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Benthic macroinvertebrates as indicators of ecological integrity of lotic ecosystems in the Šumava National Park, Czech Republic

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Abstract

Macroinvertebrate communities were monitored at 15 sampling sites of streams in the Vydra and Křemelná watersheds in the Šumava National Park in 2000–2004. A total of 87 macrozoobenthos taxa were found. Community structure based on species composition, biotic indices and functional feeding groups was determined. The relationship between the communities and their abiotic environmental factors was described using statistical methods. Species diversity of benthic communities is very high in this region, but differences in diversity were found, depending on the physical, chemical and geographical parameters of the biotopes studied. Some acidified streams had low species numbers and a marked dominant species dynamic, while communities in other streams with minimum anthropogenic influence were more diverse and stable. Changes in community composition were found, especially in the headwaters of the streams. Differences and yearly variations in the occurrence of functional feeding groups were also observed, and were more pronounced in acidified waters.

Key words: mountain streams, acidification, benthic macroinvertebrates, deforestation of watershed, statistical methods

INTRODUCTION

The influence of deforestation and anthropogenic acidification on aquatic ecosystems is an often-studied phenomenon with many historical causes and links. In the Bohemian Forest (=Šumava Mts.) region, the principal causes of deforestation have been repeated mass outbreaks of the bark beetle in non-indigenous spruce monocultures as well as inappropriate forest management practices in the past (HLADILIN 1996, ZATLOUKAL 1998). The impacts of anthropogenic acidification due to air pollution became pronounced in the 1970s and 1980s (BORMANN & LIKENS 1979). Recent trends in lake water chemistry (NO_3^-, SO_4^{2-}) of the Bohemian Forest reflect those in atmospheric deposition (KOPÁČEK et al. 1999). Since 1989, water chemistry in the Bohemian Forest lakes has been recovering from acidification (KOPÁČEK & HEJZLAR 1998). Recently, pH values have been increasing back towards their original values, but the concentrations of aluminium and other toxic metals remain elevated. Ion concentrations in streams remain substantially higher compared with precipitation and throughfall (KOPÁČEK et al. 2003). Low pH values combined with low temperatures and elevated aluminium concentrations are a limiting factor for stream biota development in the area studied (Růžičková & Kotrbová 2000). During the spring thaw, aluminium concentrations in the Vydra watershed reach values of up to 700 μg.l^{-1}, and pH values decrease below 4.5. The structure of aquatic invertebrate communities changes with the decline of pH values. Shifts in relative abundance from invertebrate grazers to shredders and changes in fish communities have been observed in acidified waters (Hermann et al. 1993). Biodiversity also depends on the stability of pH values. Chronically acidified waters have been shown to have larger numbers of macrozoobenthos taxa compared with episodically acidified waters, which usually have lower diversity values, often with one dominant taxon only (Madarish & Kimmel 2000).

Methods

Macrozoobenthos was sampled three times a year, to coincide with spring, summer and autumn periods of the stream biota. In the years 2000–2002, samples were taken in April, June and October. In 2003 only April and October samples were taken, and the last sampling was in April 2004. A total of ten stream localities were regularly monitored in the Otava River watershed, six of these in the Vydra basin (Modravský-Březník – MoB, Modravský-Modrava – MoM, Roklanský-Modrava – RoM, Hamerský – Ha, Hrádecký – Hr, and Vydra – Vy), the other four in the Křemelná basin (Křemelná – Kr, Prášilský – Pr, Jezerní – Je, and Slatinný – Sl). From 2002 to 2003, five new sampling sites were monitored in the headwater region of the Vydra stream (Roklanský-hájenka – RoH, Roklanský-pod Novohuťským – RoN, Novohuťský – No, Březnický – Br, and Luzenský – Lu). These sites were chosen to investigate the impact of deforestation on the chemistry of the streams and thus on their biota. For detailed descriptions of the sampling localities see Růžičková et al. (2004b), for the map of the watershed area see Kodrová & Růžičková (2005). Macrozoobenthos was sampled by a semiquantitative kicking method. The surface layer of the stream bottom was whirled up for the duration of 10 minutes on the 10 m long stretch and the turbulent material was caught by the net of the sampler.

The Hobent programme (Kokeš & Vojtíšková 1999) was used to calculate Margalef's index of species richness, Simpson's dominance index, the Shannon-Wiener diversity index, equitability (Pielou) and community saprobity. Using cluster analysis, sampling sites were divided into several groups based on mutual similarity. By the agglomerative hierarchical clustering the objects (localities) were described by the vector of certain number of characteristics. The following factors were used – altitude, stream width, depth of stream channel, substrate roughness (after Hynes 1970), distance from headwater, temperature, pH, conductivity, diversity, equitability and community dominance. The hydrological and geomorphologic characteristics of localities are summarized in Table 1. The physico-chemical characteristics were published in Růžičková et al. (2004a). After the method of the closest neighbor, when the distance between two objects is the minimum of the distances between all the objects, the system of subsets was created. By the "distance" is meant the Euclidian distance between two objects (Lukasová & Šarmanová 1985). Ordination gradient analysis was carried out using the Canoco programme. The method of direct linear ordination (RDA) was used. This incorporates both species data and data concerning those environmental variables which had been proven to be statistically significant for species distribution. The level of $p = 0.05$ was chosen for the randomisation test, which serves to indicate statistical significance (Lepš & Šmilauer 2000). Rare species (i.e. those comprising a total of less than 5 individuals in all samples) were excluded, as well as sites sampled irregularly or only in some seasons. There were five RDA analyses carried out: the aim of the first one was to describe the relations between all the macroinvertebrate species and the physico-chemical and hydrological

Table 1. Hydrological and geomorphological characteristics of the localities.

locality	altitude (m)	distance from headwater (km)	stream width (m)	depth of stream channel (m)	substrate roughness
MoB	1135	3.3	2.5	0.4	4.3
MoM	990	10.6	8	0.3	6.0
RoM	980	14.5	6	0.4	5.8
Ha	900	9.1	3	0.3	6.4
Hr	810	5.0	2	0.3	1.6
Vyd	650	21.2	10	1.0	6.4
Kře	810	14.9	6	0.4	2.8
Pr	810	11.4	5	0.3	3.6
Je	880	8.1	3	0.3	2.0
Sl	850	7.5	5	0.5	2.7
RoH	1170	2.3	1.5	0.3	3.7
RoN	1060	6.0	3	1.0	5.3
No	1070	3.4	2	0.4	2.4
Bř	1150	2.6	1	0.3	3.5
Lu	1158	3.1	1.5	0.3	0.9

characteristics of the area. The next three analyses tried to explain the same relations for the individual classes of insect, which were occurring most frequently – Ephemeroptera, Plecoptera, and Trichoptera. The last analysis describes the seasonal variability of species; therefore the years and the sampling seasons instead of environmental variables were used. The abbreviations of the species are listed in Table 2.

RESULTS AND DISCUSSION

A total of 14 553 individuals and 87 macrozoobenthos lower taxa were found, pertaining to six higher taxa (Turbellaria, Clitellata, Gastropoda, Arachnida, Crustacea, and Insecta). With 82 taxa and 94% of the total macroinvertebrate numbers, aquatic insects were the dominant group. In the watershed as a whole, Plecoptera were most common, comprising 53% of all the insect specimens found. Ephemeroptera were next, with 20%, followed by Trichoptera (13%), Diptera (9%), and Coleoptera (3%). *Dinocras cephalotes*, *Perla burmeisteriana*, *Ecclisopteryx dalecarlica*, *Siphonoperla neglecta*, *Ancylus fluviatilis*, and *Helodes* sp. were found in addition to the taxa listed by Růžičková et al. (2004b). *Siphonoperla torrentium*, a species which has been found in the past in the area studied, was not observed. All the species found in the sampling area within the years 2000–2004 are listed in Table 2.

Table 2. Species found in the sampling area and the abbreviations used in RDA analysis.

Ephemeroptera	
Ameletus inopinatus	Ame ino
Baetis alpinus	Bae alp
Baetis rhodani	Bae rho
Baetis vernus	Bae ver
Baetis sp.	Bae sp.
Ecdyonurus austriacus	Ecd aus
Ecdyonurus subalpinus	Ecd sba
Ecdyonurus submontanus	Ecd sbm
Ecdyonurus sp.	Ecd sp.
Epeorus sylvicola	Epe syl
Rhithrogena loyolaea	Rhi loy
Rhithrogena semicolorata	Rhi sem
Rhithrogena sp.	Rhi sp.
Ephemerella mucronata	Eph muc
Ephemerella ignita	Eph ign
Plecoptera	
Brachyptera seticornis	Bra set
Taeniopteryx hubaulti	Tae hub
Amphinemura sulcicollis	Amp sul
Nemoura flexuosa	Nem fle
Nemoura sp.	Nem sp.
Nemurella picteti	Nem pic
Protonemura sp.	Pro sp.
Leuctra nigra	Leu nig
Leuctra sp.	Leu sp.
Perlodes microcephalus	Per mic
Diura bicaudata	Diu bic
Isoperla oxylepis	Iso oxy
Isoperla rivulorum	Iso riv
Isoperla sp.	Iso sp.
Dinocras cephalotes	Din cep
Perla burmeisteriana	Per bur
Perla marginata	Per mar
Perla sp.	Per sp.
Chloroperla tripunctata	Chl tri
Chloroperla sp.	Chl sp.
Siphonoperla montana	Sip mon
Siphonoperla neglecta	Sip neg
Siphonoperla torrentinum	Sip tor
Coleoptera	
Oreodytes sanmarki	Ore san
Helodes sp.	Hel sp.
Elmis sp.	Elm sp.
Limnius sp.	Lim sp.

Trichoptera	
Rhyacophila dorsalis	Rhy dor
Rhyacophila obliterata	Rhy obl
Rhyacophila polonica	Rhy pol
Rhyacophila praemorsa	Rhy pra
Rhyacophila tristis	Rhy tri
Rhyacophila sp.	Rhy sp.
Hydropsyche pellucidula	Hyd pel
Plectrocnemia conspersa	Ple con
Plectrocnemia sp.	Ple sp.
Psychomyia pusilla	Psy pus
Brachycentrus montanus	Bra mon
Apatania sp.	Apa sp.
Anomalopterygella chauviniana	Ano cha
Drusus annulatus	Dru ann
Drusus discolor	Dru dis
Drusus sp.	Dru sp.
Ecclisopteryx dalecarlica	Ecc dal
Ecclisopteryx guttulata	Ecc gut
Ecclisopteryx madida	Ecc mad
Ecclisopteryx sp.	Ecc sp.
Chaetopterygopsis maclachlani	Cha mac
Chaetopteryx villosa	Cha vil
Halesus digitatus	Hal dig
Potamophylax cingulatus	Pot cin
Potamophylax latipennis	Pot lat
Potamophylax sp.	Pot sp.
Silo pallipes	Sil pal
Sericostoma sp.	Ser sp.
Beraeamyia hrabei	Ber hra
Odontocerum albicorne	Odo alb
Diptera	
Liponeura sp.	Lip sp.
Tipula saginata	Tip sag
Pedicia rivosa	Ped riv
Dicranota sp.	Dic sp.
Eloeophila submarmorata	Elo sub
Simuliidae	Sim
Chironomidae	Chiro
Atherix ibis	Ath ibi
Others	
Crenobia alpina	Cre alp
Ancylus fluviatilis	Anc flu
Oligochaeta	Oli
Hydracarina	Hyd
Gammarus fossarum	Gam fos
Gerris sp.	Ger sp.

The ecological indices are summarized in Figs. 1–4. The Margalef's index of species richness achieved the highest median values at the Kr, Ha, Hr and Sl sampling sites and except several distant values the species richness was well-balanced. The index values at the Vyd, Pr, Je, and Lu sites were relatively high as well, but more fluctuating. The lowest index median values were found out at all profiles of the Modravský and Roklanský streams and at No and Br sampling sites. The Simpson's dominance index median values at the Vyd, Kr, Ha, Hr, and Sl sampling sites had a low scatter and were relatively very low, only in Hrádec-

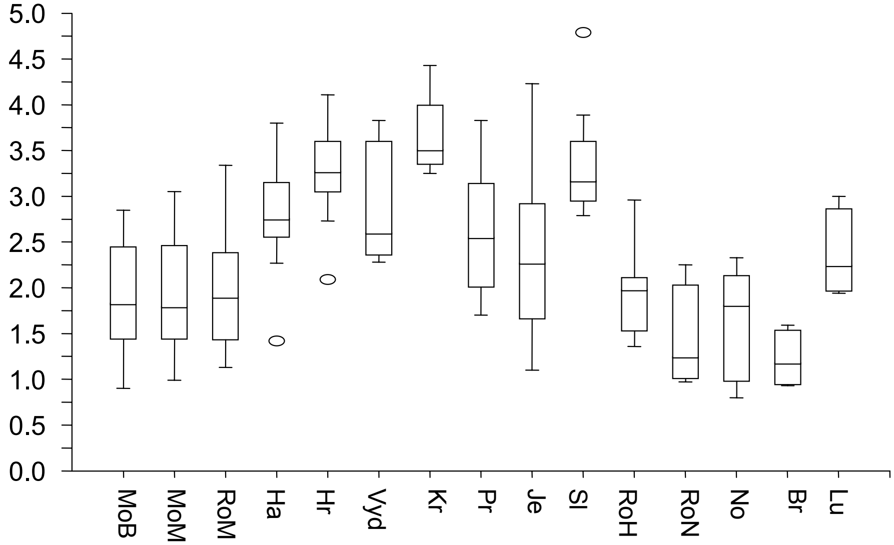

Fig. 1. Margalef's index of species richness. The interior line in the box plot rectangles represents the median value.

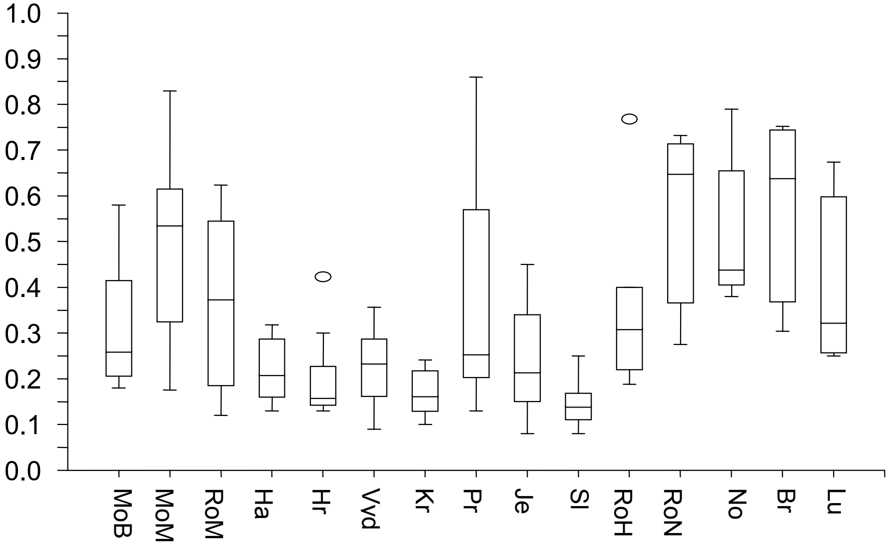

Fig. 2. Simpson's dominance index. The interior line in the box plot rectangles represents the median value.

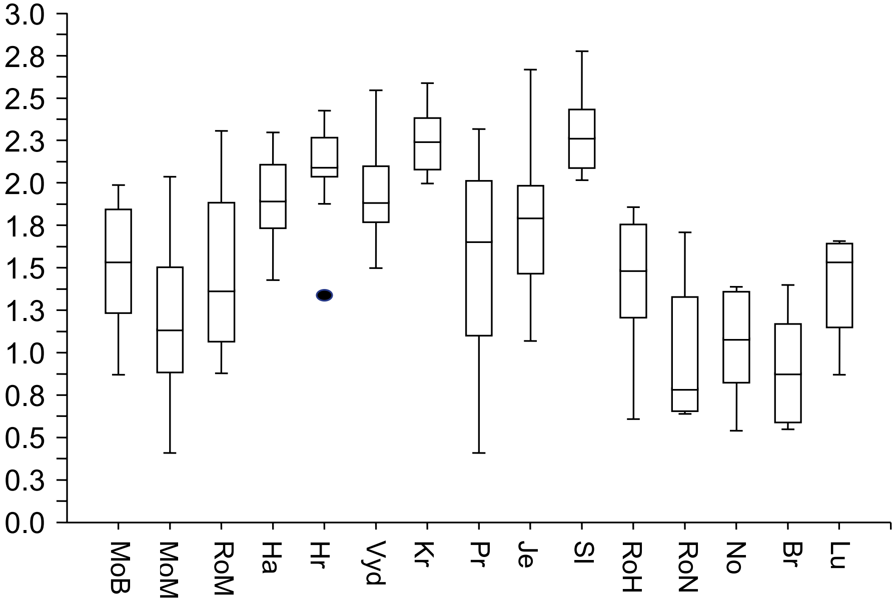

Fig. 3. Shannon-Wiener diversity index. The interior line in the box plot rectangles represents the median value.

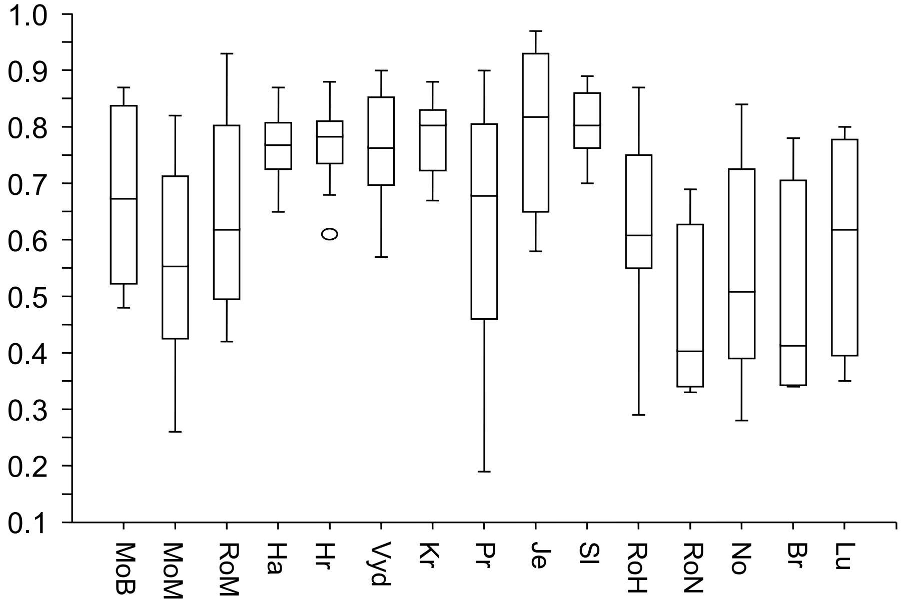

Fig. 4. Equitability (Pielou). The interior line in the box plot rectangles represents the median value.

ký stream one distant value 0.42 was observed. In other streams there were considerably high differences between the samplings. Among the values of the equitability index there was the lowest standard deviation in the Ha, Hr, Sl, Vyd, and Kr sampling sites, in other streams the equitability considerably varied. In the case of Shannon-Wiener diversity index the highest and the least fluctuating values were observed at the Vyd, Kr, Ha, Hr, and Sl sampling sites.

One result of the ecological evaluation is the percentage of individual functional feeding groups in the samples taken (Fig. 5). Ecosystem evaluation based on a faunistic structure comparison is described in the relevant literature (Wright et al. 1984, Vojtíšková et al. 2000,

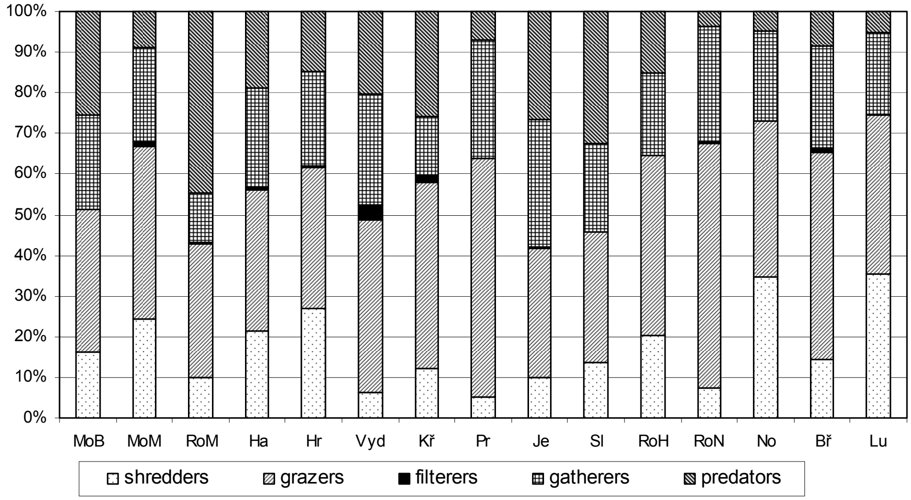

Fig. 5. Percentage of functional feeding groups at the individual sampling sites.

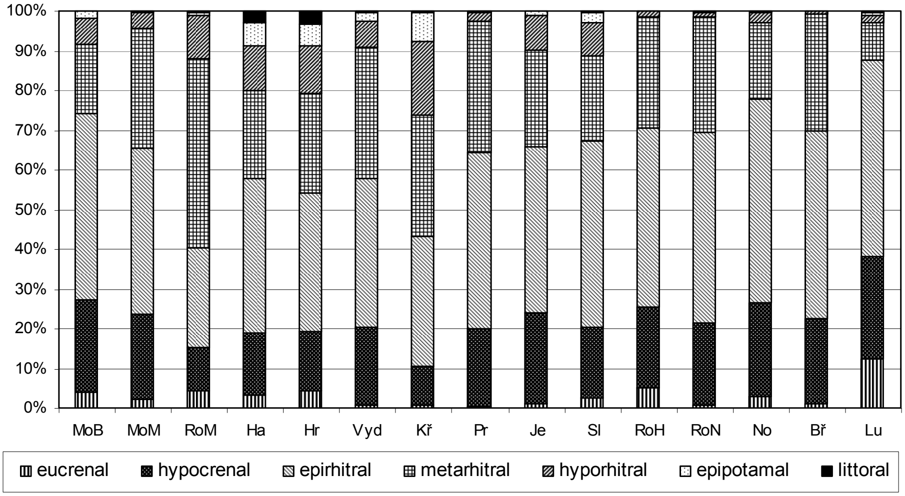

Fig. 6. Percentage of biocenotic groups at the individual sampling sites.

Zahrádková et al. 2000). Shredders as well as grazers, filterers, gatherers and predators were found in most of the samples. This is in agreement with the usual distribution described in the literature (Allen 1995, Cummins 1973, 1974, Cushing 1995, Statzer & Higler 1985, Vannote et al. 1980). Another result is the classification of individual biocenotic regions at each sampling site. On the basis of probability calculations in dependence on the occurrence of individual taxa and the environmental characteristics, each locality is classified as a complex of relevant biocenotic groups, expressed as the percentage (Fig. 6).

Localities were divided into three basic clusters, which are apparent from the dendrogram in Fig. 7. The first cluster is formed by a group of six streams at high altitude in the Vydra watershed (MoB, RoH, RoN, No, Bř, and Lu). The second cluster includes five profiles, two of which are situated in the Křemelná watershed (Pr and Je) and three of which to the Vydra watershed (MoM, RoM, and Ha). The last cluster (Kr, Sl, and Hr) might also include the Vydra profile, but this is debatable due to the rather high dissimilarity index.

The aim of the ordination gradient analysis was to describe the relationship of individual species found in the studied area to the physico-chemical gradients and hydrological factors of the environment. This results in a diagram of variability percentages explained by individual environmental variables. This process ("forward selection") excluded the environmental variables which were not significant for the analysis (Lepš & Šmilauer 2000). The following variables were rejected as not significant – conductivity, substrate, depth, width and slope**.** The likely reason why these variables were not found to be relevant for the analysis is their correlation with other variables (depth and width are correlated with distance from the headwater, conductivity is correlated with pH). Another reason could be that the range of values of some of the measured variables was relatively small (conductivity, flow gradient), or was only estimated (percentage of different substrate types in the stream bottom). The variables altitude, pH, temperature, COD and distance from headwaters were found to be statistically significant. These selected variables explained 26% of the total variability of the species composition of the localities studied. Species for which the environmental gradients explained 1% or less of the variability were then deleted from the RDA analysis graph. Fig. 8 indicates that the pH and altitude line is the most important gradient. It divides the species into two halves along a vertical axis, which approximately indicates their distribution in the area studied. Species which prefer higher altitudes and lower pH values predominate. Gradients of growing temperature, pH and distance from headwaters are located in the first quadrant, represented mainly by mayflies of the families Baetidae, Ephemerellidae, and Heptageniidae (*Baetis alpinus*, *Baetis rhodani*, *Ephemerella ignita*, *Epeorus sylvicola, Rhitrogena semicolorata*). The fourth quadrant, on the other hand, where the acid tolerant species and species from higher altitudes are expected, includes the gradient of growing chemical oxygen demand as well. Plecoptera (*Brachyptera seticornis*, *Diura bicaudata*, *Protonemura* sp., *Nemoura* sp., and *Nemurella picteti*) is the most numerous group in this quadrant. It also includes the mayfly *Ameletus inopinatus* and some caddisflies of the Limnephilidae family (*Drusus annulatus*, *Apatania* sp., *Chaetopteryx villosa*, and *Potamophylax cingulatus*). Most of the Trichoptera (*Anomalopterygella chauviniana*, *Drusus discolor*, *Ecclisopteryx guttulata*, *Chaetopterygopsis maclachlani*, *Odontocerum albicorne*, and *Brachycentrus montanus*) as well as several of the stoneflies (*Taeniopteryx hubaulti*, *Chloroperla* sp., *Siphonoperla neglecta*) and other species (*Crenobia alpina*, *Atherix ibis*) are in the second quadrant, which has no environmental factor gradient. Their occurrence is thus probably caused by several factors with none clearly predominating, or by some other untested factor.

Multivariate analysis is very often used to evaluate changes in aquatic biotopes, as it is a universal method applicable to different groups of organisms and offers many possibilities

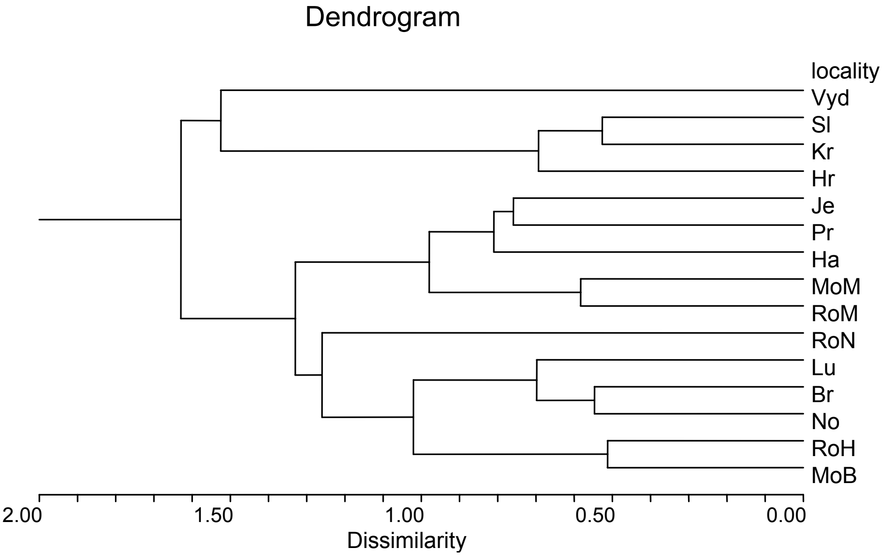

Fig. 7. Dividing the sampling sites according to the mutual similarity on the basis of the cluster analysis.

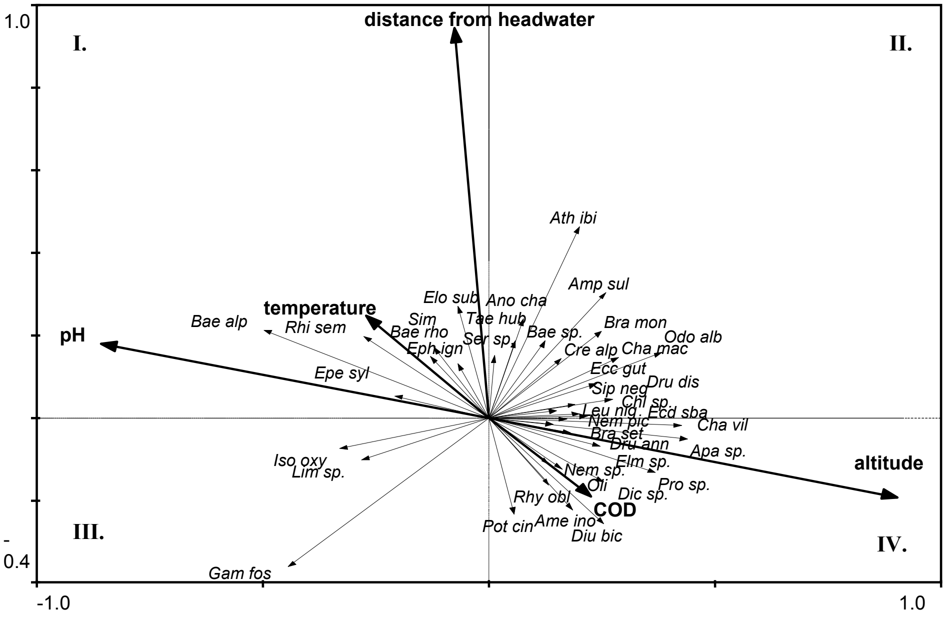

Fig. 8. Direct linear ordination (RDA) of species data and selected environmental variables.

for comparing the impact of abiotic changes on benthic organisms (Soldán et al. 1998). Substrate roughness, often considered as an important environmental factor (Allen 1995, Helešic 2000) did not classify as a significant factor in our case. This may have been caused by the method of coding the variable used (phi scale); however this is a recommended and often used method in such cases (Soldán et al. 1998, Kokeš & Vojtíšková 1999). Flow, one of the most significant environmental variables, was not measured, although especially in years of marked increase it can have a crucial influence on species distribution. However, the ordination species analysis and the time factor appear to indicate that species composition did not vary significantly, e.g. in the year 2002, when flooding occurred, in comparison with other years. The ordination analysis showed a correlation between *Ameletus inopinatus* and rising altitude, which is typical for this mountain species (Landa et al. 1998). A significant positive correlation of the species *Ephemerella ignita* and *Baetis rhodani* with temperature was also confirmed, as were a positive correlation of the Heptageniidae family with the pH gradient and a negative correlation with altitude. This family is very sensitive to acidification (Soldán et al. 1996, 1999, Růžičková & Kotrbová 2000). The most significant gradients for the Plecoptera communities were altitude and pH. *Isoperla oxylepis* and *Isoperla* sp. were typical taxa preferring higher pH and lower altitude. Correlation of the species *Taeniopteryx hubaulti* and *Perlodes microcephalus* with these gradients was also found. The genus *Capnia*, sporadically found in acidified biotopes in the past (Růžičková 1998) has not been recently observed.

Sampling sites at the Vydra headwaters

The first cluster includes six sampling sites – MoB, RoH, RoN, No, Bř, and Lu (Fig. 9). The site RoN showed the greatest dissimilarity index (1.33). Conversely, the localities Bř and No, and RoH and MoB were very similar (dissimilarity at point 0.55 and 0.51).

The localities in this cluster are situated at altitudes of over 1100 m in areas affected by forest decay and acidification. They have the lowest average pH values and the lowest pH spring minima of all the localities studied. The sum of strong acid anions is always greater than the sum of base cations (Růžičková et al. 2000, 2004a, b). The localities are unbalanced as far as biota is concerned. Most samples had large numbers of macroinvertebrates and relatively high dominance (0.18–0.77) but low species richness (0.80–3.00), diversity (0.61–1.91) and equitability (0.28–0.87) – see Figs. 1–3.

Protonemura sp., *Brachyptera seticornis, Leuctra* sp., *Ameletus inopinatus,* and *Drusus annulatus* were the dominant taxa. Plecoptera were predominant (forming quantitatively 48 to 94% of aquatic insects) with the above mentioned three taxa present almost exclusively. The acido-tolerant species *Diura bicaudata* was also present. Sporadically, *Chloroperla tripunctata* (MoB), *Siphonoperla montana* (RoN), *Amphinemura* sp., *Isoperla oxylepis*, and *Nemurella picteti* (Lu) were found. *Amphinemura* and *Leuctra* sp. are most resistant to acidification (Madarish & Kimmel 2000). Representatives of the Ephemeroptera order were much less numerous; their proportion was usually under 8%, with the exception of the site MoB, where it rose to 22% in 2000 and to 39% in 2001. Both years were characterised by slightly higher pH values than usual. *Ameletus inopinatus* was the dominant species, while *Baetis alpinus* and *Baetis rhodani* were much less numerous than at other localities studied. *Rhitrogena loyolaea* and *Rhitrogena semicolorata* appeared sporadically at sampling sites MoB, RoN, and No. The occurrence of the representatives of Trichoptera and Diptera orders remained relatively stable in the period studied. The Trichoptera community is more diverse in these localities compared with other orders. Some representatives of the families Rhyacophilidae and Limnephilidae were observed, for example *Drusus annulatus* is a very common species in the Luzenský and Modravský streams. The Diptera included genus *Dicranota* and

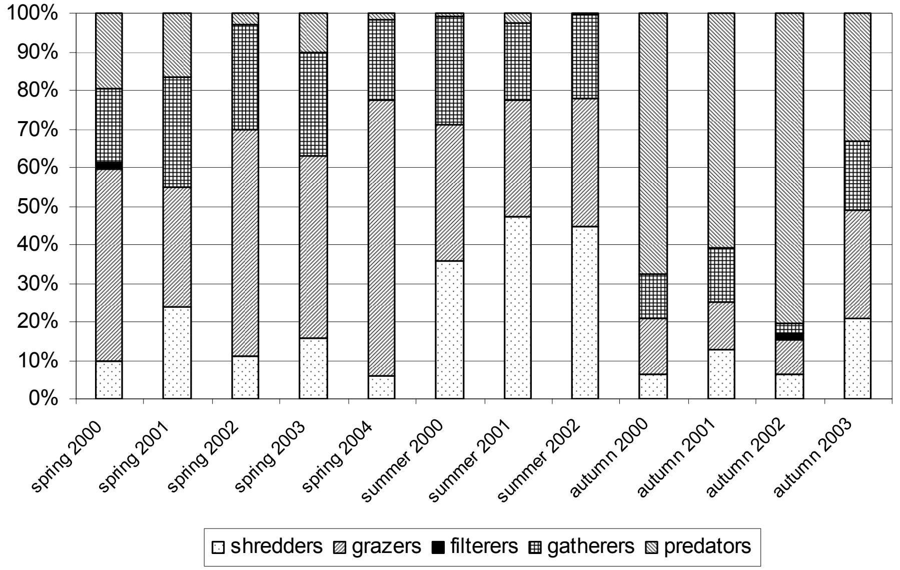

Fig. 9. Percentage of functional feeding groups in spring, summer and autumn periods (MoB sampling site).

families Chironomidae and Simuliidae. No species of the order Coleoptera or of any other group of macroinvertebrates were found, except for Oligochaeta.

Considerable seasonal changes in the relative presentation of functional feeding groups were observed at sites MoB and RoH, which were sampled regularly (Fig. 9). These changes are connected with the distribution of food resources during the course of the year in these oligotrophic localities. In spring, grazers and gatherers formed the largest proportion of the macroinvertebrates. The quantitative presence of shredders increased compared with grazers in the summer, while the proportion of gatherers remained relatively constant. The relative presence of predators was highest in the autumn. Data from the other sites were available only for the 2002 season and for spring 2003, and therefore inadequate for a discussion of seasonal changes. However, grazers were abundant in all localities in the spring. The proportion of shredders increased in the summer and decreased slightly in the autumn. The occurrence of gatherers was almost constant throughout the sampling period. Herrmann et al. (1993) observed a larger proportion of shredders compared with grazers in acidified waters. From the biocenotic point of view, the biotopes at the Vydra headwaters have epirhitral to hypocrenal character (Fig. 6).

The rest of the sampling sites in the Vydra watershed

Three different clusters include the sampling sites MoM, RoM, Ha, Hr, and Vyd (Fig. 7). The localities RoM and MoM have the lowest dissimilarity index (0.58). The site at the Hamerský stream belongs to the same cluster. This locality, however, is more similar to the Prášilský and Jezerní streams in the Křemelná watershed. This cluster is separated from the former by branching with a high dissimilarity index (1.63). The last cluster includes the Hrádecký stream, which is similar to the Slatinný and Křemelná streams, and the Vydra stream, which is again separated from the rest of the sites by a very high dissimilarity index (1.53).

The sites Modravský-Modrava and Roklanský-Modrava have been systematically studied since 1994 (Růžičková 1998, Růžičková et al. 2000, 2004b). Compared with other localities in the Vydra watershed, these sites have always shown lower numbers of individuals, lower numbers of taxa, and lower community diversity. The difference is probably caused by acidification. Both sites are characterised by elevated concentrations of nitrates and low conductivity. Low species numbers were mostly observed in the spring and in the autumn. Median values of species diversity were 1.31 for RoM and 1.09 for MoM (Fig. 3). The ranges of median values of species richness and dominance were similar to those of sites at the headwaters of the Vydra stream. Species richness was relatively low (RoM – 1.90 and MoM – 1.80), as was equitability (RoM – 0.62 and MoM – 0.55); dominance, on the contrary, was relatively high (RoM – 0.37 and MoM – 0.54) – Figs. 1, 2, 4.

Both sampling sites showed a marked difference in the relative presence of macroinvertebrates. Plecoptera predominanted in all years at MoM. At RoM, Plecoptera were prevalent in 2003 and in spring 2004 only, while in 2000 and 2001 Diptera predominated. In addition, representatives of the orders Ephemeroptera and Trichoptera were more common. In the Modravský stream, *Brachyptera seticornis*, *Protonemura* sp., *Leuctra* sp., and *Diura bicaudata* were found frequently. Interestingly, the species *Chloroperla tripunctata* appeared in spring and summer in the years 2000 and 2001, but was not present on later dates. In addition to these species, *Perlodes microcephalus*, *Nemoura* sp., and *Amphinemura sulcicollis* were also found in the Roklanský stream. The most common Trichoptera species at both sites were *Rhyacophila obliterata*, *Drusus annulatus*, and *Ecclisopteryx guttulata*, with *Drusus discolor* occurring in large numbers at the site MoM and *Anomalopterygella chauviniana*, a species found in Bohemia in the Bohemian Forest only (Novák 1996), abundant at RoM. The only Ephemeroptera family found were Baetidae, numerous in some samples from the RoM site. A decline in species richness of Ephemeroptera, Crustacea, and Mollusca or their absence indicates stream acidification (Herrmann et al. 1993). The large proportion of Diptera in the Roklanský stream was caused by the high abundance of *Atherix ibis* especially in 2000 and 2001, while in later years its numbers declined. This may have been caused by the fact that this species has a two-year life cycle**.** Other taxa found included only Oligochaeta, *Crenobia alpine*, and *Limnius* sp.

The seasonal development of functional feeding groups was very similar to the situation in the headwaters of the Modravský and Roklanský streams, with the exception of a lower predominance of shredders, especially in spring. Taking into consideration the higher stream order these results are in good agreement with research, e.g. by Cummins (1974) and Graca (2001). The two streams differed most markedly in the presence of predators, which was high at RoM in the summer and especially in the autumn, while autumn at MoM was characterised by a predominance of grazers, whose numbers rose almost to their spring values after the summer decline. The high numbers of predators could have been caused by periodic acidification (Madarish & Kimmel 2000). As far as biocenotic structure is concerned, the MoM site is classified for the most part as epirhitral**,** while RoM as metarhitral (Fig. 6).

Long-term research of the other Vydra tributaries, the Hamerský and Hrádecký streams, has also been performed. These streams are characterised by higher pH and higher conductivity (Růžičková 1998). In most samples, the sum of base cations was higher than the sum of strong acid anions. COD was usually low with the exception of the flood year 2002, when this parameter was higher and very variable in both streams (Růžičková et al. 2004a). Species richness and equitability are very high in both streams (Figs 1, 4). Dominance indices reached very low values (0.13–0.42) – Fig. 2.

A study on the long-term changes in the species composition of the orders Ephemeroptera and Plecoptera in the Hamerský stream has shown that 13 of the original 30 species were absent in the final research period (Soldán et al. 1998). The species composition and structure of macroinvertebrates was very diverse. Compared with sampling sites at higher altitudes, Ephemeroptera were more common than Plecoptera. While *Baetis alpinus* was abundant at both sites, *Baetis rhodani* was found in higher numbers only in the Hrádecký stream. Representatives of the Heptageniidae family were also found in both streams, especially *Rhitrogena semicolorata* and three species of the genus *Ecdyonurus* (*E. austriacus*, *E. subalpinus*, *E. submontanus*). *Epeorus sylvicola* was observed in the Hrádecký stream only. All the Plecoptera taxa found in the Roklanský and Modravský streams were present, and another Plecoptera species, *Isoperla oxylepis*, was numerous in both streams. In addition, *Isoperla rivulorum* was found in the Hamerský stream in the years 2002 and 2003. The Trichoptera community was not numerous, but relatively diverse. *Rhyacophila* (*R. obliterata, R. praemorsa*), *Psychomyia pusilla*, and *Plectrocnemia conspersa* were all found, as well as all the representatives of the Limnephilidae family observed at MoM and RoM. In addition, *Chaetopterygopsis maclachlani* was observed in the Hamerský stream and *Potamophylax cingulatus*, *P. latipennis*, and *Halesus digitatus* were found in the Hrádecký stream. The Diptera were represented by the Simuliidae and Chironomidae families, *Tipula saginata*, *Dicranota* sp., and *Atherix ibis*. In the Hamerský stream the species *Eloeophila submarmorata* and *Liponeura* sp. were also found. The higher percentage of Diptera observed in 2003 in the Hrádecký stream was connected with a mass summer occurrence of Chironomidae. Of the Coleoptera order, *Limnius* sp. was numerous in the Hrádecký stream. *Crenobia alpina* was present though rare in both the Hrádecký and Hamerský streams, and *Ancylus fluviatilis* was found in the Hrádecký stream. The crustacean *Gammarus fossarum* was typical for both localities. The occurrence of this species is often connected with higher saprobity due to anthropogenic influences (Whitton 1984).

From a biocenotic point of view, both streams are classified as epirhitral to metarhitral (Fig. 6), and they are the only localities studied which have a littoral zone. From a trophic group perspective, the community composition was very stable during the whole study period. The seasonal trend was indistinct, and consisted of a slight increase in the percentage of shredders in the summer and autumn compared with grazers. Filterers were found in most of the samples from the stream Hamerský but in none of the Hrádecký stream. The small proportion of filterers generally is typical for mountain streams with low direct human impact, as their waters contain little fine particulate organic matter (Krno et al. 1995).

The Vydra sampling site is characterised by the lowest altitude, relatively high pH values and average values of conductivity. Since 1994, the COD at the site has been gradually increasing (Mánek 1998, Růžičková & Kotrbová 2000). The number of species found at this site was usually lower than numbers from comparable localities, but samples contained high numbers of taxa. The diversity and dominance are comparable to values from the Hamerský and Hrádecký streams (Figs. 2, 3). The median values of species richness and equitability also resemble those of these streams, but particular indices are more variable throughout the year.

Ephemeroptera were numerous in the Vydra stream in the years 2000 and 2001, while Plecoptera occurred rarely, especially in 2001. However, their presence increased considerably in 2002 and 2003. The most numerous species were *Baetis alpinus* and *Baetis rhodani*, dominant in 2000 and 2001, and *Brachyptera seticornis* and *Protonemura* sp., which prevailed in 2002 and 2003. The Ephemeroptera species *Epeorus sylvicola* as well as the Plecoptera *Amphinemura sulcicollis*, *Leuctra* sp., and *Perlodes microcephalus* were also observed. The Trichoptera community was characterised by high diversity and low fluctuation. In addition to many representatives of the family Drusinae and the Rhyacophilidae and Psychomyidae families, found also in the Hamerský and Hrádecký streams, the following species were found at the Vydra sampling site – *Hydropsyche pellucidula*, *Brachycentrus montanus*, *Ecclisopteryx dalecarlica*, *Sericostoma* sp., *Beraeamyia hrabei*, and *Odontocerum albicorne*. Very few representatives of the Limnephilidae family were found. The Diptera community was also very rich. The most numerous taxa were *Atherix ibis* and Simuliidae, but *Tipula saginata*, *Pedicia rivosa*, *Dicranota* sp., *Eloeophila submarmorata*, and Chironomidae were also identified.

Compared with other sites, the Vydra zoocenosis has a higher amount of predators and a lower proportion of shredders (Fig. 5). Grazers are less abundant compared with other sites. The percentage of filterers increases slightly in the autumn, but on the whole, seasonal changes in trophic group occurrences are small.

Streams in the Křemelná watershed

The streams in the Křemelná watershed (Kr, Pr, Je, and Sl) were divided into two clusters, which separate already at the first level at point 1.63 and thus differ substantially (Fig. 7). The sites Slatinný and Křemelná (clustered with the Hrádecký stream) have a very low dissimilarity index (0.53). The Prášilský and Jezerní streams are more similar to the Hamerský stream and their dissimilarity index is slightly higher (0.76). Compared with the Vydra watershed, the Křemelná localities tend to have higher species diversity and species richness (Figs. 1, 3). The localities were balanced as far as biota concerned. Trophic conditions were richer than in the Vydra watershed, which is more deforested. But even some of the Křemelná sites were acidified. The Jezerní stream was characterised by lower pH and low conductivity compared with other Křemelná sites. A similar situation was typical for some Prášilský stream samples as well (Růžičková et al. 2004b). Average conductivity was very low in both streams, especially in the Jezerní stream which had the lowest values of all the localities studied.

The two streams mentioned above however had a similar biota composition, with species diversity slightly higher in the Jezerní stream (median 1.81) than in the Prášilský stream (median 1.76) – Fig. 3. Species richness and equitability were also high, although lower than in the remaining two streams in the Křemelná watershed (Figs. 1, 4). Ecological indices varied greatly in both the Jezerní and Prášilský streams.

Plecoptera dominated in both streams, but representatives of other orders were present as well. The Plecoptera *Brachyptera seticornis* and *Leuctra* sp. were especially numerous at both sites. Another Plecoptera species, *Protonemura* sp., was dominant in the Jezerní stream. The species *Perlodes microcephalus*, *Isoperla oxylepis*, and *Chloroperla tripunctata* were also relatively common. Ephemeroptera were represented by the species *Ameletus inopinatus* and *Baetis alpinus*. Some Heptageniidae species, such as *Epeorus sylvicola* or *Rhitrogena loyolaea*, were common in the Prášilský stream but very rare at the Jezerní site. Long-term research on the Ephemeroptera (Soldán et al. 1998) indicates that species composition in the Prášilský stream has remained practically the same for the last fifty years. Trichoptera were taxonomically rich but not very numerous. They consisted of species common in the whole watershed, with *Rhyacophila obliterata* the most abundant in the Jezerní stream and *Ecclisopteryx guttulata* the most common in the Prášilský stream. Regarding Diptera, Simuliidae were abundant at both sites, *Dicranota* sp. was abundant in the Jezerní stream and *Atherix ibis* is common in the Prášilský stream. Of other taxa, Oligochaeta were most numerous.

Seasonal variability in the occurrence of functional feeding groups in the Jezerní and Prášilský streams was similar to the downstream localities of the Vydra watershed. Shredders and predators were very low in all spring samples. They increased in the summer, with shredder proportions decreasing once more in the autumn. Filterers were present only in some of the samples.

The Slatinný and Křemelná streams are slightly affected by human impacts, as indicated by elevated nitrate and base cations concentrations (Růžičková et al. 2000). Conductivity and pH were the highest of all the streams studied, comparable only with the Hrádecký stream in the Vydra watershed. COD values were the highest in the Křemelná watershed, but lower than values observed in the Vydra stream**.** Species richness, diversity, and equitability were the highest in the whole studied region, and, accordingly, the dominance was the lowest (Figs 3–4).

Composition of macroinvertebrates in these two localities is the most diverse of the two watersheds studied. Ephemeroptera dominated in 2000 and 2001, later they were overtaken by the Plecoptera and the Trichoptera. *Ameletus inopinatus*, *Baetis alpinus*, and *Baetis rhodani* were the dominant Ephemeroptera species. Representatives of the family Heptageniidae (*Epeorus sylvicola*, *Rhitrogena semicolorata*, and *Ecdyonurus submontanus*) were observed. In addition, *Ecdyonurus austriacus* was common in the Slatinný stream. The genus *Heptagenia*, reported from this locality by Soldán et al. (1999) was not found. *Brachyptera seticornis*, *Leuctra* sp., and *Protonemura* sp. (Plecoptera) were common. The Perlodidae family (*Perlodes microcephalus*, *Diura bicaudata*, *Isoperla oxylepis*) was richly represented. *Perla marginata* of the Perlidae family was present, and the species *Dinocras cephalotes* was found, though very rarely, in the Křemelná stream. *Chloroperla tripunctata* was identified at both sites. The family Rhyacophilidae (Trichoptera) was represented by *Rhyacophila obliterata* and *Rhyacophila dorsalis* at both localities, and by *Rhyacophila praemorsa* and *Rhyacophila tristis* in the Slatinný stream only. *Anomalopterygella chauviniana*, *Drusus annulatus*, and *Ecclisopteryx guttulata* were often found at both localities, while *Potamophylax latipennis* and *Potamophylax cingulatus* were identified only in the stream Slatinný. Diptera were represented by *Dicranota* sp., *Eloeophila submarmorata*, *Simuliidae*, and *Chironomidae* which were common at both localities, while *Atherix ibis w*as found only in the Křemelná stream. *Limnius* sp. (Coleoptera) was numerous especially in the Slatinný stream.

The presentation of functional feeding groups at these two localities remained stable throughout the year. The groups were equitably distributed, with the exception of the filterers, which were present only in some of the Křemelná samples. The autumn increase in shredders was observed only at the Křemelná site in the years 2002 and 2003.

Conclusion

Research in the Vydra and Křemelná watersheds indicates that the quality of the lotic environments there has remained high.

In the area studied, the least stable and also the most threatened biotopes are situated in the headwater and at upstream localities of the streams, especially in the Vydra watershed. The whole region is situated at altitudes above 1000 m and stream water quality is significantly influenced by peat bogs where the streams originate or through which they flow. These extreme habitats have relatively species-poor and unstable community, formed by a few species resistant to acidification, mostly represented by Plecoptera. Species composition in downstream parts of the Modravský and Roklanský streams is similar, with relatively low biodiversity and a small number of dominant species. Compared with the other tributaries of the Vydra stream, the presentation of functional feeding groups varies strongly throughout the year. As opposed to the headwater region at upstream localities we may assume that the natural community structure could be much more diverse. As the pH values gradually increase, we can expect the community to develop towards greater biodiversity. The other streams in the Vydra watershed are very diverse and stable as far as functional feeding groups are concerned.

Of all the sites studied, streams in the Křemelná watershed have the highest macroinvertebrate diversity, especially in the Křemelná and Slatinný streams. This is partly due to the bedrock composition, the watershed is for the most part still covered by forest, the streams have higher pH values and the region is less disturbed by human settlements and tourism compared with the Vydra watershed. The presentation of functional feeding groups and species composition are very balanced and does not change much over time. Especially this region serves as an important refuge of aquatic insects for the whole Bohemian Forest area and lotic biotopes needs to be effectively protected.

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