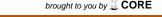
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Impact of reservoirs and channelization on lowland river macroinvertebrates: A case study from Central Europe

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Abstract

In order to assess and compare the ecological impacts of channelization and shallow lowland reservoirs, macroinvertebrate communities of a lowland metapotamal river below reservoirs with epilimnial release were studied. The study was carried out in the Dyje River (Czech Republic) at five sites located from 1.5 to 22.5 km downstream of the reservoir outfall. The five sites differed in the degree of channel modification from natural muddy banks to riprap regulation. Seven samples were collected during the years 1998 and 1999 at each site using a semiquantitative method. The data were processed using multivariate analyses and methods for assessing the ecological and functional structure of communities. Altogether, 261 species of benthic macroinvertebrates were recorded including several rare and threatened taxa. Based on the results of principal component analysis (PCA), most of the variability within the species data (the first PCA axis) was explained by the degree of channel modification, from natural muddy banks with aquatic vegetation to a man-made riprap. The second axis was strongly correlated with current velocity. The sites differed in species richness, total abundances, proportion of individual functional feeding groups, pattern of the distribution of the current preference groups, and values of several biotic indexes, all of which also corresponded to the degree of channel modification. Thus, the morphological man-made modifications of the river channel were found to be the main factor affecting lowland river macroinvertebrates and their biodiversity. Our results suggest that the biggest threat to benthic macroinvertebrate diversity of lowland rivers comes from channelization. The impact of reservoirs can be completely overwhelmed by the impact of channelization, especially when muddy banks with aquatic vegetation present a substantial part of habitat diversity and significantly contribute to the total species pool. © 2008 Elsevier GmbH. All rights reserved.

Keywords: Lowland river; Macroinvertebrates; Channelization; Lowland reservoirs; Human impact; Biodiversity loss

Introduction

The impact of reservoirs and river channelization on the ecology of river ecosystems and biodiversity has been well-studied. Several concepts were established to

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explain patterns of ecosystem alteration caused by manmade changes. Ward and Stanford (1983, 1995), for example, proposed the Serial River Discontinuity Concept to describe the influence of reservoirs in connection with the River Continuum Concept (Vannote et al. 1980). Other authors used the term "ecosystem fragmentation" for river systems influenced by regulations (e.g. Zwick 1992). More information concerning the influence of damming and other types of regulation has been also compiled in monographs (Ward and Stanford 1979; Lillehammer and Saltveit 1984; Craig and Kemper 1987; Prach 1995), in special studies (Petts 1984; Ligon et al. 1995), and in reviews by Vinson (2001), Saito et al. (2001), Bunn and Arthington (2002), Lowe (2002), Friedl and Wüest (2002), and Gergel et al. (2002). However, the knowledge is still very heterogeneous in its content and extent, and general interpretations remain rather inconsistent. The impact on river's biota depends on the reservoir size, type, and age. flow manipulations, presence or absence of an equalising reservoir, and on technical modifications of the channel downstream of the reservoir. Thus, there are many factors involved, which make general prediction of river community alterations difficult. Therefore, it is necessary to judge the reservoir impact from case to case.

Channelization involves modification of river channels for the purposes of flood control, land drainage, navigation, and reduction or prevention of erosion. Engineering techniques including resectioning, realignment, channel diversion, embankments, bank protection, floodwalls, etc. are commonly used and they have different environmental impacts (see Brookes 1988). In comparison with reservoir impact assessment, only a few papers have dealt with the identification and quantification of the environmental factors changed by the channelization. There is also a lack of information concerning the biological response of different taxonomic groups of organisms to a set of river channel modifications. Brookes (1988) published the most comprehensive review on this topic. Later studies have dealt with the effect of riparian grazing and channelization (Quinn et al. 1992), the effect of channelization in relation to flow fluctuation (Negishi et al. 2002), the effect of various technical impacts in alpine streams (Bloesch et al. 1998), the benthic community in a totally artificial concrete channel (Kubíček et al. 1995), and the comparison of benthos in braided and channelized parts of the river (Peeters and Tachet 1989). There has also been an effort to directly link observed changes in benthic invertebrates with modifications of hydrological regime (e.g. Armitage 1995; Gore 1996). Probably the most robust method, the LIFE scores, linking qualitative and semi-quantitative changes in riverine benthic macroinvertebrate communities to prevailing flow regime was proposed by Extence et al. (1999). In the last decade, much attention has been paid to the development of methods to assess morphological changes (e.g. Raven et al. 1998; Lorenz et al. 2004).

The regulation of the large rivers in the Czech Republic began more that 150 years ago, with a dramatic increase during the second half of the 20th century (Vlček 1984). Probably the most affected lowland region is the Dyje River basin due to intensive agriculture use, the construction of the largest lowland reservoirs, and river channel modification. In spite of

this, the region is one of the most unique areas in the Czech Republic, being the extension of the Pannonian Basin hosting many thermophilous and highly endangered species (Opravilová et al. 1999). This region has been designated as a Wetland of International Importance under the Ramsar Convention, as a Protected Landscape Area, and as a Biosphere Reserve due to its diverse flora and fauna, and the occurrence of many threatened habitats.

In the study area, investigations started before 1930 and more than 50 papers, theses, and other works have been carried out here. Sukop (1990) and Adámek and Sukop (1992) published the most important work, which dealt with the river below the reservoirs and also introduced the evaluation of changes in invertebrate communities. Comprehensive information on the aquatic invertebrate fauna of the target region provides the monograph edited by Opravilová et al. (1999). Horsák (2001) published a current species list of macroinvertebrates of the investigated river stretch, including a survey of previously published data.

The main purpose of this study is to compare the impact of reservoirs and channelization on lowland river macroinvertebrates. Our hypothesis is that channelization, which eliminates mainly shallow bank habitats with vegetation, has a stronger impact than the downstream effect of reservoirs.

Material and methods

Study area and sampling sites

The study area (Fig. 1) is located in S Moravia, Czech Republic (N: $48^{\circ}44'-49^{\circ}52'$; E: $16^{\circ}30'-16^{\circ}52'$) in the northern part of the Pannonian Subprovince a part of the Dyje-Morava Bioregion (Culek 1996). The entire bioregion has an average altitude of 155–185 m a.s.l. and lies in the warmest area of the Czech Republic (Quitt 1971); its climate is similar to that of the Danube Valley. The Dyje River floodplain receives rather low annual precipitation (490–520 mm). The total length of the river is 305.6 km; the mean annual discharge is 43.89 m³ s⁻¹ (at its mouth). The whole catchment area covers 13,418.7 km². The bedrock is mainly formed of sands and gravels. The natural dynamics of the floodplains were significantly affected in the 1970s and 1980s by stream regulation and the construction of the Nové Mlýny Water Reservoirs.

The reservoirs consist of three shallow impoundments with an epilimnial release. The first (upper one) with an area of 528 ha was filled in 1979, the second with an area of 1031 ha was filled in 1983, and the third has an area of 1668 ha and was filled in 1989. The reservoirs represent the biggest complex under river regulation and the

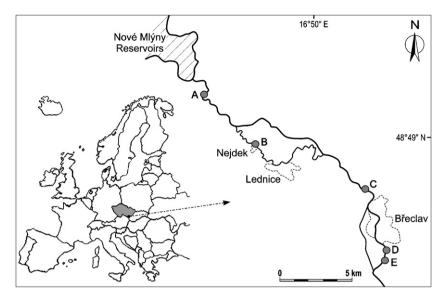


Fig. 1. Position of the study area with the sampling sites.

largest artificial modification of the environment in the lowlands of the Czech Republic. More than 3300 ha of floodplain forests, meadows, temporary and permanent pools, and about a stretch of 44 km of a natural river were destroyed. The main reasons for the construction of reservoirs were to implement government regulation aimed at flood prevention and the need for a source of water for intensive farming irrigation. At the same time, the river below the reservoirs was channelized by using a trapezoidal profile river channel design, with a riprap. The artificially affected downstream part of the river is 52 km long.

The average annual discharge was 25.66 m³ s⁻¹ in 1998 and $38.21 \,\mathrm{m}^3 \,\mathrm{s}^{-1}$ in 1999 (all data are from the Water Management Dispatching of Morava Basin). Although reservoirs usually have a permanent impact on the discharge pattern in rivers, no substantial difference between the inflow and the discharge was recorded during our research. There were no hydropeaking events, and the artificial changes in the discharge were limited to (1) maintaining the minimum ecological discharge (i.e. $8.00 \,\mathrm{m}^3 \,\mathrm{s}^{-1}$), and (2) releasing controlled floods on 4-5 May 1998 and on 3-25 April 1999. The main goal of this artificial flooding was the restoration of the hydrological regime in the former inundation area and the maintenance of unique biotopes of lowland forests, meadows, and plesio- and paleopotamic pool systems.

The research was carried out at five sites, marked from A to E, following their distance from the reservoirs (Fig. 1, Table 1). The site B was situated on a former channel, whereas the others were situated on the present main channel. The studied sites were chosen based on two different criteria. The first was the distance from the reservoirs and the second was the degree of artificial modification (see Table 1), i.e. strongly channelized sites

with a continuous riprap (sites D, E), sites with a partially destroyed (A) or totally destroyed (C) riprap and an originally unchannelized site (B). To separate the impact of reservoirs from that of channelization it was important that affected (A, D, E) and preserved (B, C) sites alternated along the distance from the reservoirs (cf. Fig. 1). Furthermore, at the site B there was a small, partially destroyed boulder chute. Both submerged (*Potamogeton* sp. and *Ceratophyllum* sp.) and emergent (predominantly *Phalaris arundinacea*) macrophytes occurred only at the more natural sites B and C.

Data collection and explanatory variables

Samples were collected four times during 1998 (spring, late spring, summer, and autumn) and three times during 1999 (spring, summer, and autumn) at the five sampling sites. Macroinvertebrates were obtained from riparian zone using a hand net of 0.2 m in diameter and a mesh size of 0.5 mm (EN 27 828 1994). Samples were taken semi-quantitatively (kick samples), 5 min of sampling were divided between different habitats proportionally to their representation in a sampling site. Large specimens were picked out from the samples in the field and then the samples were put into plastic bottles. Both the separated specimens and the bulk samples were fixed in 4% formaldehyde. Citations of all taxonomic literature used for identification of the species are available in Horsák (2001).

Several environmental variables were measured for each site/sample during fieldwork: water temperature, oxygen, pH, and conductivity (using portable instruments), mean water depth of a sampled stretch, and an approximate flow velocity (using the float method). Detailed description of studied sites, especially in terms

Table 1. Location and basic characteristics of sampling sites

Sampling site	Distance from reservoir (km)	Mean depth (cm)	Mean velocity (m/s)	Dominant substrate type	Type of impact	Character of banks
A: Below reservoirs (48°50′57.5″N, 16°44′04.6″E)	1.5	81	0.43	Mud/organic	Channelization	Muddy, without vegetation
B: Old flow-through arm (48°48′52.1″N, 16°46′33.7″E)	6.5	63	0.61	Mud/organic, boulder chute, gravel	Remains of boulder chute	Muddy, littoral vegetation, macrophytes
C: Upstream of Břeclav town (48°46′56.8″N, 16°52′47.1″E)	17.0	86	0.47	Mud/organic, sand	Historical channelization	Muddy, littoral vegetation, macrophytes
D: Downstream of Břeclav town (48°44′34.9″N, 16°53′32.1″E)	22.0	57	0.52	Gravel/organic	Channelization	Gravel with riprap
E: Downstream of Břeclav town (48°44′26.1″N, 16°53′30.9″E)	22.5	48	0.58	Boulder/organic	Channelization	Riprap

of presence and extent of riprap and macrophytes, muddy banks, character of substrate, was also done. Degree of modification was determined on a four-grade scale: 0 – without bank modification, 1 – remnants of former riprap, 2 – former riprap more or less preserved, 3 – completely preserved riprap. Water samples were taken for laboratory measurement of NO_3 , NH_4 , and PO_4 concentrations.

Statistical analyses

We used basic statistics to describe the differences in species richness, total abundances, and relative abundances of major taxonomic groups between the sites. To describe the functional differences in community composition, we assessed functional feeding groups and current preferences of the taxa based on the knowledge of individual species ecology (Moog 1995; Barbour et al. 1997; Helešic and Kubíček 1999; Šporka 2003). Further, we calculated two indices indicating the degree of artificial modification: Czech saprobic index for organic pollution assessment and LIFE scores for assessing flow-related stress on the macroinvertebrate communities (AOEM consortium 2002).

The species-by-sites matrix was classified by cluster analysis (Ward's method, Euclidean distance) to evaluate the dissimilarity of individual communities. The species abundance data were log-transformed as $Y = \log(n+1)$ in order to reduce the influence of predominant species. To describe ecological differences among the studied sites based on variability in species composition and measured variables, a principal component analysis (PCA) was undertaken. We calculated Spearman rank correlations (r_s) to examine possible correlations between explanatory variables and site

scores on the first four ordination axes for continuous and ordinal variables. The Mann–Whitney *U* test was used for the testing of differences between two groups of independent samples. Sequential Bonferroni corrections of the significance level were used for multiple comparisons of environmental variables (Holm 1979). The CANOCO 4.5 package (ter Braak and Šmilauer 2002) was used for PCA techniques, the PC-ORD package (McCune and Mefford 1999) for cluster analysis, and STATISTICA 7 (www.statsoft.com) for the other (uni-dimensional) analyses. The ASTERICS software was used for the calculation of the indexes (AQEM consortium 2002).

Results

Species richness and relative abundance

Altogether, 261 species of aquatic invertebrates were recorded at the study site (for details see Horsák 2001). The groups with the highest species richness were Diptera (57 species), Oligochaeta (37), Mollusca (31), Coleoptera (20), Heteroptera (17), Trichoptera (14), and Nematoda (13) (see Appendix).

The highest numbers of species were found at sites B and C, whereas site E had the lowest species richness (Fig. 2). The mean numbers of taxa collected at sites A and D were similar, but the variability between individual samples was different (Fig. 2). Site D displayed unusually large variability in the number of taxa between the samples, which covered nearly the whole variability of all the remaining samples.

The macroinvertebrate communities of the affected sites (A, D, E) consisted mainly of three taxonomic groups, i.e. Oligochaeta, Diptera (esp. Chironomidae)

and Heteroptera (esp. *Micronecta scholtzi*), which made up for 82–92% of the total macroinvertebrate abundance (Fig. 3). At the less affected sites B and C, these three taxa reached together only 46% and 52%,

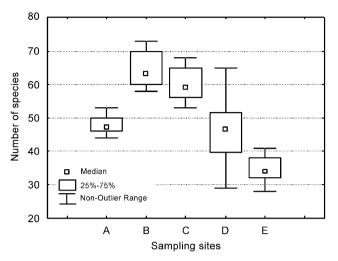


Fig. 2. Number of recorded species in samples from sites A–E.

respectively. At these sites we found a sharp increase of other taxa, especially molluscs, which formed 34% (B) and 28% (C) of the total abundance at these sites. The remaining 20% or so was equally distributed among the following taxa: Coleoptera, Odonata, Ephemeroptera, Trichoptera, and Crustacea. Regarding the individual taxonomic groups, the community structures of sites B and C were more diverse and showed more evenly distributed abundances than those at sites A, D and E (Fig. 3).

Functional feeding groups, current preferences, and biotic indexes

The trophic structure of the communities on the more affected sites (A, D, E) was very similar with gathering collectors being the most abundant (72–74%, Fig. 4). A very low percentage of shredders was also characteristic. Site C differed slightly by a smaller share of gathering collectors (64%), a higher share of shredders, scrapers, and predators. The most different was site B with a

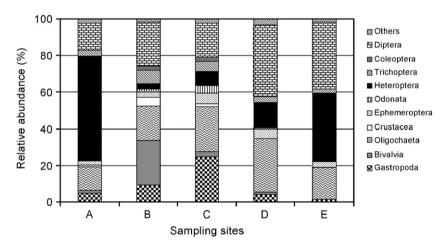


Fig. 3. Relative abundances of major taxonomic groups in all samples from sampling sites A–E.

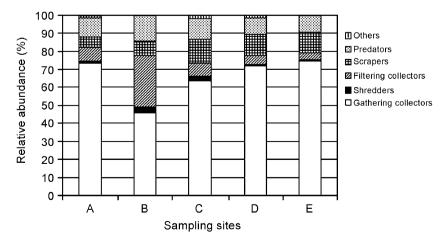


Fig. 4. Relative abundances of the six functional feeding groups in all samples from sampling sites A–E.

higher share of filtering collectors (up to 28%), predators, and shredders.

The sites most affected by channelization (A, D, E) also showed similar patterns of species water velocity preferences (Fig. 5). However, different patterns were found at the less affected sites B and C. At site B rheoto limnophilous taxa were much more abundant than at site C (Fig. 5).

Using the saprobic index, we did not confirm any significant differences in organic pollution for individual sites (Mann–Whitney U test, P > 0.05) due to a broad overlap of the values among the sites. By contrast, significant differences were found using the LIFE scores where low values were observed for sites B and C (Fig. 6), but only site B was significantly different from all other sites (Mann–Whitney U test, P < 0.05). Site C significantly differed from sites A and B, whereas no differences were found when site C was compared with sites D and E (Mann–Whitney U test, P > 0.05).

Community composition and their predictors

On the basis of the cluster analysis, the samples were classified into four groups on an arbitrary chosen cut level (Fig. 7). The samples were separated according to the sites, which indicated that the differences in species composition due to site were lager that those due to seasonal variation (Fig. 7). The only exception was the samples from sites D and E, which were grouped in one cluster.

Percentage variance of the species data explained on the first PCA axis was 21.3% that on the second axis was 11.0%. Relations of all explanatory variables to the first two ordination axes are given in Table 2; there was no significant relation with other axes. The sites were arranged along the first axis in the PCA diagram in relation to the character of riverbank (Fig. 8). The factor with the highest loading on the first axis, reflecting correlations with the sample scores, was the degree of the channel modification ($r_s = -0.89$, P > 0.001). The sites with preserved riprap and without submerged

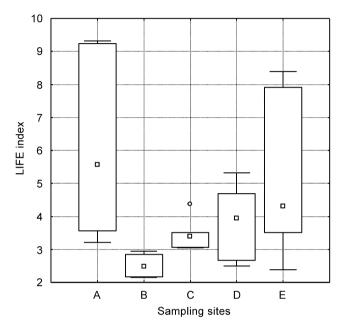


Fig. 6. Values of LIFE index of individual samples and their variability within sampling sites A–E.

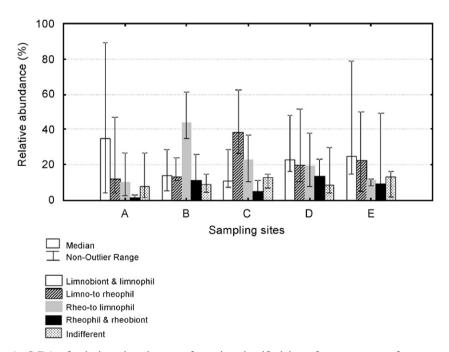


Fig. 5. Median values (\pm S.D.) of relative abundances of species classified into five current preference categories. All collected samples from the sampling site (A–E) were used for the calculation.

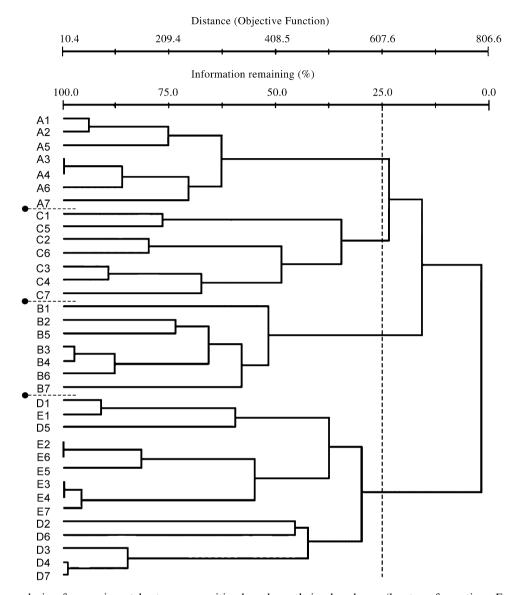


Fig. 7. Cluster analysis of macroinvertebrate communities based on their abundance (log-transformation, Euclidean distance, Ward's method). A, B, C, D, E: sites, 1: spring 1998, 2: late spring 1998, 3: summer, 4: autumn 1998, 5: spring 1999, 6: summer 1999, 7: autumn 1999. Dash line means cut level.

vegetation were plotted on the left side of the diagram. In contrast, the sites situated towards the right side of the diagram were characterized by the higher share of submerged vegetation and muddy banks. This type of bank was suitable mainly for many mollusc species (e.g. Viviparus acerosus, Physella acuta, Fig. 9). The second axis can be explained as a gradient of current velocity and mean site's depth (see Table 2). The sites with higher current velocity were placed in the lower part of the PCA diagram, which was indicated by the rheophilous bug Aphelocheirus aestivalis (Fig. 9). Sites with lower velocity were placed on the opposite site of the diagram. These conditions were indicated by the occurrence of species, which are more frequent in standing water bodies (e.g. Cloeon dipterum, Ranatra linearis). These results agreed with the results of the analysis of current

preferences (Fig. 5). The PCA diagram clearly demonstrated the strong difference of site B: whereas the assemblages of sites A, C, D and E formed continuous communities, site B fell outside the continuum (see Fig. 8).

Discussion

Species composition gradients and community features

The degree of riverbank modification was found to be the most important factor explaining the variation in species composition of the studied sites. Although the distance from the reservoirs was also significantly

Table 2. Relationships between all variables and samples scores on the first two PCA axes

Variables	PCA 1		PCA 2		
	$r_{ m s}$	P	r_{s}	P	
Water temperature	0.056	0.748	0.134	0.442	
Oxygen supply	-0.286	0.096	-0.306	0.073	
Water pH	-0.139	0.426	-0.173	0.319	
Water conductivity	-0.204	0.239	-0.012	0.946	
Distance from dam	-0.648	< 0.001	-0.272	0.114	
Depth	0.421	0.012	0.667	< 0.001	
Degree of modification	-0.891	< 0.001	0.140	0.424	
Nitrate concent.	-0.164	0.347	-0.014	0.934	
Ammonia concent.	0.145	0.406	0.179	0.304	
Phosphate concent.	0.091	0.604	-0.029	0.868	
Surface velocity	0.016	0.927	-0.900	< 0.001	
M–W U test					
Riprap vs. muddy and vegetation	_	< 0.001	_	0.522	

Values of Spearman rank correlations (r_s) and their probabilities (P) for continuous and ordinal variables; and significance of Mann–Whitney U test for nominal variable. Significant values are in bold; after using Bonferroni correction the current cut level was P = 0.003.

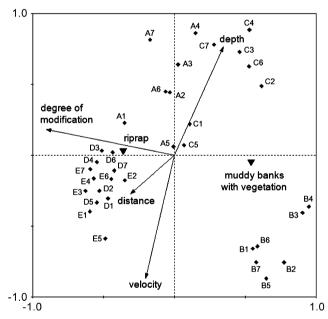
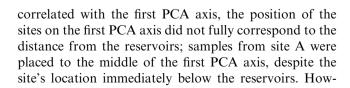


Fig. 8. PCA diagram of sites (A–E) on the first two ordination axes with posteriori plotted explanatory variables; only those significantly correlated with the first two ordination axes were used (see Table 2). Percentage variance of the species data explained: first axis 21.3%, second axis 11.0%. Species–environment relation: first axis 35.3%, second axis 18.1%. For explanation of abbreviation, see Fig. 7.



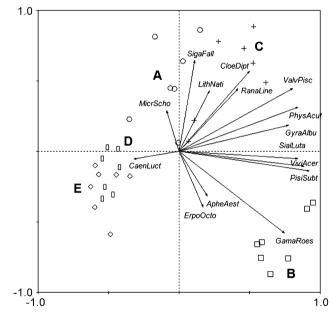


Fig. 9. PCA diagram of sites (A–E) on the first two ordination axes with plotted species with higher fit: Viviparus acerosus, Lithoglyphus naticoides, Valvata piscinalis, Physella acuta, Gyraulus albus (snails), Pisidium subtruncatum (clam), Erpobdella octoculata (leech), Gammarus roeselii (shellfish), Caenis luctuosa, Cloeon dipterum (mayflies), Aphelocheirus aestivalis, Sigara falleni, Micronecta scholtzi, Ranatra linearis (bugs), Sialis lutaria (dobsonfly).

ever, site A was intermediate in terms of the riverbank modification. We think that the significant relationship between distance from the reservoirs and the main direction in data variability in PCA might rather reflect the influence of longitudinal gradient itself than the impact of reservoirs. Nor the other statistical methods used showed any significant variability of the benthic macroinvertebrates composition caused by the impact of the reservoirs (Figs. 4–6). On the contrary, site A was more similar to the most downstream sites D and E regarding their species diversity (Fig. 2), trophic community structure (Fig. 4), and current preferences analysis as well (Fig. 5). The current preferences distribution at site A differed from those at sites D and E only by the share of limnobionts and rheobionts (see Fig. 5). We assume this difference to be caused by the presence of muddy banks at site A, rather than the manifestation of a reservoir impact. Whereas some authors observed a close relation between changes of community structure and current conditions (e.g. Brittain and Saltveit 1989), we conclude that in this respect there is no or only a minor impact of the impoundments on the benthic macroinvertebrates of the studied river section. The only evidence of a reservoir impact in the community structure we found was the high abundance of Hydra oligactis (more than 24%) at site A (just 1.5 km below the reservoirs). The reason for the high abundance of hydroids was probably a high proportion of zooplankton, a prey of hydroids, in the impoundment outlet water (cf. Armitage 1976, 1978). In general, it is more common to find net-spinning caddis larvae and suspension-feeding black fly larvae below the dams that discharge surface water (Boon 1988), but the muddy substrates at site A were unfavorable for these larvae. In conclusion, the above-mentioned results corresponded well to the Serial Discontinuum Concept (Ward and Stanford 1983), according to which lowland and shallow reservoirs have relatively low ecological impacts on the downstream river.

Biotic indication of negative impacts

Since the number of studied sites was low and thus the risk of bias was rather high, we tried to validate the results using additional independent techniques. On the basis of saprobic index, we confirmed that the level of organic pollution did not differ along the studied river stretch, even though sites D and E were located below a relatively large town. The fact that the whole studied region is naturally nutrient-rich can be a possible explanation of this unexpected situation, where organic pollution produced by the reservoirs has rather marginal effect. Communities of this area are adapted to dwell in such a trophic-rich environment and therefore the degree of organic pollution was not an important control of species structure and composition.

As indicated by the LIFE index, flow-related stress on the macroinvertebrate communities was relatively low at the sites B and C, at the former being significantly lower than at all the other sites (Fig. 6). The higher discharges at site B did not lead to a strong increase in water velocity and hydraulic stress due to a high retention capacity of the floodplain area along the former channel. By contrast, increased hydraulic stress was found at the sites in the main channel, the most unfavorable conditions being observed at the sites A and E. Thus, the channel modification was likely to have more negative impact on macroinvertebrates than the discharge pattern of the reservoirs. Relatively higher values and high variability of the hydraulic stress were encountered at site A probably because the higher discharges could not be buffered by a water exchange with channels and pools as it happened at the other sites (C–E).

Habitat diversity and the role of natural banks

In general, the differences between the macroinvertebrate communities of the unchannelized (sites B, C) and channelized stretches (sites A, D, E) observed in our study were similar to those reported in previous studies. The overall abundance and species richness of macroinvertebrates in the channelized stretches are usually lower than those in the natural ones (Moyle 1976; Quinn et al. 1992; Negishi et al. 2002). The extent of the impact and response of macroinvertebrates depends on the type, age and state of channelization. The main differences in the species number between the unchannelized and channelized stretches were caused by the presence of stretches with shallow and slow-flowing water with muddy banks, rich macrophyte growth and with no or only slight channel modification (B and C). Macrophytes represent a specific habitat type of great importance for the maintenance of overall macroinvertebrate diversity (e.g. Harper et al. 1998). Within their stands, dense shoots strongly reduce the flow and promote sedimentation of fine particles, while along these patches the flow is accelerated (Sand-Jensen and Mebus 1996; Sand-Jensen and Pedersen 1999). Several species were restricted to or preferred macrophyte stands, including rare (e.g. Baetis pentaphlebodes) and endangered species (e.g. Pisidium moitessierianum, Lithoglyphus naticoides), and many other common inhabitants of standing waters. Abundant FPOM sediments within macrophyte vegetation resulted in higher abundances of gastropods (more than 25% of total abundance) and mud-dwelling larvae of dragonflies (e.g. Platycnemis pennipes, Ischnura elegans). We found an increase in the number of limno- to rheophilous taxa in the less affected sites. In contrast, the faunal assemblages of the channelized sites, had low species richness and total abundances. Only three taxa (Oligochaeta, Chironomidae and M. scholtzi) formed together more than 80% of the total abundance. Nearly all groups associated with special slow-flowing habitats

(e.g. Hydrophilidae, Planorbidae, Sphaeriidae, Zygoptera) were missing or of a very low abundance.

The results discussed above are in agreement with those published by Quinn et al. (1992) and Negishi et al. (2002). These authors interpret differences caused by the morphological changes of the river bottom as the reason for general reduction of habitat diversity. Other studies (Duvel et al. 1976; Whitaker et al. 1979; Bloesch et al. 1998), however, did not reveal any differences between assemblages of channelized and unchannelized stretches. However, these works concern rather small streams without any specific bankside habitats. It is probable that if slow-flowing bankside habitats, most endangered by channelization, are absent, no difference would appear. On the other hand, at site B the remnant of a boulder chute led to the increase in species diversity. The macroinvertebrate community of this site was similar to that of site C, but the artificial occurrence of swiftflowing habitat with coarse inorganic substratum resulted in a higher share of filtering collectors (i.e. Hydropsyche spp. and Simuliidae) and members of the rheo- to limnophilous group. Thus, not only the species richness has to be considered, but functional aspects of community structures as well.

Conclusion

The lowland part of the Dyje River is a relatively rare stream type within the Czech Republic. Natural conditions of the studied river stretch were represented by the relatively shallow, muddy, and slow-flowing reaches with muddy banks, rich in both submerged and emergent vegetation. After the construction of the reservoirs and channelization of the river, the current velocity increased, natural banks were destroyed by using a riprap regulation and many animals dwelling here became extinct (Opravilová et al. 1999). After 30 years, the stabilization of banks was naturally nearly removed within some stretches and the environmental conditions and macroinvertebrate communities reverted towards the original state observed in the first half of the 20th century (see monograph by Opravilová et al., 1999). Our investigation suggested that the removal of shallow vegetated sections as a result of channelization had a greater effect on the macroinvertebrate communities than the flow regulations and the increase of organic pollution caused by the reservoirs.

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Appendix

Number of species in individual taxonomic groups recorded from studied sites (A–E)

Taxon	No. of species						
	A	В	C	D	E	Total	
Demospongia	0	0	1	2	2	2	
Cnidaria	1	1	1	1	1	1	
Platyhelminthes	2	2	3	1	1	4	
Nematoda	6	8	5	8	3	13	
Gastropoda	7	14	14	7	3	18	
Bivalvia	8	10	9	10	3	13	
"Oligochaeta"	22	19	16	18	21	37	
Hirudinida	5	4	5	7	2	8	
Tardigrada	0	0	0	1	0	1	
Hydrachnellae	4	0	3	4	1	6	
Cladocera	5	4	2	2	2	9	
Ostracoda	3	1	2	0	0	3	
Copepoda	6	5	7	6	4	10	
Isopoda	2	1	1	1	2	2	
Amphipoda	2	1	2	0	0	3	
Ephemeroptera	6	5	7	8	8	9	
Odonata	4	4	4	5	0	7	
Heteroptera	10	12	12	9	5	17	
Neuroptera	0	1	0	0	0	1	
Megaloptera	1	1	1	1	0	1	
Coleoptera	5	13	12	7	5	20	
Trichoptera	9	9	8	9	7	14	
Lepidoptera	0	0	1	0	1	1	
other Diptera	9	15	7	14	7	28	
Chironomidae	11	21	23	21	18	29	
Ectoprocta	2	1	2	2	1	3	

References

Adámek, Z., Sukop, I., 1992. Invertebrate communities of former southern Moravian floodplains (Czechoslovakia) and impact of regulation. Regul. Rivers: Res. Manage. 7, 181–192.

AQEM consortium, 2002. Manual for the Application of the AQEM System, Version 1.0 \(\sqrt{www.aqem.de} \).

- Armitage, P.D., 1976. A quantitative study of the invertebrate fauna of the River Tees below Cow Green Reservoir. Freshwater Biol. 6, 229–240.
- Armitage, P.D., 1978. Downstream changes in composition, numbers and biomass of bottom fauna in the Tees below Cow Green Reservoir and in an unregulated tributary Maize Beck, in the first five years after impoundment. Hydrobiologia 58, 145–156.
- Armitage, P.D., 1995. Faunal community change in response to flow manipulation. In: Harper, D.M., Ferguson, A.J.D. (Eds.), The Ecological Basis for River Management. Wiley, Chichester, pp. 59–78.
- Barbour, T.M, Gerritsen, J., Snyder, D.B., Stribling, J.B., 1997. Tolerance and Functional Feeding Group Assignments for Benthos. Appendix B. EPA 841-D-97-002.
- Bloesch, J., Peter, A., Frauenlob, G., 1998. Effects of technical impacts on alpine stream benthos and fish, and restoration proposals. Verh. Int. Ver. Theor. Angew. Limnol. 26, 1193–1200.
- Boon, P.J., 1988. The impact of river regulation on invertebrate communities in the UK. Regul. Rivers: Res. Manage. 2, 389–409.
- Brittain, J.E., Saltveit, S.J., 1989. A review of the effect of river regulation on mayflies (Ephemeroptera). Regul. Rivers: Res. Manage. 3, 191–204.
- Brookes, A., 1988. Channelized Rivers: Perspectives for Environmental Management. Wiley, Chichester.
- Bunn, S.E., Arthington, A.H., 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environ. Manage. 30, 492–507.
- Craig, J.F., Kemper, J.B., 1987. Regulated Streams Advances in Ecology. Plenum Press, London.
- Culek, M., 1996. Biogeografické členění České republiky. Biogeographical division of the Czech Republic. ENIGMA, Praha (in Czech).
- Duvel, W.A., Volkmar, R.D., Specht, W.L., Johnson, F.W., 1976. Environmental impact of stream channelization. Water Res. Bull. 12, 799–812.
- EN 27 828, 1994. Water quality-methods for biological sampling-guidance on handnet sampling of aquatic benthic macroinvertebrates (ISO 7828: 1985).
- Extence, C.A., Balbi, D.M., Chadd, R.P., 1999. River flow indexing using British benthic macroinvertebrates: a framework for setting hydroecological objectives. Regul. Rivers: Res. Manage. 15, 543–574.
- Friedl, G., Wüest, A., 2002. Disrupting biogeochemical cyclesconsequences of damming. Aquat. Sci. 64, 55–65.
- Gergel, S.E., Turner, M.G., Miller, J.R., Melack, J.M., Stanley, E.H., 2002. Landscape indicators of human impacts to riverine systems. Aquat. Sci. 64, 118–128.
- Gore, J.A., 1996. Response of aquatic biota to hydrological change. In: Petts, G.E., Calow, P. (Eds.), River Biota Diversity and Dynamics. Blackwell Scientific Publication, London, pp. 209–230.
- Harper, D., Smith, C., Kemp, J., Crosa, G., 1998. The use of 'functional habitats' in the conservation, management and rehabilitation of rivers. In: Bretschko, G., Helešic, J. (Eds.), Advances in River Bottom Ecology. Backhuys Publishers, Leiden, pp. 315–326.

- Helešic, J., Kubíček, F., 1999. Hydrobiology of the Dyje River in the National Park Podyjí, Czech Republic. Folia Fac. Sci. Nat. Univ. Masaryk. Brunen. Biol. 102, 1–138.
- Holm, S., 1979. A simple sequentially rejective multiple test procedure. Scan. J. Stat. 6, 65–70.
- Horsák, M., 2001. Contribution to our knowledge of macroinvertebrate fauna of the Dyje river downstream of the Nové Mlýny reservoirs (Czech Rebublic). Scr. Fac. Sci. Nat. Univ. Masaryk, Brun. Biol. 27 (Suppl.), 41–62.
- Ligon, F.K., Dietrich, W.E., Trush, W.J., 1995. Downstream ecological effects of dams. BioScience 45, 183–192.
- Lillehammer, A., Saltveit, S.J., 1984. Regulated Rivers. Universitetsforlaget AS, Oslo.
- Lorenz, A., Hering, D., Feld, C.K., Rolauffs, P., 2004. A new method for assessing the impact of hydromorphological degradation on the macroinvertebrate fauna of five German stream types. Hydrobiologia 516, 107–127.
- Lowe, W.H., 2002. Landscape-scale spatial population dynamics in human-impacted stream systems. Environ. Manage. 30, 225–233.
- Kubíček, F., Helešic, J., Komárek, O., 1995. The benthic community in artificial concrete channels. Folia Fac. Sci. Nat. Univ. Masaryk. Brun. Biol. 91, 63–76.
- McCune, B., Mefford, M.J., 1999. PC-ORD. Multivariate Analysis of Ecological Data. Version 4. MjM Software Design, Gleneden Beach.
- Moog, O., 1995. Fauna Aquatica Austriaca, Version 1995. Bundesministerium für Land- und Forstwirtschaft, Wasserwirtschaftskataster, Wien.
- Moyle, P.B., 1976. Some effects of channelization on the fishes and invertebrates of Rush Creek, Modoc County, California. Calif. Fish Game 62, 179–186.
- Negishi, J.N., Inoue, M., Nunokawa, M., 2002. Effects of channelisation on stream habitat in relation to a spate and flow refugia for macroinvertebrates in northern Japan. Freshwater Biol. 47, 1515–1529.
- Opravilová, V., Vaňhara, J., Sukop, I., 1999. Aquatic invertebrates of the Pálava Biosphere Reserve of UNESCO. Folia Fac. Sci. Nat. Univ. Masaryk. Brun. Biol. 101, 1–279.
- Peeters, E.T.H.M., Tachet, H., 1989. Comparison of macrobenthos in braided and channelized sectors of the Drôme River, France. Regul. Rivers: Res. Manage. 4, 317–325.
- Petts, G.E., 1984. Impounded Rivers, Perspectives for Ecological Management. Wiley, New York.
- Prach, K., 1995. Sixth international symposium on regulated rivers. Regul. Rivers: Res. Manage. 10, 1–391.
- Quinn, J.M., Williamson, R.B., Smith, R.K., Vickers, M.L., 1992. Effects of riparian grazing and channelisation on streams in Southland, New Zealand. 2. Benthic invertebrates. New Zealand J. Mar. Freshwater Res. 26, 259–273.
- Quitt, E., 1971. Klimatické oblasti Československa. Climatic regions of Czechoslovakia. Stud. Geogr. 16, 1–47 (in Czech).
- Raven, P.J., Holmes, N.T.H., Dawson, F.H., Fox, P.J.A., Everard, M., Fozzard, I.R., Rouen, K.J., 1998. River habitat quality – the physical character of rivers and streams in the UK and Isle of Man. Bristol (Environment Agency): River Habitat Survey Report No. 2, May 1998.

- Saito, L., Johnson, B.M., Bartholow, J., Hanna, R.B., 2001. Assessing ecosystem effects of reservoir operations using food web-energy transfer and water quality models. Ecosystems 4, 105–125.
- Sand-Jensen, K., Mebus, J.R., 1996. Fine-scale patterns of water velocity within macrophyte patches in streams. Oikos 76, 169–180.
- Sand-Jensen, K., Pedersen, O., 1999. Velocity gradients and turbulence around macrophyte stands in streams. Freshwater Biol. 42, 315–328.
- Šporka, F., 2003. Vodné bezstavovce (makroevertebráta) Slovenska, súpis druhov a autekologické charakteristiky. Slovak aquatic macroinvertebrates checklist and catalogue of autecological notes. Slovenský hydrometeorologický ústav, Bratislava (in Slovak).
- Sukop, I., 1990. Influence of the water works at Nové Mlýny on macrozoobenthos of the Dyje River in the vicinity of Biosphere Reserve Pálava (southern Moravia). Ekológia (Bratislava) 9, 73–86.
- ter Braak, C.J.F., Šmilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide. Software for Canonical Community Ordination (version 4.5). Biometris, Wageningen and České Budějovice.

- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37, 130–137.
- Vinson, M.R., 2001. Long-term dynamics of an invertebrate assemblage downstream from a large dam. Ecol. Appl. 11, 711–730.
- Vlček, V., 1984. Zeměpisný lexikon ČSR-vodní toky a nádrže. GEOGRAPHICAL lexicon of CSR-Water streams and reservoirs. Academia, Praha (in Czech).
- Ward, J.V., Stanford, J.A., 1979. The Ecology of Regulated Streams. Plenum Press, New York.
- Ward, J.V., Stanford, J.A., 1983. The serial discontinuity concept of lotic ecosystems. In: Fontaine, T.D., Bartell, S.H. (Eds.), Dynamics of Lotic Ecosytems. Scientific Publishers, Ann Arbor, pp. 29–42.
- Ward, J.V., Stanford, J.A., 1995. The serial discontinuity concept: extending the model to floodplain rivers. Regul. Rivers: Res. Manage. 10, 159–168.
- Whitaker, G.A., McCuen, R.H., Brush, J., 1979. Channel modification and macroinvertebrate community diversity in small streams. Water Res. Bull. 15, 874–879.
- Zwick, P., 1992. Stream habitat fragmentation-a threat to biodiversity. Biodiversity Conserv. 1, 80–97.