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Effect of meander restoration on macroinvertebrate biodiversity: the case of the Borová stream (Blanský Les, Czech Republic)

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Abstract
This study brings a view on the effects of restoration of a formerly channelized small submontane stream situated in the Blanský Les Protected Landscape Area (South Bohemia, Czech Republic) on macroinvertebrate assemblages as an indicator group. The restoration project was carried out during two stages (1998 and 2000). It consisted of excavating a new channel to restore the historic meandering pattern. The evaluation of this project is primarily based on the comparison of composition between pre-restoration (1995) and post-restoration (2000–2003) macroinvertebrate samples focusing on species richness, species composition, and representation of rare Ephemeroptera and Plecoptera species. The analyses showed a substantial increase in species richness that was especially prominent shortly after the restoration intervention. This increase was not only due to the creation of lentic habitats, but was even observed at every single sampling site of the stream. The DCA ordination of species composition of the pre- and post-restoration sites indicated a considerable increase in the between-site diversity. This was apparently caused mainly by the establishing of lentic habitats, whereas diversity of lotic sites showed only a slight increase, which was most prominent during the last year of the sampling period. The shift in the species composition was profound for lotic sites as well. Although the restoration intervention considerably increased species richness and markedly changed species composition, there was no detectable increase of rare or vulnerable Ephemeroptera and Plecoptera species.

Key words: stream restoration, meander reconstruction, species richness, Ephemeroptera, Plecoptera

Introduction

European freshwater systems have suffered during the last century by the consequences of industrial, agricultural, and urban development. This development is associated with river regulation for flood control, land drainage, navigation, hydroelectric power etc. For instance, 8500 km (25%) of rivers in England were heavily channelized between 1930 and 1980 (Brookes 1988). Half of the agricultural land was drained and 80–98% of natural watercourses have been channelized in Denmark (Markmann 1990). In the Czech Republic, 25.4% of agricultural land was drained, 40.2% of natural watercourses have been modified, and the total length of watercourses has been shortened by about one third (Soldán et al. 1998). All these factors considerably decreased freshwater biota in species number as well as quantitative presentation. The situation became alarming in the 1970s and scenarios of future development were quite pessimistic at that time (Lepš et al. 1990). The turn of this century has witnessed a major turn in freshwater management. Many efforts have been undertaken to reduce the impairment of stream ecosystems by wastewater, fertilizers, and other pollution. This lead to a remarkable improvement of water quality in most parts of Central Europe. Nevertheless, the structural degradation of stream morphology still presents the most severe disturbance in freshwater systems. Governments invest considerable efforts and resources to reduce these damages and restoration of freshwater systems has been recognized as a European priority as a promising and possibly the most important tool for preserving the Earths' biodiversity (Moss 2000, Cardinale et al. 2002, Hooper at al. 2005).

Although restoration ecology is a young academic discipline, it has undertaken a considerable shift in attitudes towards restoration projects that originally strived for structural and functional returns of channelized watercourses to a pre-disturbed state (Cairns 1982). Today restoration ecology tends to call for a new paradigm (Choi 2007, Temperton 2007). The past--oriented static approach is often criticized for its inapplicability to dynamic ecosystems and changing environmental conditions. Besides various socio-economic landscape uses, there are also climate changes that detectably influence water macroinvertebrates (Durance & Ormerod 2007). The stress is rather put on rehabilitation of ecological functions then on strictly rearranging the species composition or landscape surface (Temperton 2007). Under the circumstances of climatic change accompanied by severe weather fluctuations and problems with frequent floods and erosion, emphasis is also placed on socio-economic and political framework as well as on scientific background.

Although restoration projects can be viewed as applied experiments of ecological knowledge, the vast majority of projects are not implemented within any experimental context. In spite of long-term popularity of restoration projects, their efficiency with respect to purported goals has rarely been assessed (Karr & Chu 1999, Lake 2000). Bernardt et al. (2005) has reported that, although the worldwide annual expenditures on various restoration projects excess 1 billion USD, only 10% of the cases report any monitoring whatsoever and the evaluations are often inadequate.

Morphologically degraded stream sections are typically characterized by low habitat heterogeneity and consequently lower biodiversity compared to more natural sections (Sear at al. 1998). Much of the biodiversity is presented by benthic macroinvertebrates – much more than that of fishes or macrophytes (Allan & Flecker 1993). Macroinvertebrates are particularly suitable for assessments of restoration projects, owing to their high plasticity in biological traits and habitat requirements (Rosenberg & Resh 1993). They are species-rich, typically occur in high abundances, and respond to particular interventions in a relatively short time. Compared to the fish, they have a relatively fast life cycle and react even to the small--scale changes, yet they have lower-order sizes. Moreover, a considerable amount of restoration projects are being done in small streams and, although fish diversity is quite an easy and popular tool in assessing success of restoration projects (Rabeni & Jacobson 1993, Jungwirth 1995, Cowx & Welcome 1998, Pretty et al. 2003), it fails in these cases.

An implicit assumption of stream restoration projects is to maximize habitat diversity leading to system restoration (Osborne et al. 1993, Muhar et al. 1995, Stanford et al. 1996). There are some theories that predict how stream morphology affects species richness. According to a habitat templet concept (Southwood 1977, Townsend & Hildrew 1994), species richness increases with increased spatial heterogeneity – either due to a greater number of niches available or because of reduced likelihood of competitive exclusion in a patchy environment. Using the patch dynamic concept (Resh et al. 1994), highest species richness occurs at intermediate levels of temporal variability and the highest levels of spatial variability. Statzner & Higler (1986) suggested that maximum richness should occur where major changes in stream slope create areas of high in-stream hydraulic variability. Minshall (1988) and Poff & Ward (1990) also emphasize the influence of habitat and flow heterogeneity on species richness. Concerning restoration projects, Lancaster & Hildrew (1993) and Negishi et al. (2002) recommend the construction of flow refuges, i.e., places not subjected to raised hydraulic forces during high flows. This is consistent with the theory that spatial habitat heterogeneity buffers against temporal disturbances (Quinn & Hickey 1990, Scarsbrook & Townsend 1993, Townsend & Hildrew 1994, Minshall & Robinson 1998). Moreover, the scale of spatial heterogeneity also represents a very important question. It should be appropriate for macroinvertebrates' requirements, which are usually different from our intuitive perceptions of landscape heterogeneity.

This study brings a view on the effects of the restoration of a formerly channelized, small, submontane stream (situated in the Blanský Les Landscape Protected Area, South Bohemia, Czech Republic) on macroinvertebrate assemblages as an indicator group. It is primarily based on comparison of composition between pre-restoration and post-restoration macroinvertebrate samples and attempting to discuss: How was species composition and species richness of macroinvertebrate assemblages affected by restoration and how the restoration influenced rare or vulnerable species representation.

In practice, restoration objectives are mainly achieved by the introducing of various in-stream structures (Nickelson et al. 1992, Rabeni & Jacobson 1993, Roni et al. 2005) such as cobble ridges, woody debris, boulder dams, timber logs, or transverse sills. These structures alter channel morphology and promote deposition of organic debris. However, the streambeds typically retain their straight, horizontal profiles. Contrary to this widespread approach, a comprehensive design was used in this case. The whole streambed has been re-meandered with a number of small pools. These measures can certainly increase morphological heterogeneity and mimic the pre-disturbance state. On the other hand, the intervention included substantial disturbance and the use of heavy technique which had seriously affected the biota.

Material and methods

Locality description

The Borová stream is 6 km long with a spring area at the altitude of 660 m, 48º53'03" N, 14º11'56" E. It is situated in the south-western part of the Blanský Les Protected Landscape Area, 5 km north-western from the Chvalšiny village. It first passes through a shallow valley covered by cattle pastures surrounded by woodlands and then through the small village of Borová. It drains into the Chvalšinský Potok stream (a part of the Vltava River basin). Its left-side tributary, the Zrcadlový Potok stream, is about 3 km long. It springs at the elevation of 720 m, passes through mixed, predominantly deciduous forest and enters the Borová stream at the elevation of 620 m.

Locality history and restoration project

Until the 1980s, the stream has run through the valley as a shallow, meandering stream surrounded by small-sized, traditionally managed meadows and fields. In 1982–1984, the entire valley was drained and the stream was channelized into an unnaturally deep (120–180 cm), straight drainage ditch. Banks were stabilized by grass concrete lining. The channelized section was 3.13 km long and included the mouth of the Zrcadlový Potok tributary.

The restoration project primarily aimed to diversify the flow and increase water retention in the landscape. It consisted of the construction of a new streambed, 25–60 cm deep, with several meanders in the downstream part and several pools designed to increase heterogeneity. These measures increased the total length of the stream by the factor of 1.25 and consequently reduced its slope. The old channel was filled with soil – only a part was transformed into a cascade of pools. However, the drainage tubing at the surrounding pastures had to remain undisturbed except for the spring area where a small wetland was established. The restoration proceeded in two phases: the upstream section (1.8 km long) was restored in 1998 and the downstream section (1.2 km) in 2000. The banks were lined with sod and native woody species. Speckled alder, black alder, bird cherry, goat willow, ash, and maple were planted along the exposed concave parts of meanders to stabilize the banks. A short section (ca. 100 m) was restored in a traditional way, i.e., by the establishing of transverse sills, because the necessary agreement of the land owner was not secured.

Sampling of benthic macroinvertebrates

Prior to the restoration in July and August 1995, short-time biological surveys were carried out in order to monitor the pre-restoration state (Flíček 1995, Fuka & Flíček 1995, Matěna & Soldán 1995). Benthic macroinvertebrates were sampled at seven sites using the semi-quantitative kick and sweep technique (Kershaw & Frost 1968) and by hand-picking of specimens from stones and macrophytes. Adults of Plecoptera and Trichoptera were occasionally collected from surrounding vegetation. The objective of the surveys was to collect as many species per site as possible, hence the time spent on sampling varied between the sites. All sampled individuals were preserved and counted. The total catch was 1615 specimens in 49 species.

Post restoration sampling proceeded monthly from June 2001 to September 2003. However, only samples from July and August (months with available pre-restoration data) are analyzed here. The kicking sample technique was used again, but now in a more rigorous way, with identical sampling effort (20 minutes) per site and visit. There were twelve sampling sites in total (Fig. 1). Seven were identical to the pre-restoration survey: two in the section restored in 1998, two in that restored 2001, one in the part restored in a traditional way, and two in the non-restored Zrcadlový Potok tributary. They are referred as "lotic sites". The additional five sites were the "lentic sites", which did not exist before the restoration.

For each sample, the depth/width of the stream and the presence of canopy layers overshadowing the site were recorded. Water velocity was measured by using a timer and a cork float. The substrate roughness of the bottom was characterised as percentage cover by par-

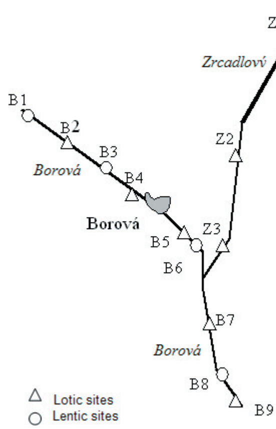

Fig. 1. Map of the locality studied with sampling sites.

Table 1. Characteristics of particular sites according to the physical factors (mean ± standard error).

	B1 (lentic)	B2[1] (lotic)	B3 (lentic)	B4[1] (lotic)	B5[1] (lotic)	B6 (lentic)	B7[1] (lotic)	B8 (lentic)	B9[1] (lotic)	Z1 (lentic)	Z2[1] (lotic)	Z3[1] (lotic)
pH	7.2±0.12	7.2±0.10	7.2±0.11	7.2±0.13	7.4±0.09	7.0±0.09	7.3±0.09	7.6±0.16	7.6±0.12	7.3±0.15	7.4±0.10	7.4±0.10
Conductivity (μS.cm^{-1})	128±3.8	131±3.5	136±2.9	135±2.9	229±12.3	230±6.5	228±10.6	214±8.5	207±8.2	231±40.1	301±17.8	298±14.8
Turbidity (NTU) [2]	2.2±0.37	3.7±0.76	5.5±1.18	5.0±1.36	8.1±1.15	7.4±1.17	9.0±0.08	12.9±1.80	10.0±1.59	6.7±1.57	2.7±0.31	8.3±1.77
Dissolved oxygen (mg.l^{-1})	8.7±0.48	9.9±0.30	9.0±0.22	10.3±0.25	10.2±0.28	8.5±0.49	9.6±0.035	9.8±0.60	10.9±0.45	8.7±0.62	10.7±0.29	10.3±0.39
Temperature (°C)	11.0±1.04	11.3±0.86	12.2±0.98	12.1±0.98	12.2±1.12	13.3±1.23	12.9±1.18	14.1±1.35	13.7±1.32	9.6±0.75	9.9±0.79	10.7±1.07
Current velocity [3]	2	2	0	2	3	0	2	0	2	0	2	2
Boulders (%)	0	60±3.0	0	57±4.3	64±3.1	0	62±1.4	0	11±1.9	5±2.1	25±2.8	6±1.5
Gravel (%)	2±1.4	37±3.4	2±2.0	29±3.4	15±2.8	0	22±3.4	0	78±2.5	31±6.2	46±2.3	61±5.0
Sand (%)	3±1.7	2±0.9	2±0.9	11±3.6	20±1.7	0	11±3.6	0	8±2.0	3±1.5	29±3.0	30±4.8
Mud (%)	29±4.3	1±0.5	46±6.2	3±1.2	2±1.0	42±4.7	4±1.9	48±4.8	1±0.5	9±3.0	2±1.6	2±1.0
Macrophyta (%)	52±5.0	1±0.4	47±5.2	0	0	48±4.6	1±0.4	48±5.7	1±0.4	0	0	0
Leave litter (%)	0	0	0	0	0	0	0	0	0	53±6.5	0	0
Algae (%)	16±6.3	0	3±2.7	0	0	10±4.4	0	4±2.1	2±1.3	0	0	0
Depth (cm)	33±2.0	15±1.1	38±3.2	23±1.7	28±2.2	39±3.9	32±1.8	21±0.9	23±2.2	32±1.7	18±1.3	18±1.4
Width (cm)	184±4.4	37±1.7	310±2.5	58±5.2	86±1.6	226±8.2	87±1.7	1000±0	77±2.9	62±1.2	131±6.6	45±1.6

[1] sites included to the analysis comparing pre- and post-restoration state
[2] NTU (Nephelometric Turbidity Units); nephelomether measures the light intensity scattered at 90° from the light source
[3] current velocity was coded: 0: 0–0.04 m.s^{-1}, 1: 0.004–0.2 m.s^{-1}, 2: 0.2–0.3 m.s^{-1}, 3: 0.3–0.6 m.s^{-1}

ticular substrates, i.e., boulder, sand, gravel, mud, leaves, filamentous algae, and submerged macrophytes at the site (cf. Gordon et al. 1992). In addition, the physical variables were measured with a portable water-quality checker, the Horiba U-10 (pH, temperature, conductivity, turbidity, and dissolved oxygen). Physical-chemical data of particular sites are enclosed as Table 1.

The collected macroinvertebrates were preserved in 70% alcohol and later sorted in the laboratory. All animals excluding Diptera and Oligochaeta were identified to the lowest feasible taxonomic level, desirably species.

The study partly represents a before-after-control intervention (BACI) design (Underwood 1994). However, the control site differed in many respects from the affected one (higher slope, running through forested area and thus exposed to lower insolation and containing higher amounts of detritus). Hence, the interpretation of the differences between the streams Borová and Zrcadlový Potok has a rather limited value.

Data analyses

Pre-restoration data was available only as a cumulative dataset from July to August 1995 (for particular sites), so we combined these two months also in case of post restoration data. The four datasets from 1995, 2001, 2002 and 2003 (for each site) were used to answer the following tasks.

Effects of the restoration on composition of macroinvertebrate communities

Detrended correspondence analysis (DCA) in CANOCO, version 4.5 (ter Braak & Šmilauer 1998) was used to ordinate the pre- and post-restoration sites according to their macroinvertebrate assemblages. The lentic sites, which did not exist before the intervention, formed a distinct cluster separated from both pre- and post-restoration lotic sites, so they were excluded from further analyses, which were thus based on seven mutually matching lotic sites.

Species richness of the pre- and post-restoration states

Since sampling effort varied between pre- and post-restoration surveys and varied also among sites, during the pre-restoration survey, the rarefaction method was used (Krebs 1989). This method allowed us to compare species richness across datasets of different sizes, because it calculates: how many species would be found in the larger sample if it contained as many individuals as the smaller sample. The different sized samples are compared using the Chao-1 Estimator (Chao 1984) and its standard deviation is computed for each sample separately (Colwell & Coddington 1994). The calculations were performed using the on-line Rarefaction calculator (Brzustowski 2011).

The comparisons proceeded as follows: First all sampled sites were compared, including the lentic sites created during the restoration, but not existing prior to it. Then the lentic sites were excluded in order to see the effects of restoration on lotic habitats. Both comparisons were carried out for all sites together and for each site separately.

Proportion of rare species in pre- and post-restoration state

This analysis was restricted to the Ephemeroptera and Plecoptera, for which there is good information on their conservational status.

In order to express the commonness/rarity of the collected Ephemeroptera and Plecoptera, a number from a six-grade-scale was assigned to each species according to its status in the Czech Republic: 1 – solitary, 2 – rare, 3 – medium distributed, 4 – abundant, 5 – very abundant, 6 – common (Soldán et al. 1998). Changes in proportional abundances of these categories, before and after the restoration, were compared using regression. The numbers expressing the situation in the Czech Republic were independent variable and the difference in proportional abundance of particular species was dependent variable (this variable was transformed by extraction in order to obtain normality of the data). The pre-restoration state was compared with the state in 2003.

Results

The tested July–August dataset contains 7581 individuals of 173 taxa identified mostly to species level (Appendix 1). The average sample contained 176 individuals (median = 166, SD = 92, SE = 14) and 22 species (median = 23, SD = 7, SE = 1). Dominant species were *Gammarus roesselii*, *Baetis rhodani*, *Cloeon dipterum*, *Pyrrhosoma nymphula*, and *B. vernus* (respectively 20, 9, 8, 5, and 3% of the total catch), followed by *Leuctra albida* and *Hydropsyche* sp. that made up more than 3%, and *Protonemura nitida*, *Gyraulus*, *Radix peregra*, and *Leuctra autumnalis* that formed about 2% of all collected individuals. Another eight species reached more than 1%, whereas 27 species were singletons.

Changes in species composition and species richness after the restoration

The DCA ordination of species composition of pre-restored and post-restored sites convincingly separated lentic from lotic sites, and pre-restoration from post-restoration sites (Fig. 2). The newly established lentic sites are shifted to the right along the first ordination axis in relation to the position of lotic sites. The pre- vs. post-restoration sites are divided along the second ordination axis.

When the pre- and post-restoration data were analyzed separately, the length of gradient of the former situation was lower (2.19) compared to the latter (3.34). This suggests that the habitats diversity increased after the restoration. However, the increase was apparently due to the lentic sites, because the length of gradient of post-restoration lotic sites was only slightly longer (2.35) than that of pre-restored lotic sites. Hence, the restored lotic sites underwent a change in macroinvertebrate assemblage composition but there was no increase of a relative distances among the sites (Fig. 2). The lengths of gradients for the end of collecting

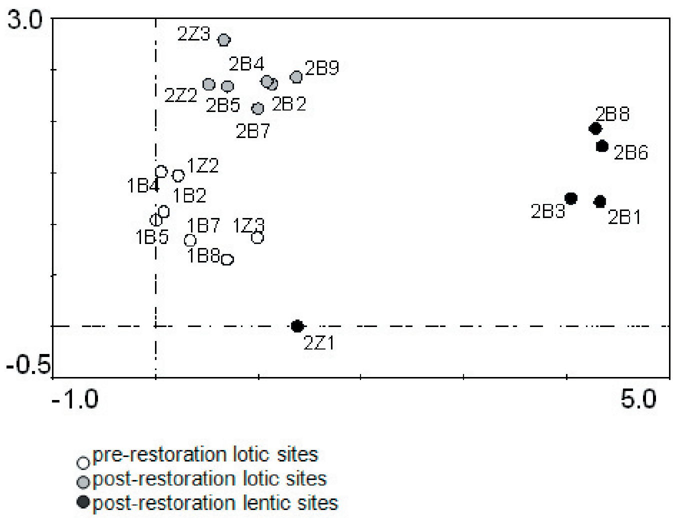

Fig. 2. Pre- and post-restoration sampling sites visualized by detrended correspondence analysis (DCA).

period (year 2003) were also higher than that computed for collated data from all post-restoration years (3.83 for all sites and 2.46 for lotic sites).

The restoration caused a considerable increase in species richness. This effect is weaker, but remains significant after exclusion of lentic sites (Fig. 3). Fig. 4 describes shifts in species richness at a few particular sites. All restored lotic sites (B2, B4, B5, and B8) exhibit significant increase in species richness. This trend is also apparent at site B7 restored in a traditional way. The non-restored sites Z2 and Z3 (Zrcadlový Potok stream) did not show any increase in species richness.

At each single restored sampling site, it is possible to observe a similar pattern of changes in species richness that increased most markedly shortly after the intervention (2001) and then gradually decreased. This decrease was just temporary as it apparently does not continue. At the end of the sampling period (2003) the species richness stabilized or even slightly increased (Fig. 4).

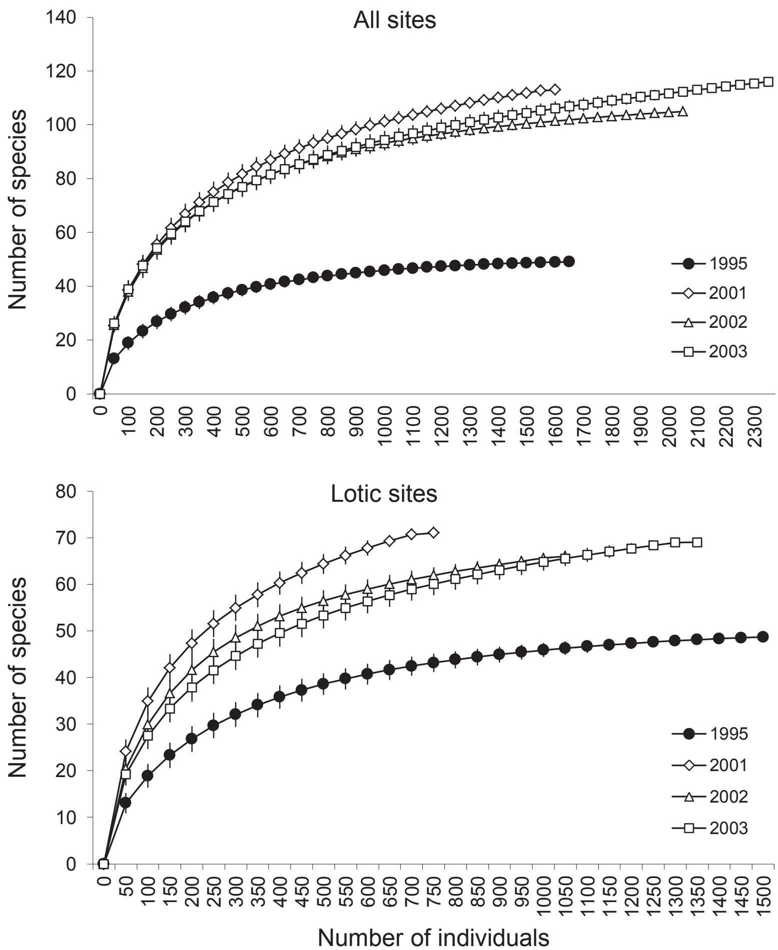

Fig. 3. Comparison of species richness of the pre- restoration situation (1995) with the post- restoration years (2001–2003) at all sampled sites together (a), including lotic sites (b).

Table 2. Number of Ephemeroptera and Plecoptera individuals and species collected during July–August in samples from pre- and post-restoration period.

Year	Ephemeroptera (individuals/species)	Plecoptera (individuals/species)
1995	608/12	217/8
2001	457/18	140/10
2002	573/15	174/10
2003	515/18	239/11

Proportion of rare species in pre- and post-restoration state

In total, 2159 specimens of 21 Ephemeroptera species and 770 specimens of 17 Plecoptera species were collected. In the pre-restoration period (1995), it was 608 specimens of 12 Ephemeroptera species and 217 specimens of 8 Plecoptera species, whereas during the last year of sampling, 515 specimens of 18 Ephemeroptera species and 239 specimens of 10 Plecoptera species were gathered (Table 2). Species that were collected only in the pre-restored period were just four Plecoptera species: *Amphinemura standfussi*, *Brachyptera seticornis*, *Protonemura intricate*, and *Nemoura marginata*. The last 3 species were also collected in the post-restoration period, but not during the July–September period. This was mainly caused by differences in their phenology and/or sampling method, because during the pre--restoration period, the adults from surrounding vegetation were also collected. Whereas 9 new Ephemeroptera and 12 new Plecoptera species appeared during the last sampling year (2003), (or 10+13 during the whole sampling post-restoration period).

The number of species increased considerably (Table 2, Fig. 3). Some of the newly appeared species are connected mainly to the lentic sites, which were absent in the channelized stream (e.g. *Cleon dipterum*), but the majority of them are typically lotic species (all Plecoptera species, *Baetis fuscatus*, *Caenis horaria*, *Ecdyonurus torrentis*, *E. venosus*, *Epeorus assimilis*, *Habroleptoides confusa*, *Habrophlebia lauta*, *Paraleptophlebia submarginata*, and *Rhithrogena semicolorata*) (Appendix 1). Most of these species prefer moderate flow and some of them are typical for lower altitudes. The correlation coefficient of regression for proportional change of rareness of Ephemeroptera and Plecoptera species was $r = 0.086$. This means that there was no significant shift towards rarer Ephemeroptera and Plecoptera species during the studied period.

Discussion

Results of this work show that the macroinvertebrate assemblage of the restored section of a small stream contained higher species richness in comparison to channelized conditions that preceded the restoration. However, the restoration did not increase abundances of rare Ephemeroptera and Plecoptera species.

The increase of species richness was influenced mainly by establishment of completely new lentic habitats missing before the intervention. As expected, the lentic habitats were colonized by a set of typically lentic species that were absent in the pre-restoration biotope state. On the other hand, there was still a significant increase in species richness concerning lotic habitats. This was consistent with the presumption that the return of the strait channel back to its meanders contributed to the richness of functional habitats and thus increased lotic species richness. The effect was apparent at each single stream site, even at site 7 that was restored in a traditional way (replacement of transverse sills that slow water current, creating artificial riffles and adding boulders to the bed). The old streambed was retained so there remain a number of microhabitats such as roots and mosses that logically lacked in the

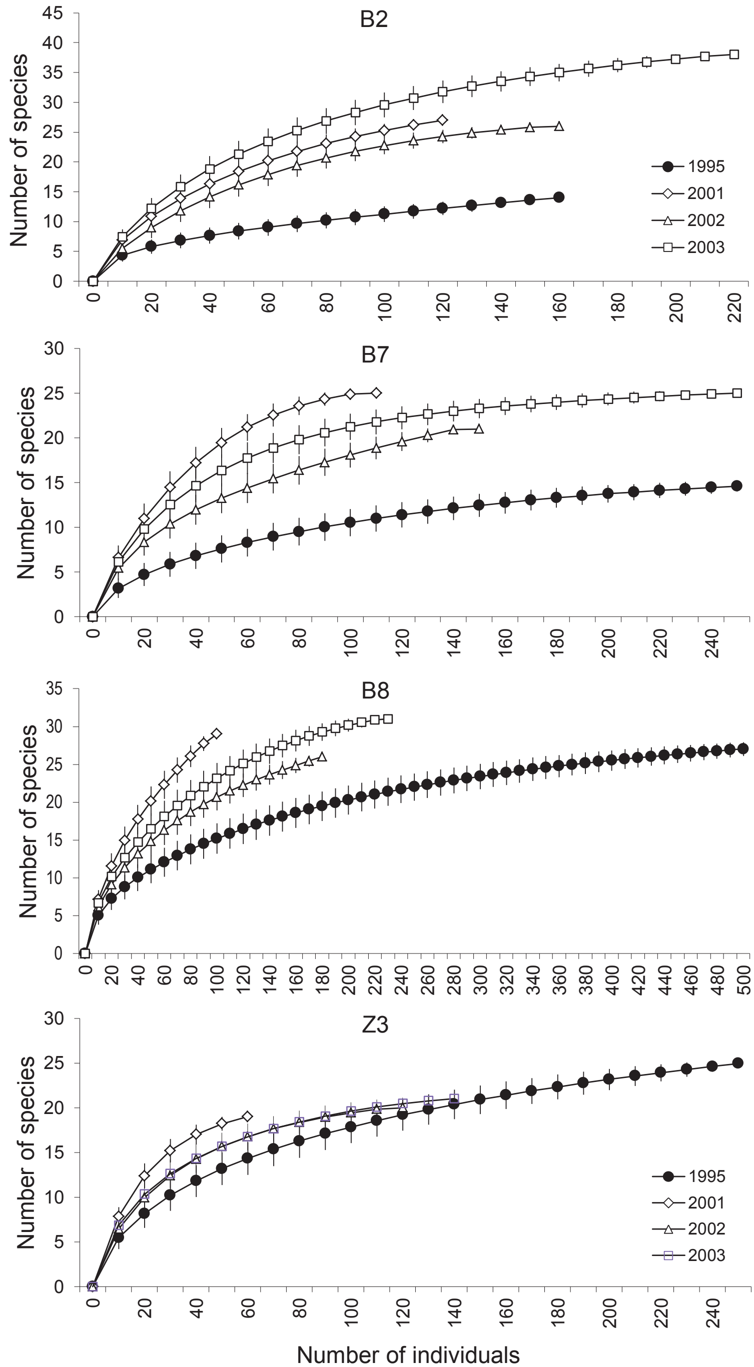

Fig. 4. Comparison of species richness of the pre-restoration situation (1995) with the post- restoration years (2001–2003) at particular sites.

newly established streambed. The section maintained in this way was just of ~100 m in the middle part, so there could be found also macroinvertebrates drifting from the upstream part. Anyway there is not possible to compare which restoration technique is more effective. Muotka et al. (2002) came with an idea that it is useful to leave relatively large areas of the stream bed untouched to serve as colonization centres (mainly for mosses that were key factor in boreal small stream retention capacity). This idea may be applicable in general colonization of other species. In this case it paradoxically enriched the whole stream bed with the next type of biotope with fast water current, submersed tree roots, and mosses. Moreover, the non-restored part was the only part with tree canopy producing leaf litter. This could potentially hasten colonization of the newly created part with detritovorous species and gather collectors. This study shows that leaving such a small part of stream non--restored, or restoring it in the traditional (cheaper) way had at least no negative effect on the species richness. To the contrary, the increase in species richness was significant at this part, and stayed relatively stable for all the three sampled years. Nevertheless, there is not enough data to discuss how much of the stream (and which parts) could stay non-restored or be restored in a cheaper way to accelerate colonization rate and achieve the required effect.

Similar patterns were observed in post-restoration changes in species richness at all the sites, where the new bed was created, as well as on the whole data. There was a substantial increase in species richness shortly after the intervention when a new streambed was established. This was followed by a slight decrease, but this trend did not continue. In the following year, numbers of species seemed to stabilize, or even increase. However, no such post-restoration changes occurred at the sites Z2 and Z3 (Fig. 4), which were unaffected by any intervention. Although the restricted number of studied sites does not allow any unequivocal conclusion, it could be suggested that the changes are most likely due to post-restoration succession. If so, the intervention would cause an initial increase in species richness, but this hypothesis deserves to be tested on more extensive data.

Considering the lotic sites and judging from a comparison of the length of gradients in the ordination analyses, there was no distinct increase in inter-site variation between species communities of the restored lotic sites compared to the pre-restoration situation. Although the fact that the length of gradient for the lotic sites computed for the last year of the collecting period (2003) was longer than that computed for data of the whole post-restoration period suggests that sites may diversify in time according to the species composition. Nevertheless, this diversification was quite slight. In other words, the restoration systematically restructured the species composition of assemblages in the stream, but the differences in diversity of particular sites remained nearly unchanged. All restored lotic sites showed an increase in species richness at the same time, compared to the pre-restoration conditions. A likely interpretation of these contradictive observations is as follows: The intervention increased habitat heterogeneity at a small scale within individual sampling sites, homogeneously along the watercourse. Samples of aquatic macroinvertebrates frequently reveal a higher diversity within the sites than among them, even if only one microhabitat type (such as boulder surface, riffle, etc.) is studied (e.g., Downes et al. 1993, Li et al. 2001, Brooks et al. 2002). Many stream macroinvertebrates are good colonizers, which settle a high number of sufficient microhabitats along the watershed almost homogeneously. In this study, the individual sampling sites were quite large (about 2 m long segments of streambed) compared to the macroinvertebrates' habitat distinguishing ability, and all potential microhabitats within one sampling site, e.g., riffle, the banks and mainstream, were sampled. The spatial scale considered in this study was possibly too crude to assess habitat heterogeneity from a macroinvertebrate point of view. The increase of species richness following the restoration may be interpreted in terms of increased microhabitat diversity along the stream.

The DCA ordination of sites according to their species composition shows a shift of restored lotic sites along the first ordination axis towards the lentic sites (Fig. 2). The shift was likely due to the establishment of habitats suitable for species that prefer slower current velocity. Sections with lower current velocity were absent in the stream prior to the restoration. Our interpretation indicates that the post-restoration shift in macroinvertebrate assemblage composition towards positive values of the first ordination axis (Fig. 2) was due to the decreased current velocity and/or due to the building of pools in the system. In addition, some lentic species were perhaps detected in lotic sections simply because they were washed out from their preferred habitat. On the other hand, the more pronounced shift along the second axis could have been caused by a change of the macroinvertebrate composition towards communities typical for lower altitudes. The channelization, apart from the simplification of morphological diversity of the streambed, also increased current velocity which reassembled conditions typical for streams of higher elevation and slopes. As such, it could have exhibited a "mountainisation" effect on the stream biota since mainly stonefly species, common for higher altitudes (*Nemoura cinerea*, *Protonemura intricata*, *Brachyptera seticornis*, *Amphinemura standfussi*, and *Leuctra autumnalis*), were associated with the pre-restoration conditions. Contrary to this, the re-meandered stream (with a number of pools) slowed the current, reduced the slope and also created conditions sufficient for species rather typical for lower altitudes (e.g., *Beatis fuccatus*, *Rhithrogena semicolorata*, *Amphinemura borealis*) that were logically missing in the pre-restoration samples.

It could be argued that it was too early to assess the effect of the restoration as only a few years had passed since the intervention and the assemblage might still be undergoing dramatic changes. A more long-term study that would cover several years before and after the intervention might be desirable. However, there are only few long-term surveys of macroinvertebrate responses to interventions similar to the case of the Borová stream. Despite the lack of similar studies, the emerging pattern suggests that the assemblages vary dramatically in the first few years. This is soon followed by a year-to-year decrease of variation in both composition and abundances of constituent species. Muotka et al. (2002) found radical changes in assemblage composition between two sampling occasions in the zero vs. fourth and second vs. sixth year following restoration, but no considerable changes occurred between the third and eighth year. Laasonen at al. (1998), who studied stream macroinvertebrates in the years 0–16 following a restoration, obtained a similar conclusion: species composition changed negligibly after a recovery period of 5 years. Another example could be a stream severely affected by oil spillage, which required 3 years for re-colonization of macroinvertabrates (Eggers 2000).

The examples above allow us to consider the period of three to five years (covered in this study) as sufficient enough to unravel the most prominent trends in species richness.

Considering the rarity/commonness of species, it seems that the post restoration state was not connected with scarcer species than the state prior to the restoration. The restoration intervention considerably changed species composition, but the new colonizers were as common as the former inhabitants of the non-restored stream. This may be interpreted in the following way: The restoration intervention established a lot of new microhabitats, but did not create special habitats suitable for uncommon species such as habitat specialists or more sensitive species.

On the other hand, there is a number of objections that dispute this interpretation. Firstly, the six-grade-scale of rareness may not be sensitive enough to detect a slight shift towards more uncommon species. Secondly, rare species are infrequent in landscape that decreases the probability of immigration. Even though the diversity of macroinvertebrates usually increases markedly after the initial recolonization (Laasonen et al. 1998, Muotka et al. 2002, Lepori et al. 2005), immigration of new species may require much more time (Moerke et al. 2004, Spänhoff et al. 2006). In addition, the chosen groups of species (Ephemeroptera and Plecoptera) may not be ideal candidates for such a test, due to their low dispersal capability. Although suitable habitats could have been created for rare species, they might not have been able to re-colonize them in the given period. More suitable candidates for such a research are Odonata, Heteroptera, or Coleoptera, since their dispersal ability is much better.

Summing this restoration project up, it is possible to say that there was a positive effect in the increase of species richness; however, this has been caused mainly by "ordinary" species that are not rare in the Czech Republic.

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Appendix 1. The list of 205 taxa collected at the Borová and Zrcadlový Potok (Z.P.) streams during the pre--restoration period (July–August 1995) and the post-restoration period (July 2001–October 2003). Species of higher taxa are listed alphabetically. Relative abundances of species (for data from July–August): **** 35–10%, *** 10–2%, ** 2–0.5%, * <0.5%, s singletons; # species collected just during the pre-restoration period; & species collected in the post-restoration period, but not during July–August.

Taxa		Pre-restoration		Post-restoration	
		Borová	Z.P.	Borová	Z.P.
Tricladida					
	Dugesia gonocephala (Dugès, 1830)	**	**	s	*
Hirudinea					
	Erpobdella octoculata (Linnaeus, 1758)	**	0	0	0
	Glossiphonia complanata (Linnaeus, 1758)	*	0	0	0
	Helobdella stagnalis (Linnaeus, 1758)	*	0	0	*
Mollusca					
	Galba truncatula (O.F. Müller, 1774)	*	0	0	0
	Gyraulus sp.	***	*	0	0
	Pisidium sp.	***	***	s	s
	Planorbidae gen. sp. juv.	*	0	0	s
	Radix ampla (W. Hartmann, 1821)	*	0	0	0
	Radix auricularia (Linnaeus, 1758)	**	0	0	0
	Radix peregra (Müller, 1774)	***	0	0	0
	Radix ovata (Draparnaud, 1805)	**	0	0	0
	Radix sp.	***	s	s	*
Crustacea					
	Asellus aquaticus (Linnaeus, 1758)	***	*	0	0
	Gammarus roeseli Gervais, 1835	****	****	****	****
Ephemeroptera					
	Baetis alpinus (Pictet, 1843)	*	0	s	***
	Baetis fuscatus (Linnaeus, 1761)	*	0	0	0
	Baetis muticus (Linnaeus, 1758)	*	**	**	0
	Baetis niger (Linnaeus, 1761)	*	*	***	0
	Baetis rhodani (Pictet, 1843)	***	***	****	****
	Baetis vernus Curtis, 1834	***	**	***	****
	Caenis horaria (Linnaeus, 1758)	*	0	0	0
	Centroptilum luteolum (Müller, 1776)	*	0	***	***
	Cloeon dipterum (Linnaeus 1761)	****	0	0	0
	Ecdyonurus dispar (Curtis, 1834)	**	*	0	**
	Ecdyonurus torrentis Kimmins, 1942	**	**	0	0
	Ecdyonurus venosus (Fabricius, 1775)	*	s	0	0
	Electrogena lateralis (Curtis, 1834)	*	**	**	0
	Epeorus assimilis Eaton, 1865	*	0	0	0
	Ephemera danica Müller, 1764	**	0	**	0
&	*Ephemerella mucronata* (Bengtsson, 1909)	0	0	0	0
	Habroleptoides confusa Sartori et Jacob, 1986	*	0	0	0
	Habrophlebia lauta Eaton 1884	**	*	0	0
&	*Leptophlebia marginata* (Linnaeus, 1767)	0	0	0	0

Appendix 1. Continued.

Taxa		Pre-restoration		Post-restoration	
		Borová	Z.P.	Borová	Z.P.
&	*Leptophlebia vespertina* (Linnaeus, 1758)	0	0	0	0
	Paraleptophlebia submarginata (Stephens, 1835)	*	*	0	0
	Rhithrogena semicolorata (Curtis, 1834)	*	*	0	0
	Seratella ignita (Poda, 1761)	***	0	*	*
	Siphlonurus aestivalis (Eaton, 1903)	0	*	*	0
Odonata					
	Aeshna cyanea (Müller, 1764)	**	0	0	0
&	*Aeshna grandis* (Linnaeus, 1758)	0	0	0	0
	Aeshna juncea (Linnaeus, 1758)	*	0	0	0
	Anax imperator Leach, 1815	*	0	0	0
	Calopteryx splendens (Harris, 1782)	s	0	0	0
	Calopteryx virgo (Linnaeus, 1758)	*	0	0	0
	Coenagrion puella (Linnaeus, 1758)	*	0	0	0
	Cordulegaster boltoni (Donovan, 1807)	*	0	0	0
	Ischnura elegans (Van der Linden, 1820)	**	0	0	0
	Lestes sponsa (Hansemann, 1823)	*	0	0	0
	Lestes viridis (Van der Linden, 1825)	**	0	0	0
	Libellula depressa Linnaeus, 1758	*	0	0	0
	Platycnemis pennipes (Pallas, 1771)	*	0	0	0
	Pyrrhosoma nymphula (Sulzer, 1776)	***	0	0	0
&	*Sympetrum flaveolum* (Linnaeus, 1785)	0	0	0	0
Plecoptera					
	Amphinemura borealis (Morton, 1894)	*	**	0	0
#	*Amphinemura standfussi* (Ris, 1902)	0	0	**	0
&	*Brachyptera seticornis* (Klapálek, 1902)	0	0	**	*
&	*Isoperla oxylepis* (Despax, 1936)	0	0	0	0
&	*Isoperla rivulorum* (Pictet, 1841)	0	0	0	0
	Isoperla sp.	*	*	0	0
	Leuctra albida Kempny, 1899	***	***	0	0
	Leuctra aurita Navás, 1919	*	0	0	0
	Leuctra autumnalis Aubert, 1948	0	*	****	s
	Leuctra braueri Kempny, 1898	*	**	0	0
	Leuctra digitata Kempny, 1899	*	0	0	0
&	*Leuctra hippopus* Kempny, 1899	0	0	0	0
	Leuctra nigra (Olivier, 1811)	0	*	0	0
&	*Leuctra prima* Kempny, 1899	0	0	0	0
	Nemoura sp.	*	0	0	0
&	*Nemoura cambrica* Stephens, 1836	0	0	0	0
	Nemoura cinerea (Retzius, 1783)	*	0	*	***
	Nemoura flexuosa Aubert, 1949	*	0	**	0
&	*Nemoura marginata* Pictet, 1835	0	0	0	**

Appendix 1. Continued.

	Taxa	Pre-restoration		Post-restoration	
		Borová	Z.P.	Borová	Z.P.
&	*Nemoura sciurus* Aubert, 1949	0	0	0	0
	Nemurella pictetii Klapálek, 1900	0	**	0	0
	Perla burmeisteriana Claassen, 1936	s	0	0	0
	Protonemura auberti Illies, 1954	*	**	0	0
	Protonemura hrabei Rauser 1956	*	0	0	0
&	*Protonemura intricata* (Ris, 1902)	0	0	*	**
	Protonemura lateralis (Pictet, 1836)	*	*	0	0
&	*Protonemura meyeri* (Pictet, 1841)	0	0	0	0
	Protonemura nitida (Pictet, 1835)	**	****	**	***
&	*Protonemura praecox* (Morton, 1894)	0	0	0	0
&	*Siphonoperla torrentium* (Pictet, 1841)	0	0	0	0
Heteroptera					
	Aquarius najas (De Geer, 1773)	*	0	0	0
	Corixa punctata (Illiger, 1807)	*	0	0	0
	Gerris gibbifer Schummel, 1832	*	0	0	0
	Gerris lacustris (Linnaeus, 1758)	**	0	0	0
	Hesperocorixa linnaei (Fieber, 1848)	*	0	0	0
	Hesperocorixa sahlbergi (Fieber, 1848)	*	0	0	0
	Ilyocoris cimicoides (Linnaeus, 1758)	*	0	0	0
	Nepa cinerea cinerea Linnaeus, 1758	**	0	s	0
	Notonecta glauca glauca Linnaeus, 1758	**	0	0	0
	Paracorixa concinna (Fieber, 1848)	*	0	0	0
	Sigara distincta (Fieber, 1848)	*	0	0	0
&	*Sigara dorsalis* (Leach, 1817)	0	0	0	0
	Sigara falleni (Fieber, 1848)	**	0	0	0
	Sigara fossarum (Leach, 1817)	*	0	0	0
&	*Sigara lateralis* (Leach, 1817)	0	0	0	0
	Sigara nigrolineata nigrolineata (Fieber, 1848)	*	0	0	0
	Sigara semistriata (Fieber, 1848)	*	0	0	0
	Sigara striata (Linnaeus, 1758),	*	0	0	0
	Velia caprai Tamanini, 1947	*	***	s	0
Megaloptera					
	Sialis lutaria (Linnaeus, 1758)	**	0	0	0
	Sialis fuliginosa Pictet, 1836	*	*	**	0
Trichoptera					
	Allogamus uncatus (Brauer, 1857)	*	s	0	0
&	*Anabolia nervosa* (Curtis, 1834)	0	0	0	0
	Drusus annulatus (Stephens, 1837)	s	0	0	0
#	*Drusus biguttatus* (Pictet, 1834)	0	0	*	0
	Drusus trifidus McLachlan, 1868	*	0	0	0
	Ecclisopteryx dalecarlica Kolenati, 1848	*	0	0	0

Appendix 1. Continued.

Taxa		Pre-restoration		Post-restoration	
		Borová	Z.P.	Borová	Z.P.
	Ecclisopteryx madida (McLachlan, 1867)	s	0	0	0
	Glyphotaelius pellucidus (Retzius, 1783)	s	0	0	0
&	Grammotaulius nigropunctatus (Retzius, 1783)	0	0	0	0
	Halesus digitatus (Schrank, 1781)	*	**	0	0
	Halesus rubricollis (Pictet, 1834)	*	0	0	0
	Halesus sp.	*	*	*	0
	Hydropsyche angustipennis (Curtis, 1834)	*	*	0	s
	Hydropsyche bulgaromanorum Malicky, 1977	*	**	0	0
	Hydropsyche pellucidula (Curtis, 1834)	**	**	s	s
	Hydropsyche sp.	***	***	*	0
#	*Limnephilus* sp.	0	0	*	0
	Limnephilus centralis Curtis, 1834	s	0	0	0
	Limnephilus lunatus Curtis, 1834	*	s	0	0
	Limnephilus stigma Curtis, 1834	*	0	0	0
&	*Micrasema* sp.	0	0	0	0
#	*Notidobia ciliaris* (Linnaeus, 1761)	0	0	*	0
	Oligotricha striata (Linnaeus, 1758)	s	0	0	0
	Philopotamus ludificatus McLachlan, 1878	s	0	0	0
	Plectrocnemia conspersa (Curtis, 1834)	*	***	0	**
	Potamophylax cingulatus (Stephens 1837)	*	0	0	0
	Potamophylax latipennis (Curtis 1834)	**	***	*	**
	Potamophylax sp.	*	*	**	0
	Rhyacophila dorsalis (Curtis, 1834)	*	**	0	0
#	*Rhyacophila evoluta* McLachlan, 1879	0	0	*	s
	Rhyacophila fasciata Hagen, 1859	**	**	**	**
&	*Rhyacophila glareosa* McLachlan, 1867	0	0	0	0
	Rhyacophila obliterata McLachlan, 1863	*	**	**	0
	Rhyacophila sp.	*	***	**	0
	Sericostoma sp.	**	***	**	0
	Silo pallipes (Fabricius, 1781)	s	0	s	0
Coleoptera					
	Agabus bipustulatus (Linnaeus, 1767)	*	0	0	0
	Ilybius chalconatus (Panzer, 1797)	s	0	0	0
	Agabus guttatus (Paykull, 1798)	*	**	0	0
	Agabus paludosus (Fabricius, 1801)	*	0	0	0
	Agabus sp.	*	0	0	0
	Agabus sturmii (Gyllenhal, 1808)	*	0	0	0
	Anacaena globulus (Paykull, 1798)	*	*	0	0
	Anacaena limbata (Fabricius, 1792)	*	0	0	0
	Anacaena lutescens (Stephens, 1929)	*	0	0	0
	Anacaena sp.	*	0	0	0

Appendix 1. Continued.

Taxa		Pre-restoration		Post-restoration	
		Borová	Z.P.	Borová	Z.P.
#	*Dryops* sp.	0	0	0	**
&	*Dryops ernesti* (Gozis, 1886)	0	0	0	0
	Dytiscus sp.	*	0	*	s
	Elmis aenea (P.J.W. Müller, 1806)	*	0	0	0
	Elmis maugetii Latreille, 1798	*	**	0	0
	Elmis sp.	*	0	0	0
	Elodes sp.	*	*	*	0
&	*Enochrus* sp.	0	0	0	0
	Gyrinus natator (Linnaeus, 1758)	0	*	0	0
	Gyrinus sp.	*	0	0	0
	Gyrinus substriatus Stephens, 1829	*	*	0	0
	Haliplus fulvus (Fabricius, 1801)	**	0	0	0
	Haliplus heydeni Wehncke, 1875	**	0	0	0
	Haliplus lineatocollis (Marsham, 1802)	**	0	0	0
	Haliplus sp.	*	0	0	0
	Helophorus aquaticus (Linnaeus, 1758)	*	0	0	0
&	*Helophorus brevipalpis* Bedel, 1881	0	0	0	0
	Helophorus flavipes Fabricius, 1792	s	0	0	0
	Helophorus sp.	*	0	0	0
	Hydaticus sp.	s	0	0	0
	Hydraena dentipes Germar, 1842	s	0	0	0
	Hydraena excisa Kiesenwetter, 1849	0	*	0	0
	Hydraena gracilis Germar, 1824	*	**	0	0
	Hydraena riparia Kugelann, 1794	*	0	0	0
	Hydrobius fuscipes (Linnaeus, 1758)	s	0	0	0
	Hydroglyphus geminus (Fabricius, 1792)	s	0	0	0
#	Hydrophilidae sp.	0	0	0	s
	Hydroporus discretus Fairmaire et Brisout, 1859	0	s	0	0
	Hydroporus palustris (Linnaeus, 1761)	s	0	0	0
&	*Hydroporus planus* (Fabricius, 1781)	0	0	0	0
&	*Hydroporus* sp.	0	0	0	0
	Hyphydrus ovatus (Linnaeus, 1761)	*	0	0	0
	Ilybius fenestratus (Fabricius, 1781)	*	0	0	0
	Ilybius fuliginosus (Fabricius, 1792)	**	0	0	0
	Ilybius sp	*	0	0	0
	Laccobius bipunctatus (Fabricius, 1775)	*	0	0	0
	Laccobius minutus (Linnaeus, 1758)	*	0	0	0
	Laccobius sp.	*	0	0	0
	Laccobius striatulus (Fabricius, 1801)	*	0	0	0
	Laccophilus minutus (Linnaeus, 1758)	*	0	0	0
	Laccophilus sp.	*	0	0	0

Appendix 1. Continued.

Taxa		Pre-restoration		Post-restoration	
		Borová	Z.P.	Borová	Z.P.
	Limnebius truncatellus (Thunberg, 1794)	*	*	0	0
	Limnius perrisi (Dufour, 1843)	*	**	0	0
	Limnius volckmari (Panzer, 1793)	*	0	0	0
	Nebrioporus sp.	s	0	0	0
	Orectochilus villosus (O.F. Müller, 1776)	*	0	0	0
	Oreodytes sanmarki (C.R. Sahlberg, 1826)	*	0	0	0
	Oulimnius tuberculatus (P.J.W. Müller, 1806)	s	0	0	0
	Platambus maculatus (Linnaeus, 1758)	*	**	0	0
#	*Rhantus* sp.	0	0	*	0
	Rhantus exsoletus (Forster, 1771)	s	0	0	0
&	*Rhantus frontalis* (Marsham, 1802)	0	0	0	0
&	*Rhantus suturalis* (MacLeay, 1825)	0	0	0	0
	Scarodytes halensis (Fabricius, 1787)	*	0	0	0
	Stictotarsus doudecimpustulatus (Fabricius, 1792)	s	0	0	0

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