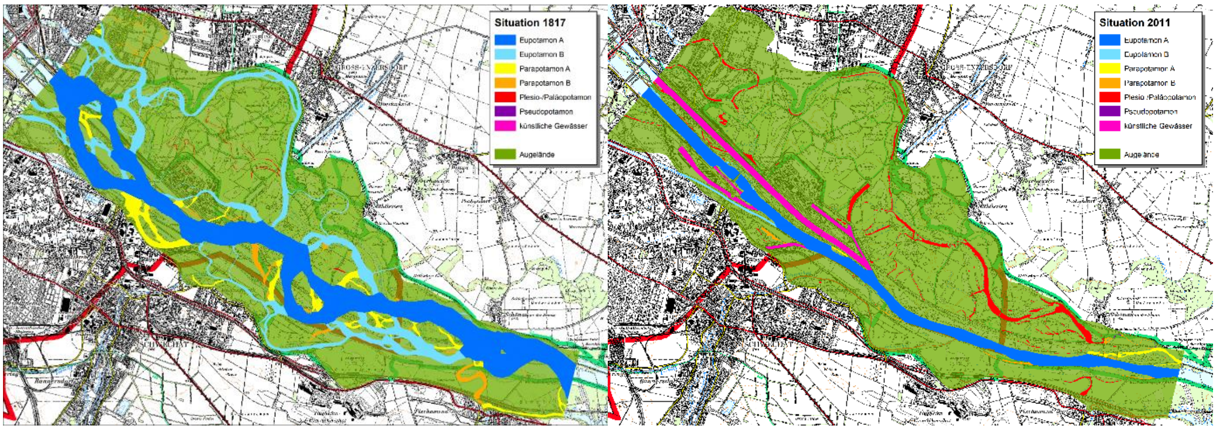

Fig. 27: Habitat types along the Danube River at Vienna in 1817 (left) and in 2011 (right); the classification of habitats distinguishes hydrological gradients according to Amoros et al. (1987) from Graf et al. (2013)

In the context of the so-called 'McDonaldization' of the biosphere (Lövei, 1997) 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. The role of navigation in the McDonaldization-process is hardly investigated comprehensively in all its aspects, therefore poorly understood and still remains underestimated. 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 & Reiss (1983), Zwick (1984; 1992) and Fochetti & Tierno de Figueroa (2006). Caspers reported already in 1980 that the benthic macroinvertebrates coenosis in the Rhine River, which can be seen as the 'pioneer' system of human-induced alterations, can be characterised as uniform and species-poor assemblage at Bonn. As pointed out earlier, the benthic assemblages are nowadays clearly dominated by non-indigenous, invasive or cosmopolitan elements which probably have strong negative effects and misbalance the ecological functioning of the whole system (Fig. 24).

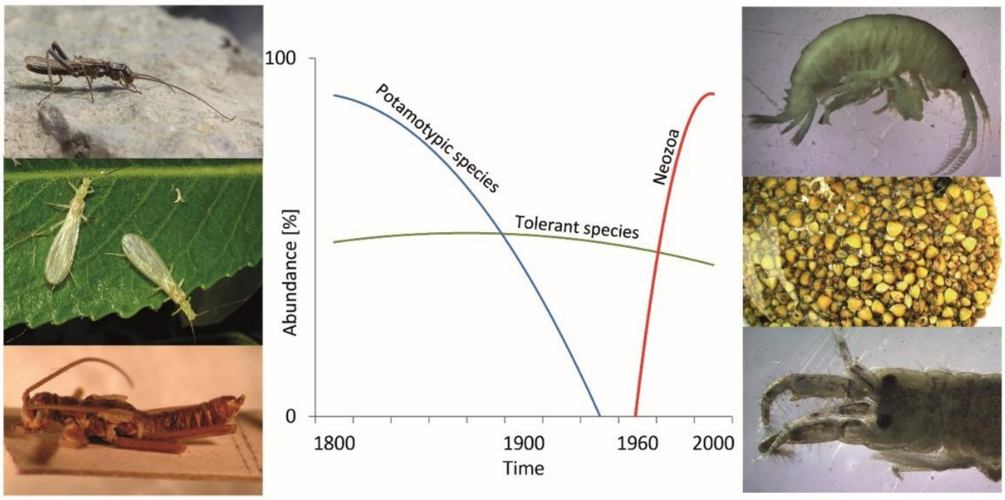

Fig. 28: Concept on the development of the large river fauna in Central Europe from 1800 to 2000; photos: left, indigenous species of the Danube: B. trifasciata, X. apicalis, T. araneoides (pinned specimen, Museum Budapest, Photo: D. Murányi); right, invasive species: Corbicula fluminea, Dikerogammarus villosus, Chelicocoropium curvispinum (Graf & Pletterbauer, unpublished)

The seriousness of the neozoa problem may be illustrated exemplarily by the recently documented structure of benthic assemblages of the Danube River during the Joint Danube Survey 2 (ICPDR 2008) expeditions which sampled along the whole river: Among the ten most frequent macroinvertebrate species sampled, nine are assigned as neozoa (Graf et al., 2008), above all occurring in very high densities and frequency (Fig. 13). In general these findings were confirmed by the JDS3 expedition (Borza et al., 2015). Detailed analyses of JDS data reveal clear habitat preferences for hard substrates for invasive species and soft bottom preferences for non-invasives, respectively (Borza et al., subm.). Land-water interface of large rivers is mostly interrupted by rip-rap structures. In combination with vessel-induced waves, which are especially harmful for merolimnic taxa, they seem to be support the success of invasiveness of Ponto-Caspian species.

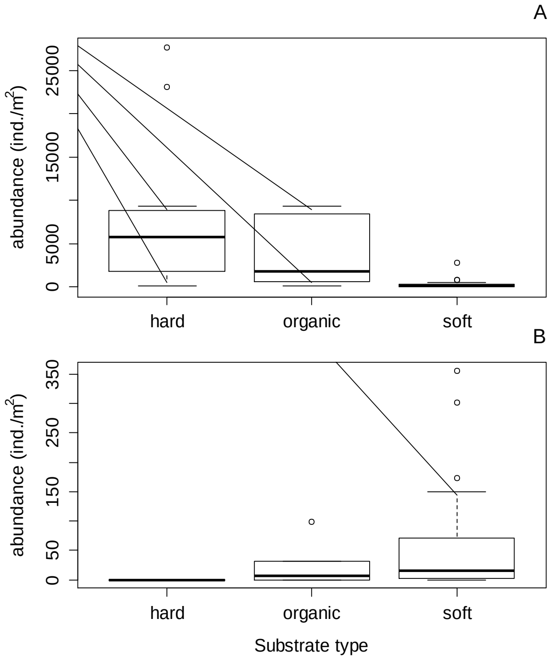

Fig. 29: Cumulative abundance (boxplots, in individual/m2) of invasive (A) and non-invasive (B) Ponto-Caspian peracarid species on different substrate types downstream of rkm 700 in the Danube during Joint Danube Survey 3 (Borza et al., subm.)

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Appendix

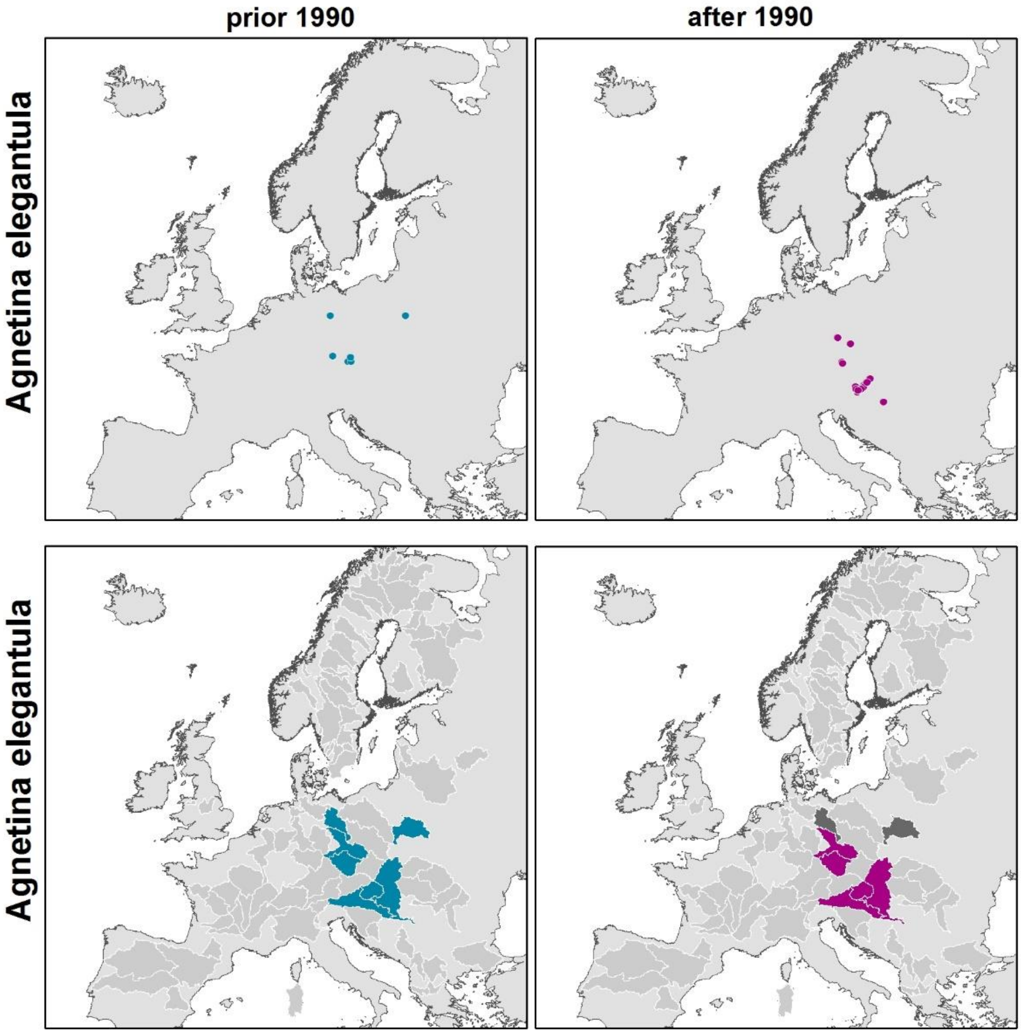

Fig. 30: Location of records (upper panel) and according large river catchments (lower panel) of Agnetina elegantula before 1990 (left) and after 1990 (right)

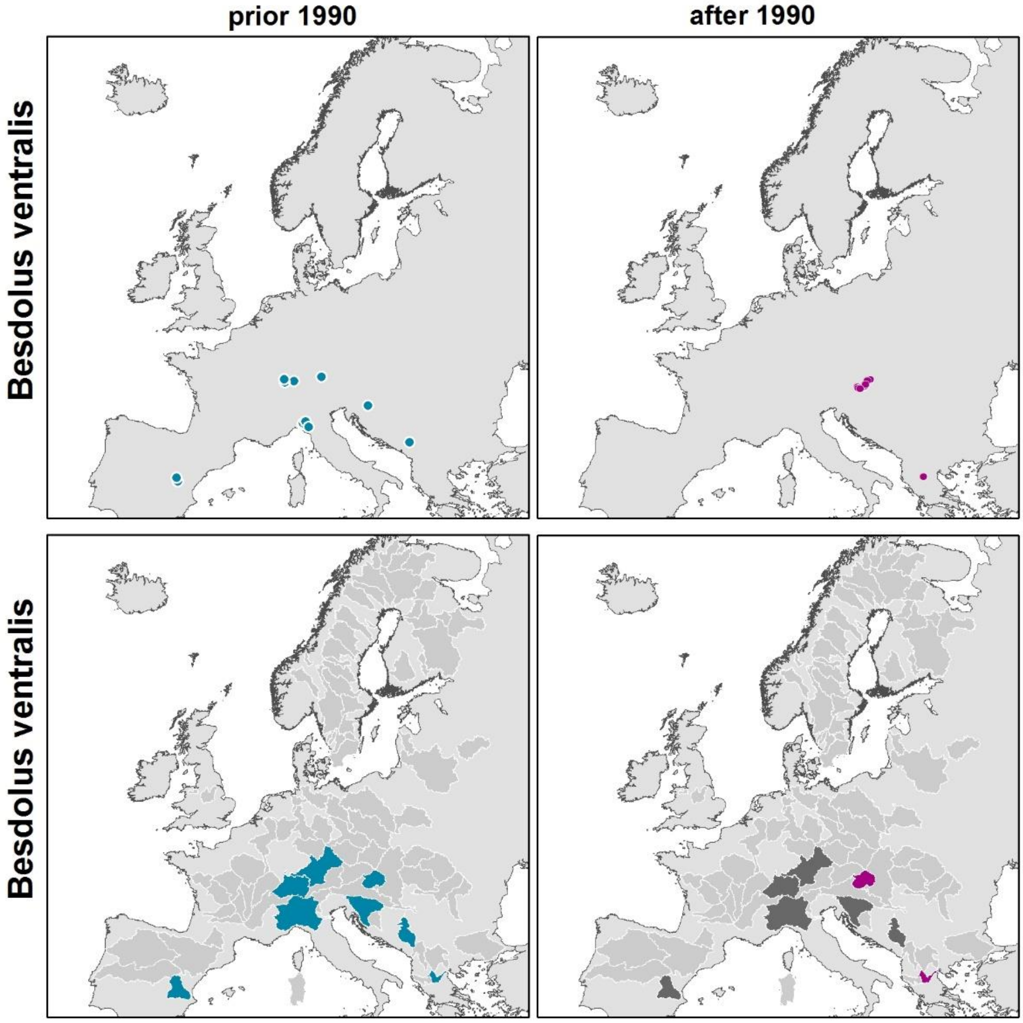

Fig. 31: Location of records (upper panel) and according large river catchments (lower panel) of Besdolus ventralis before 1990 (left) and after 1990 (right)

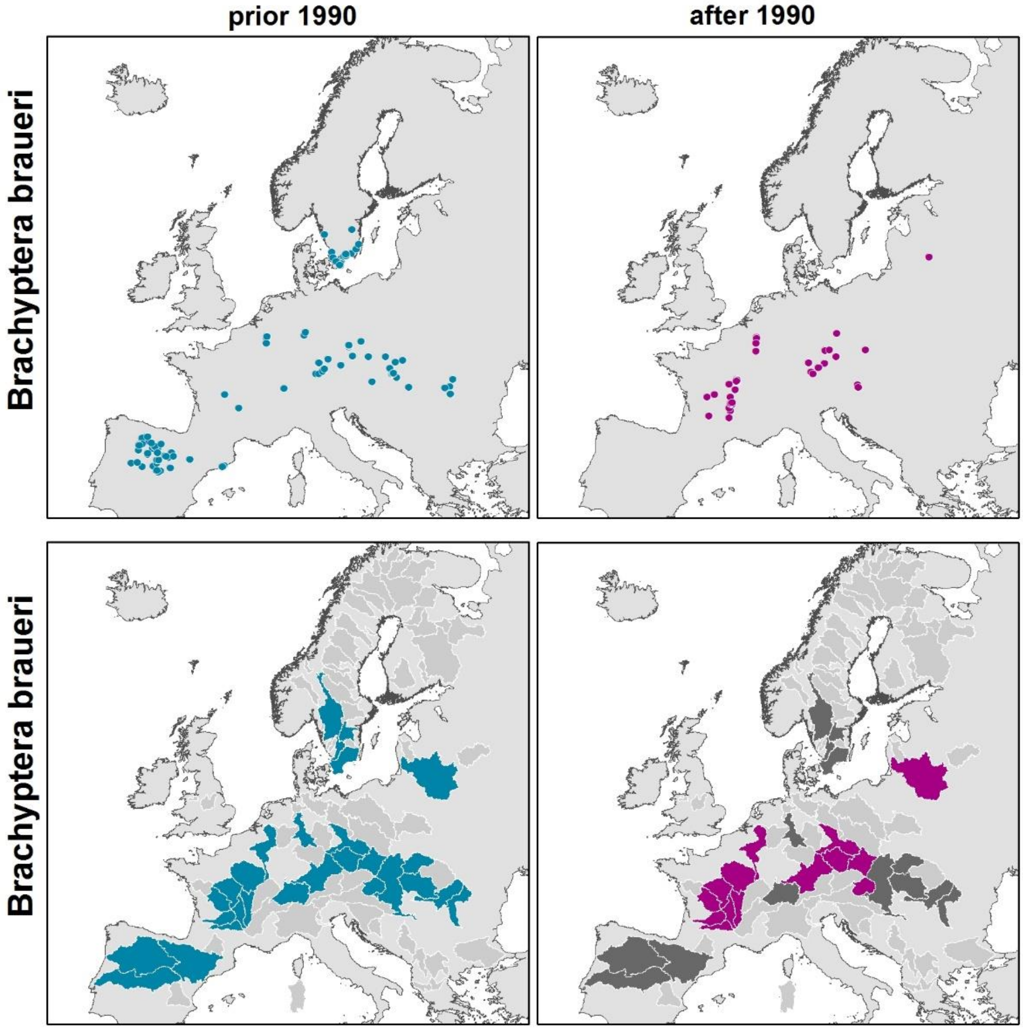

Fig. 32: Location of records (upper panel) and according large river catchments (lower panel) of Brachyptera braueri before 1990 (left) and after 1990 (right)

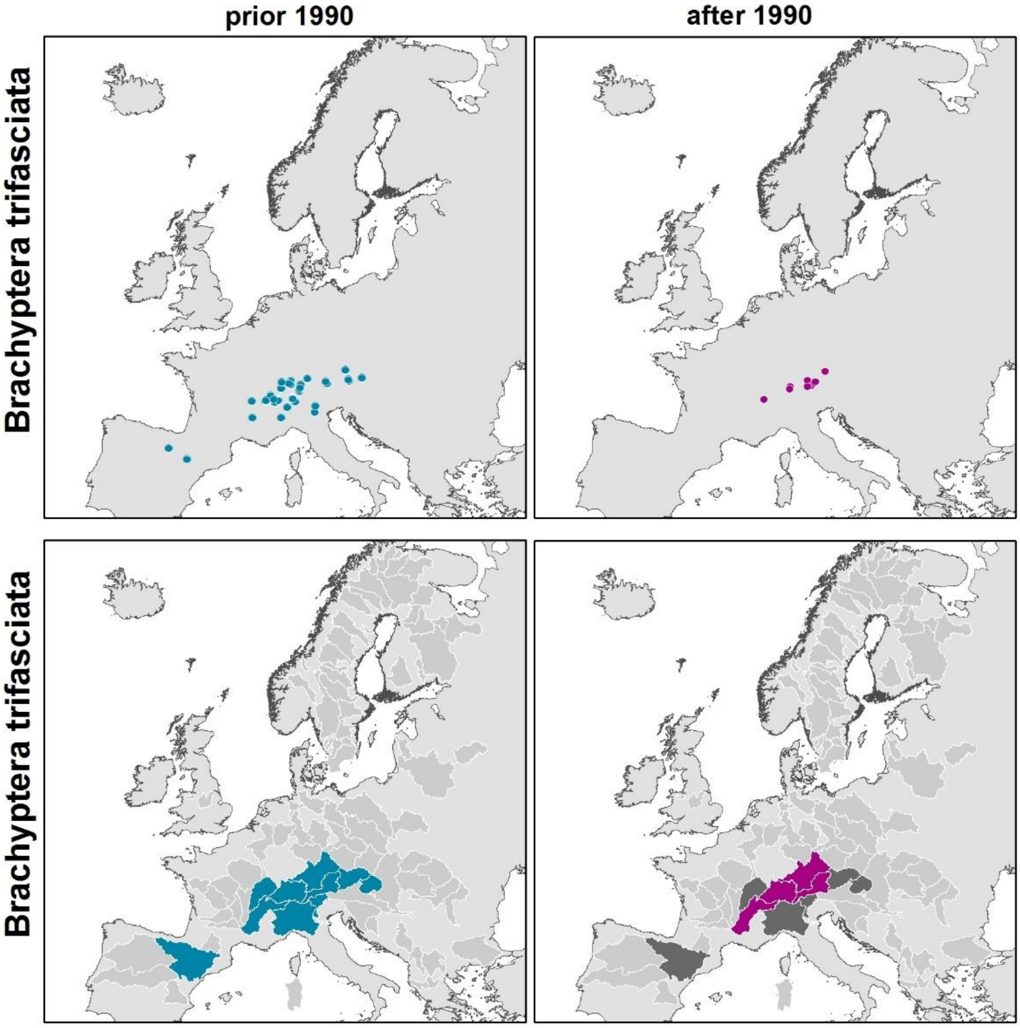

Fig. 33: Location of records (upper panel) and according large river catchments (lower panel) of Brachyptera trifasciata before 1990 (left) and after 1990 (right)

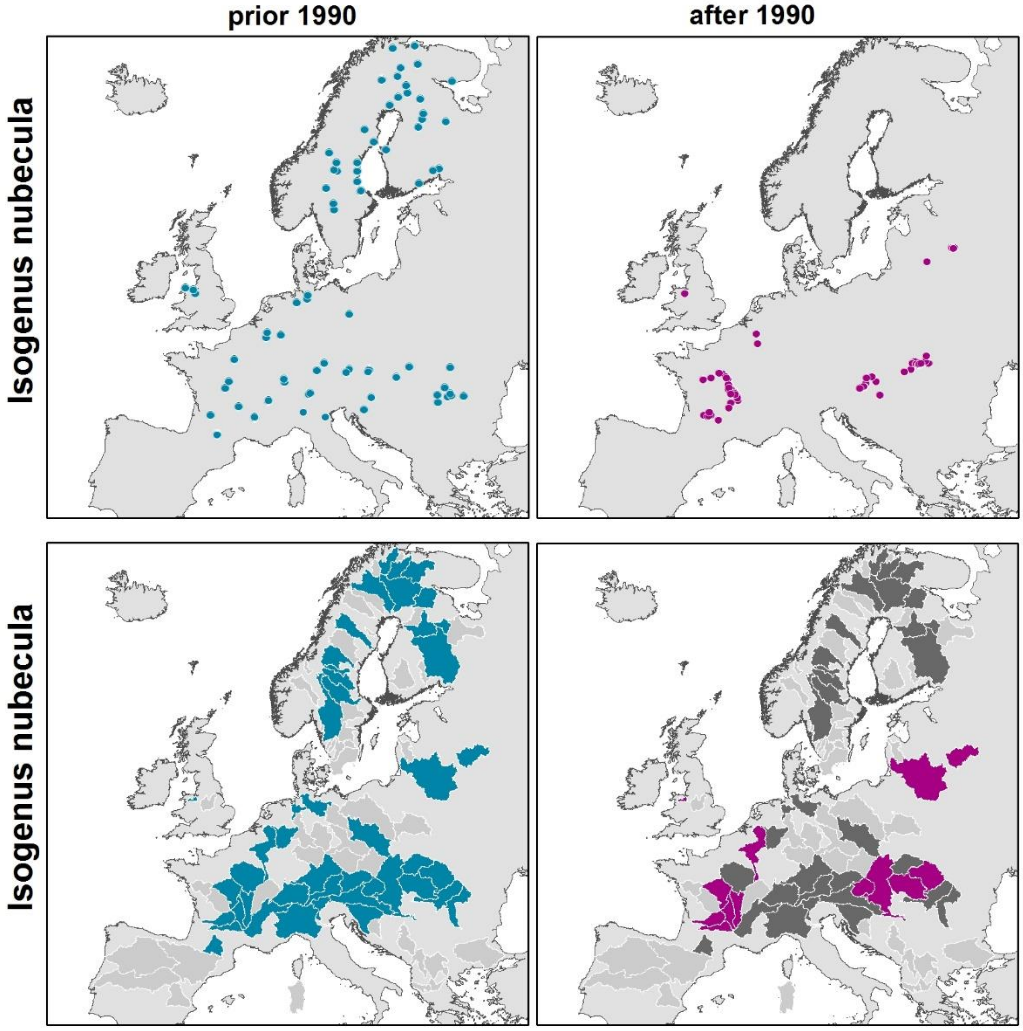

Fig. 34: Location of records (upper panel) and according large river catchments (lower panel) of Isogenus nubecula before 1990 (left) and after 1990 (right)

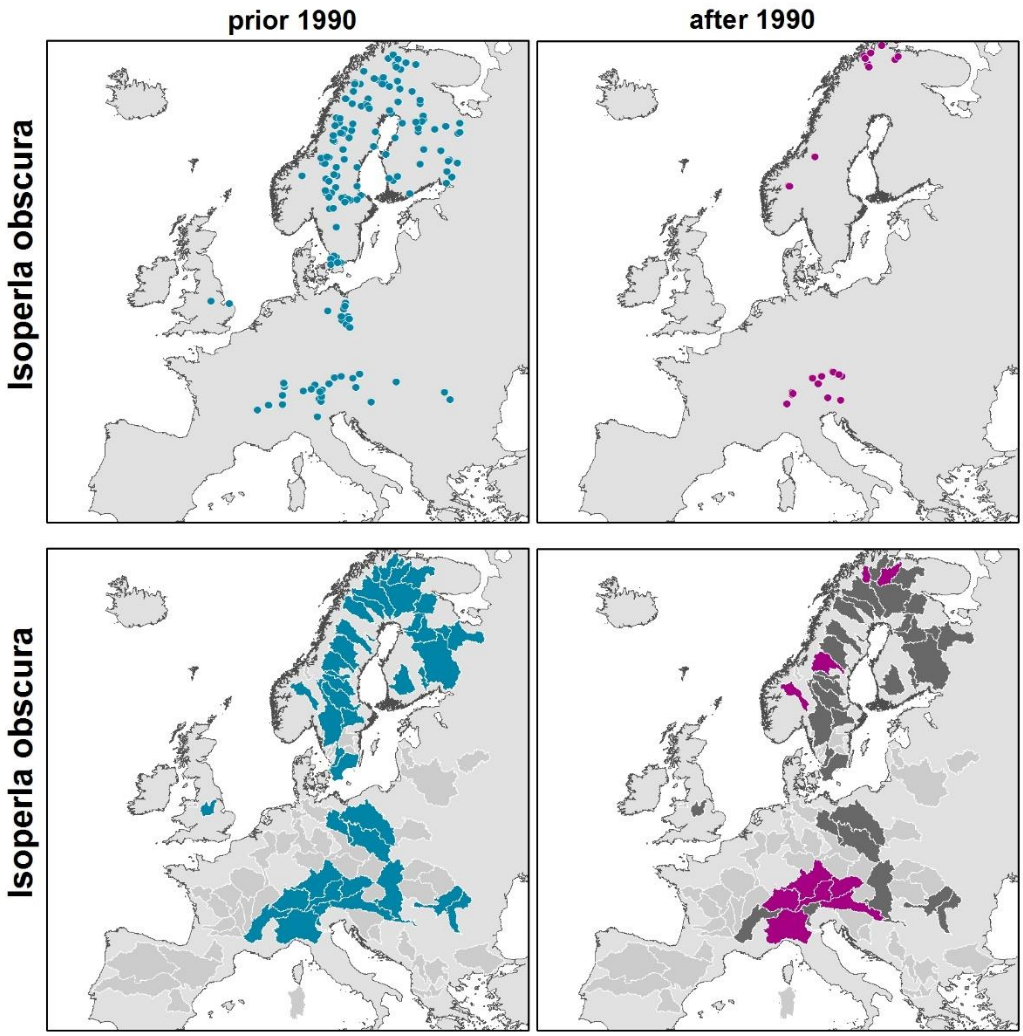

Fig. 35: Location of records (upper panel) and according large river catchments (lower panel) of Isoperla obscura before 1990 (left) and after 1990 (right)

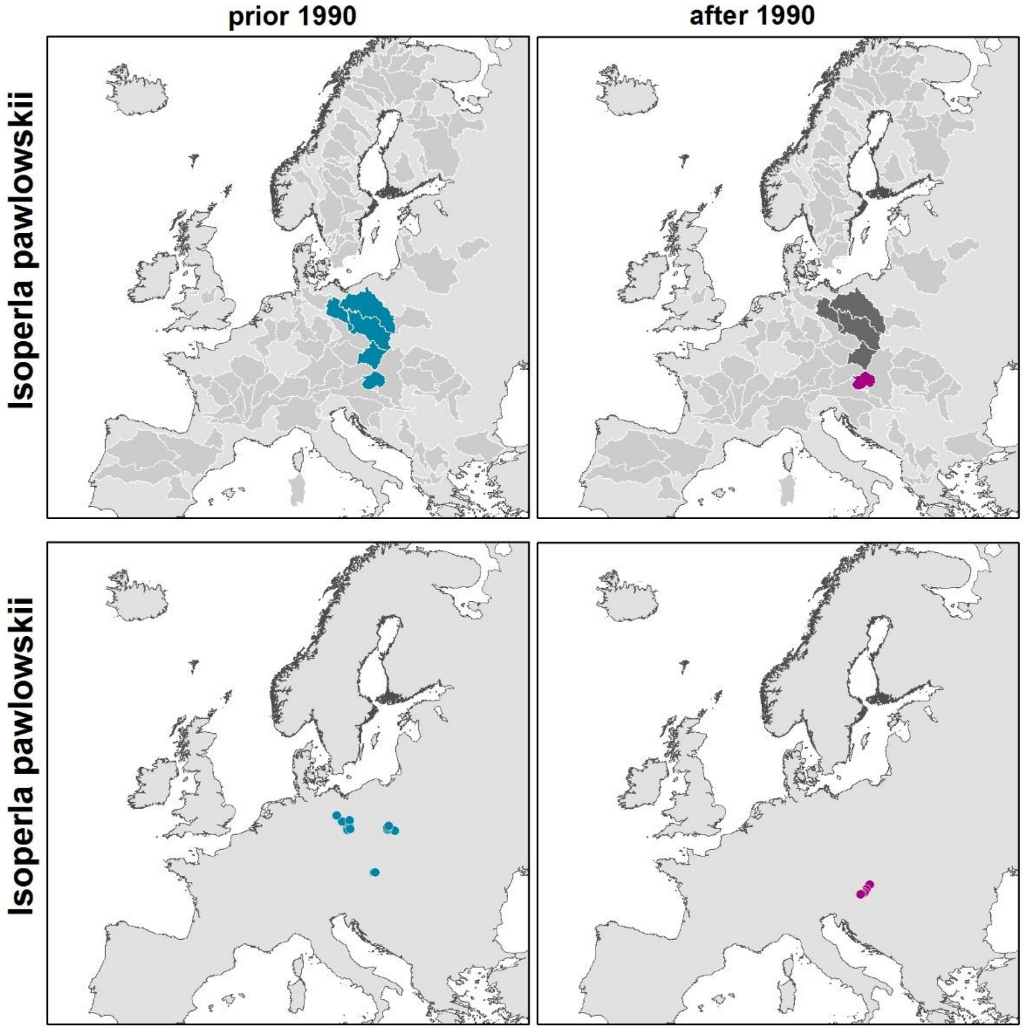

Fig. 36: Location of records (upper panel) and according large river catchments (lower panel) of Isoperla pawlowskii before 1990 (left) and after 1990 (right)

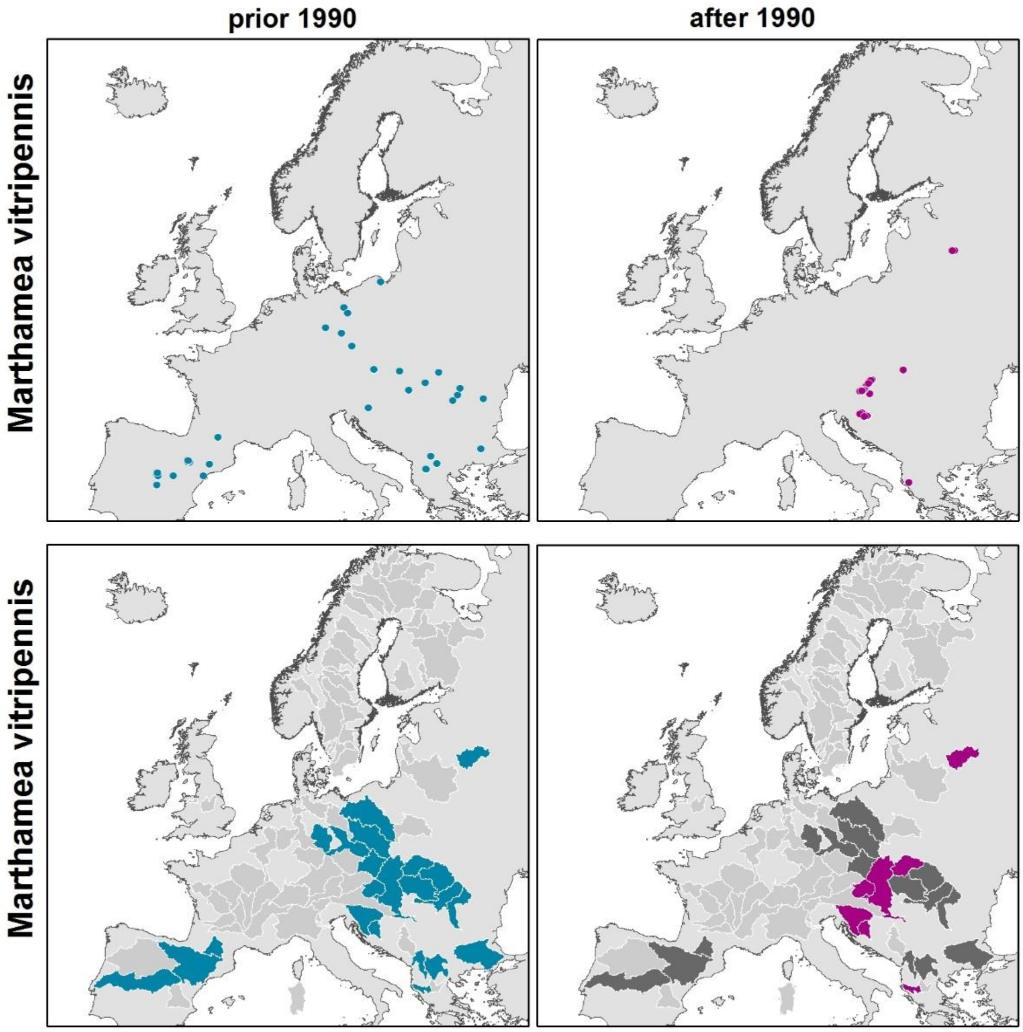

Fig. 37: Location of records (upper panel) and according large river catchments (lower panel) of Marthamea vitripennis before 1990 (left) and after 1990 (right)

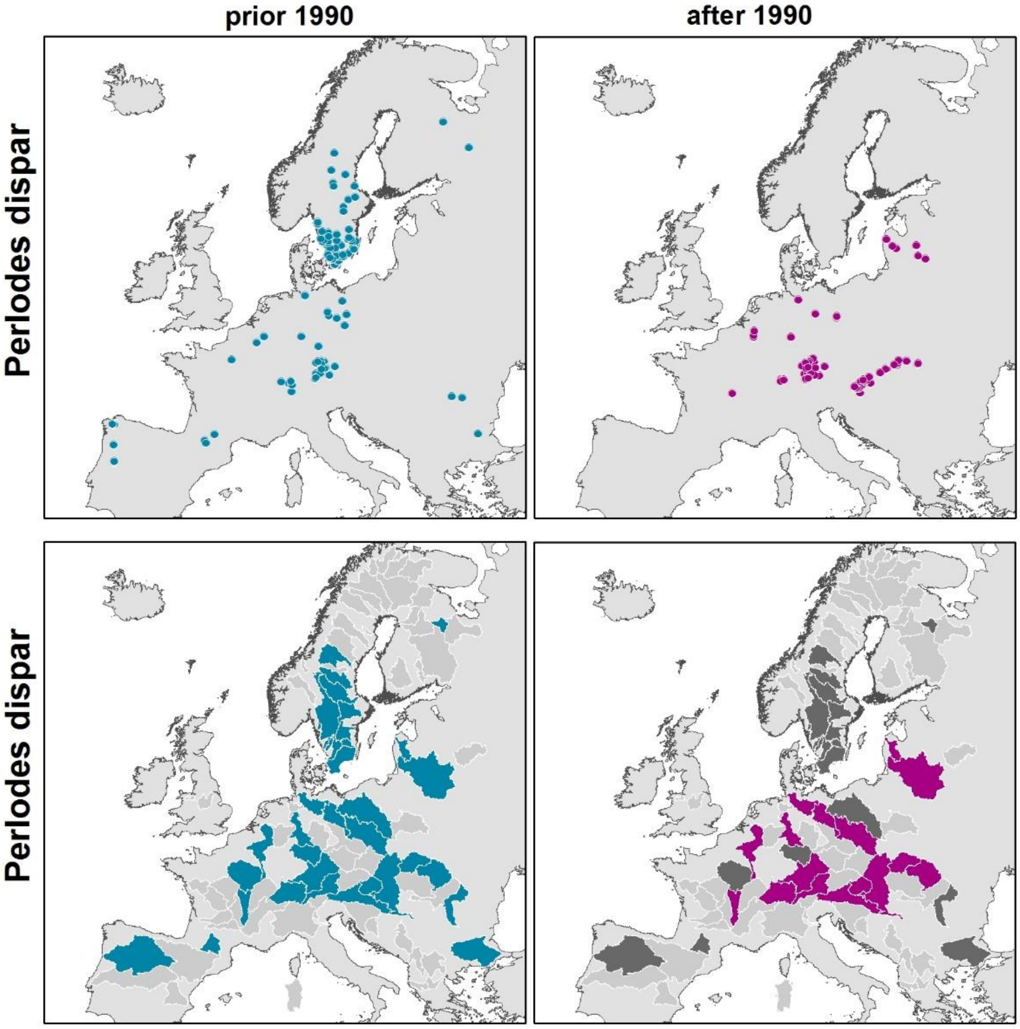

Fig. 38: Location of records (upper panel) and according large river catchments (lower panel) of Perlodes dispar before 1990 (left) and after 1990 (right)

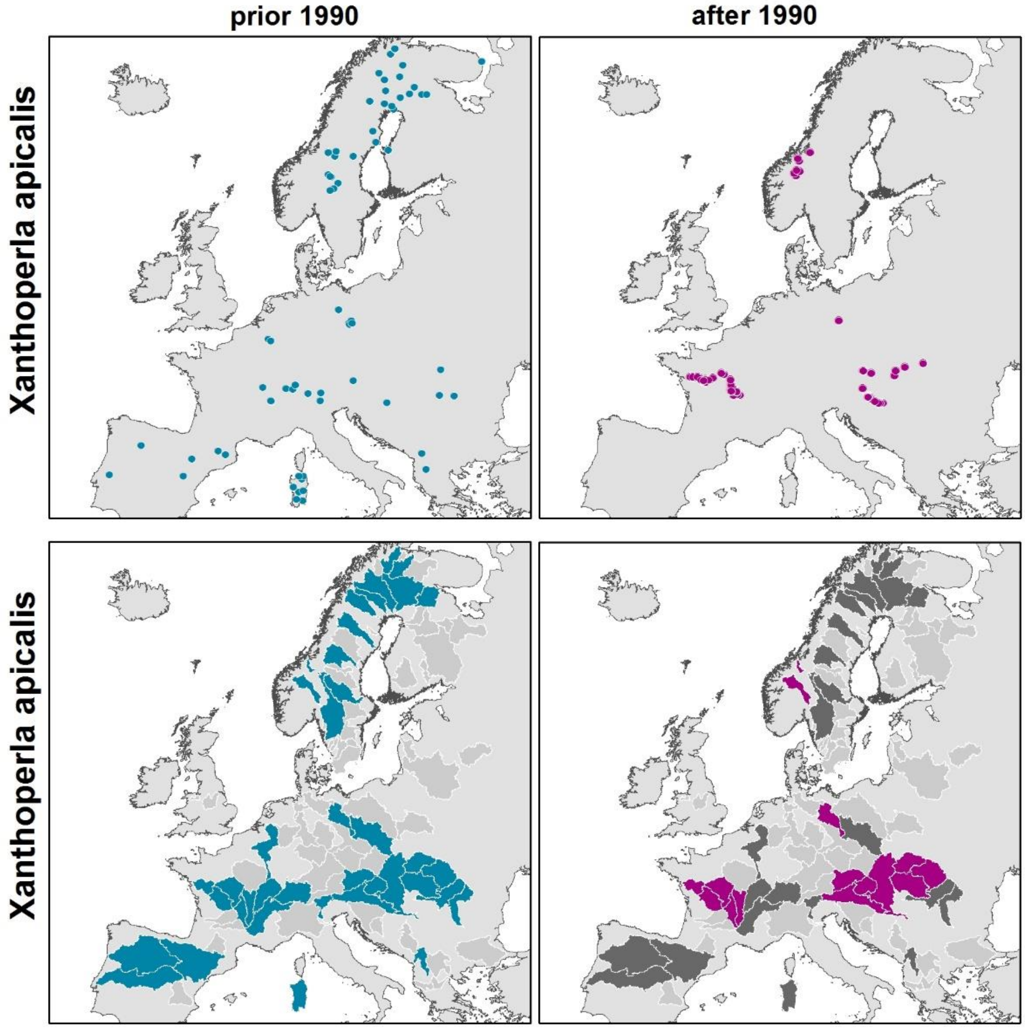

Fig. 39: Location of records (upper panel) and according large river catchments (lower panel) of Xanthoperla apicalis before 1990 (left) and after 1990 (right)