Silva Gabreta	vol. 3	p. 95–114	Vimperk, 1999

Long-term changes of diversity of mayflies (*Ephemeroptera*) in the Křemelná river basin (Šumava Mts., Czech Republic)

Dlouhodobé změny diverzity jepic (*Ephemeroptera*) v povodí Křemelné (Šumava)

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Abstract
All-season samples of larvae were taken semiquantitatively within the past 50 years in 4 sampling periods (1946–1950, 1955–1960, 1970–1980, and 1990–1995) at 6 localities of the Křemelná river basin (the Šumava Mountains, Czech Republic). Of these, 4 represented rhithral habitats, and 2 habitats of glacial lake or artificial canal, respectively. Altogether 25 species and 4865 larvae were collected. Long-term changes of mayfly taxocoenes were evaluated by means of currently used indexes (dominance, species richness and diversity, evenness), TWINSPAN hierarchic classification and ordination of localities and species (DCA). Indicator species, position of individual localities within final TWINSPAN groups, and/or in ordination space and their respective shifts are interpreted with respect to tendencies in diversity changes and effects of man-induced changes of some environment variables. Relatively not affected habitats of the Křemelná and its tributaries show almost stable and high diversity however affected, first of all, by acidification and stream bed regulation in some sampling periods. The Prášilské lake and an artificial habitat exhibit diversity strongly reduced due to acidification and discharge manipulation, respectively. In general, this area shows diversity condition close to natural state and high water quality. Some aspects of its protection are discussed.

Key words: *Ephemeroptera*, Šumava Mts., diversity, 50 years long-term changes, multicriterial analysis

Introduction

The *Ephemeroptera* larvae represents one of the most important parts of benthic macroinvertebrates reaching up to 42 % of their standing crop at some localities of the Šumava Mts. (Růžičková 1998). Thanks to detailed biodiversity research program on aquatic insects carried out in 1946–1950, 1955–1960, 1970–1980 and 1990–1995, our knowledge of Ephemeroptera of this region is relatively extensive. Altogether more than 150 localities have been thoroughly investigated to define their species composition, quantitative presentation and importance from the biodiversity protection point of view (Landa & Soldán 1981, 1982; Soldán & al. 1996). All-season samples from some of these localities have been considered to evaluate large-scale regional changes of aquatic habitats in the Labe basin (Landa & Soldán 1989) or in the whole Czech Republic (Soldán & al. 1998). However, inevitably limited number choice of these localities led us to select only several ones, moreover necessarily representing different river basins and bioregions, from the whole area. Consequently, some samples and even those collected from particularly important regions of the Šumava Mts. remain untouched regardless that those from the late 1940's are still available, too.

In 1994–1996, aquatic insects communities of some localities of the Křemelná river basin were investigated (Růžičková & Benešová 1996, Růžičková 1997, 1998). As far as the *Ephemeroptera* are concerned these authors present the occurrence of altogether 6 genera (*Baetis, Ecdyonurus, Epeorus, Ephemerella, Heptagenia,* and *Rhithrogena*) from the following localities: Křemelná river (6 genera, quantitative presentation of mayflies 31 %), Hrádecký brook (4 genera, 28 %), Prášilský brook (6 genera, 29 %), Jezerní brook (1 genus, 21 %), and Slatinný brook (6 genera, 28 %). The authors also discussed possible effects of acidification and pollution (here expressed mostly by water conductivity changes). The values of average Shannon-Weaver species diversity (here expressed for the whole community) ranged from 2.4–2.8 (Růžičková 1998). However, since the material collected was determined at the generic level, the species diversity values are very approximative not describing the state of the *Ephemeroptera* taxocenes in particular.

Basin of the river Křemelná undoubtedly represents one of the most valuable area of the mountains on one hand but also the area subjected to man-made environmental changes on the other. Since data on the occurrence and quantitative presentation of mayflies in this area from the period of more than the past 50 are at disposal, this group can provide a background or example to evaluate long-term changes of an aquatic habitat in the future in general. The objective of the present paper is to describe the composition of mayfly taxocoenes of selected localities and to discuss long-term tendencies in their development.

Material and methods

At the localities of running waters, samples were taken at about 100 m section of stream which included as many of habitats contained as possible, namely ones with fast-flowing water (riffles) and those of moderate and slow current (pools) and all types of substrates occurring here. Average width and depth of the stream and substrate roughness were estimated to represent an average state for selected 100 m long stream segment. The scale by Gordon & al. (1979) was use to estimate substratum (sediment) particle size categories. Sampling technique was slightly modified in the Prášilské lake with main attention to the littoral zone and submerged vascular plants. Samples were taken semiquantitatively by „kicking techniques" (cf. e.g. Kershaw & Frost 1968, Minshall 1969, Lillehammer 1974) repeated at least five times at each locality using a metal cup and larvae were collected also individually from larger stones.

We selected pure collection time of 10–15 minutes (sorting of material in situ not included) devoted to each locality in each season. Samples were realised in three seasons: spring (March, April), spring-summer (May–June) and full summer one (August–September). This seasonal approach is quite sufficient to cover the occurrence of all species of mayflies with different seasonal cycles (Landa 1968, Soldán & al. 1998). To evaluate long-term changes, samples (or, more precisely, total numbers of species/individuals) were classified into four collection periods, namely 1946–1950 (period 1), 1955–1960 (period 2), 1970–1980 (period 3), and 1990–1995 (period 4). Samples from 2–4 years of each period were analysed to complete full seasonal aspect. Material was collected by V. Landa during the former two periods and by T. Soldán during the latter two ones and is deposited in 75 % alcohol in the Institute of Entomology in České Budějovice.

Besides currently used indexes of diversity (dominance according to Simpson, species diversity according to Shannon-Weaver and Brillouin, species richness according to Margalef, and evenness according to Sheldon – for definition see Brillouin 1962 and Odum 1997) the following procedures of multicriterial analysis were used: (i) Methods and programme TWINSPAN (Two Way INdicator SPecies ANnalysis: HILL 1979) gradually dividing data set into two groups according to the most important indicator species that are newly found at each step. All species and samples (total numbers of individuals from all seasons) were included into analysis. To evaluate our data set by this way, the dominance values were used. Cut levels for definition of pseudospecies were established as follows: 0, 1, 2, 5, 10. These levels are thus related to individual degrees of dominance. Minimum group size for division was 2 samples. Species *Baetis alpinus, B. rhodani* and *B. vernus* were downweighted. (ii) Ordination of localities and species according to the method of indirect gradient analysis – DCA (Detrended Correspondence Analysis) using the program CANOCO for Windows (TER BRAAK & ŠMILAUER 1998). All species and samples (total numbers of individuals from all seasons) were included into analysis. Species data were transformed logarithmically, species *Baetis alpinus, B. rhodani* and *B. vernus* were downweighted, all samples from the locality Prášilské lake, Prášily (F) were downweighted, too.

Description of study area

Six localities of the Křemelná river basin (total area of 171.6 km^2) were selected to study long-term changes of diversity of mayflies. Localities were selected in order to represent all existing habitat types except for astatic waters. Two of them are situated in epirhithral zone (D, E), two in meta- and hyporhithral one (A, B), and two represented a glacial lake (F) or an artificial habitat (C, respectively). However, our choice has been rather limited since data from the collection period No. 1 (1946–1950) represented random or incidental samples however collected by the same methods. The localities selected represents all altitudinal zones at elevations of 645–1,079 m and are approximately evenly distributed within the Křemelná river basin. The following localities were selected and studied:

A – Křemelná river, Čeňkova Pila (collecting site near the mouth, coordinates according to uniform grid system 6846, number of hydrological order 1-08-0-019 (IV.), altitude of 645 m a.s.l., distance from source 30 km, average width/depth 10/0.7 m, average discharge 4.43 m^3.s^{-1}, estimated substrate roughness at collecting site: cobble 50 %, pebble and granule 30 %, coarse sand 20 %);

B – Křemelná river, Vysoké Lávky (coordinates 6846, number of hydrological order 1-08-01-019 (IV.), altitude of 810 m a.s.l, distance from source 17 km, average width/depth 5/0.5 m, average discharge 4.00 m^3.s^{-1}, estimated substrate roughness: cobble 50 %, pebble and granule 30 %, coarse sand 20 %);

C – Vchynický canal (sometimes called also Vchynicko–Tetovský or Plavební canal), Srní (coordinates 6946, number of hydrological order 1-08-01-036 (IV.), altitude of 825 m a.s.l., distance from the mouth 2.5 km, average width/depth 2.5/0.4, discharge strongly fluctuating, estimated substrate roughness: cobble 30 %, pebble and granule 30 %, coarse and fine sand 25 %, silt 15 %);

D – Prášilský brook, Prášily (coordinates 6846, number of hydrological order 1-08-01-028 (IV.), altitude of 830 m a.s.l., distance from source 8.5 km, average width/depth 2.5/0.25 m, average discharge 1.43 m^3.s^{-1}, cobble 35 %, pebble and granule 45 %, coarse and fine sand 20 %);

E – Slatinný brook, Gerlova Huť (coordinates 6845, number of hydrological order 1-08-01-020 (IV.), altitude of 930 m a.s.l., distance from source 3.5 km, average width/depth 1.2/0.15 m, average discharge 0.50 m^3.s^{-1}, estimated substrate roughness: cobble 25 %, pebble and granule 35 %, coarse and fine sand 20 %, silt 20 %);

F – Prášilské lake, Prášily (coordinates 6946, number of hydrological order 1-08-01-029

(IV.), altitude of 1079 m a.s.l., total area 3.72 ha, max. depth 14.9 m, estimated substrate roughness at collecting site in littoral zone: cobble 20 %, pebble and granule 20 %, sand and silt 30 %, submerged vegetation 30 %).

The above data on nomenclature of watercourses, number of hydrological order and average discharge, follows those by VLČEK (1984). All the localities studied are situated in the orographic unit No. I (DEMEK 1987), in the bioregion 1.62 (CULEK 1996) and in the faunistic district No. VI according to LANDA & SOLDÁN (1989).

Since analysis of main environmental variables (e.g. water chemistry, conductivity and others) with the exception of actual water temperature and acidity (LANDA & al. 1984) was not performed within the research periods 1 and 2 we failed to include them to multicriterial analysis.

Recent data sampled in 1994–1996 concerning maximal summer water temperature, pH, alkalinity, conductivity, total hardness, ammonium nitrogen, nitrate nitrogen, phosphate phosphorus, total phosphorus, dissolved oxygen and biochemical oxygen demand at localities of Křemelná river, Vysoké Lávky (B), Prášilský brook, Prášily (D), and Prášilské lake, Prášily (F) were published by SOLDÁN & al. (1998). Recent values of pH (6.0–6.3) and conductivity (22–41 $\mu S.cm^{-1}$) of the Křemelná river (pH even 7.5 at Vysoké Lávky), Prášilský brook and Slatinný brook are presented also by RŮŽIČKOVÁ (1997, 1998) and RŮŽIČKOVÁ & BENEŠOVÁ (1996). Some data concerning water sulphate hardness and concentration of some ions from the Křemelná basin were published by VESELÝ (1994). However, there are hardly any data of water chemistry (except pH) sampled by comparable methods of localities selected from the 1940–1970's. Consequently long-term tendencies in their development can be roughly estimated only. The only exception was the locality Prášilské lake, Prášily (F) subjected to regular sampling of environmental variables for at least the past 80 years (see e.g. review by VESELÝ 1994).

Results

Altogether 4865 specimens of larvae belonging to 25 species, 12 genera and 8 families (*Ameletidae, Siphlonuridae, Baetidae, Heptageniidae, Leptophlebiidae, Ephemeridae, Ephemerellidae,* and *Caenidae*) were collected at selected localities of the Křemelná river basin in 1946–1995. Species found at individual localities and their quantitative presentation as well as principal ecological indexes are apparent from Tables 1–6. Total numbers of species found in individual research periods are apparent from Fig. 1, dominance of individual species at two selected localities, i.e. Křemelná river, Vysoké Lávky (B) and Slatinný brook (E), respectively, is presented in Fig. 2.

Divisive hierarchic classification of all 6 localities in all individual collection periods with indicator species and eigenvalues of divisions depicted is apparent from Fig. 3, respective coenological table is presented in Table 7. The first division classifies localities into two larger groups (or clusters) with indicator species *Baetis alpinus* (*0), indicators for the right side of dichotomy were not found. The group *1 summarizes four sampling periods of the Prášilské lake (F) only and in further division (D3 in Fig. 3) to early sampling periods (F1, F2) and later ones (F3, F4) according to the presence of indicator species *Siphlonurus lacustris*. Further division (D2) of the group *00 classifies the localities included as follows: the group *00 is characterized by 5 indicator species, first of all by *Rhithrogena iridina* and *R. semicolorata* while the group *01 includes the only indicator species, *Ecdyonurus austriacus*. The former group (*00) gives rise to two final groups (division D4), one of them (*000) being characterized by indicator species *Siphlonurus lacustris*, the other (*001) shows no indicators. The latter group (*01) gives rise to two final groups as well, one of them (*010) being characterized

Table 1. – Long-term changes of mayfly diversity at the locality Křemelná river, Čeňkova Pila (A)

species found/ collection period	1946–1950		1955–1960		1975–1980		1990–1995	
	N	%	N	%	N	%	N	%
Ameletus inopinatus	12	5.56	65	8.16	16	2.23	8	1.39
Siphlonurus lacustris	8	3.70	22	2.76	6	0.83	24	4.17
Baetis alpinus	39	18.06	134	16.81	272	37.83	185	32.12
Baetis fuscatus	3	1.39	-		5	0.70	-	
Baetis rhodani	4	1.85	94	11.79	39	5.42	69	11.98
Baetis vernus	22	10.19	43	5.40	139	19.33	91	15.80
Ecdyonurus forcipula	3	1.39	-		1	0.14	-	
Ecdyonurus submontanus	8	3.70	-		-		-	
Ecdyonurus venosus	13	6.02	85	10.66	19	2.64	55	9.55
Electrogena lateralis	-		2	0.25	-		-	
Epeorus sylvicola	34	15.74	175	21.96	62	8.62	29	5.03
Rhithrogena carpatoalpina	-		5	0.63	-		-	
Rhithrogena hercynia	2	0.93	33	4.14	18	2.50	9	1.56
Rhithrogena hybrida	-		2	0.25	-		-	
Rhithrogena iridina	26	12.04	5	0.63	89	12.38	55	9.55
Rhithrogena semicolorata	17	7.87	31	3.89	15	2.09	9	1.56
Habrophlebia lauta	-		3	0.38	-		-	
Leptophlebia vespertina	5	2.31	12	1.51	-		1	0.17
Ephemera vulgata	1	0.46	-		-		-	
Ephemerella ignita	8	3.70	77	9.66	30	4.17	22	3.82
Ephemerella mucronata	11	5.09	-		8	1.11	19	3.30
Caenis macrura	-		9.0	1.13	-		-	
Total No. of species (S)	17		17		14		13	
Total No. of individuals (N)	216		797		719		576	
Species richness (Margalef)	6.85		5.51		4.55		4.35	
Dominance (Simpson)	0.10		0.12		0.21		0.17	
Species diversity (Shannon)	3.58		3.31		2.79		3.00	
Species diversity (Brillouin)	-2.96		-4.96		5.33		-4.81	
Evenness (Sheldon)	0.70		0.58		0.49		0.62	

mainly by *Ecdyonurus venosus* and *E. austriacus*, the other (*011) is free of indicators again. The most important shifts within the TWINSPAN classification are represented by the localities Vchynický canal (C) and Prášilský brook, Prášily (D), both being components of three final groups in their individual sampling periods.

Results of detrended correspondence analysis are apparent from Figs. 4–7. The ordination plot of localities shows those with relatively high diversity (i.e. Křemelná, Čeňkova Pila and Vysoké Lávky – A and B, except for the latter in sampling period 2) to be concentrated in the centre of diagram, mostly in quadrant I (Fig. 4). Similarly, the locality Prášilské lake, Prášily (F) exhibiting very poor species composition is situated with a homogeneous group in quadrant II. Sampling periods of the locality Slatinný brook, Gerlova Huť (E) showing apparent changes in species dominance, are almost concentrated in quadrant III. Sampling periods of

Table 2. – Long-term changes of mayfly diversity at the locality Křemelná river, Vysoké Lávky (B)

species found/ collection period	1946–1950		1955–1960		1975–1980		1990–1995	
	N	%	N	%	N	%	N	%
Ameletus inopinatus	2	1.02	-		9	2.29	-	
Siphlonurus lacustris	9	4.57	-		21	5.34	17	3.74
Baetis alpinus	66	33.50	284	76.14	132	33.59	207	45.49
Baetis rhodani	18	9.14	31	8.31	37	9.41	24	5.27
Baetis vernus	7	3.55	55	14.75	82	20.87	112	24.62
Ecdyonurus forcipula	5	2.54	-		-		4	0.88
Ecdyonurus venosus	11	5.58	-		34	8.65	18	3.96
Epeorus sylvicola	41	20.81	-		22	5.60	38	8.35
Rhithrogena hercynia	-		-		6	1.53	2	0.44
Rhithrogena iridina	31	15.74	-		43	10.94	22	4.84
Rhithrogena semicolorata	5	2.54	-		-		-	
Ephemerella ignita	-		3	0.80	-		-	
Ephemerella mucronata	2	1.02	-		7	1.78	11	2.42
No. of species (S)	11		4		10		10	
No. of individuals (N)	197		373		393		455	
Species richness (Margalef)	4.36		1.17		3.47		3.39	
Dominance (Simpson)	0.20		0.61		0.19		0.28	
Species diversity (Shannon)	2.75		1.06		2.76		2.33	
Species diversity (Brillouin)	-3.60		-6.08		-4.51		-5.13	
Evenness (Sheldon)	0.61		0.52		0.68		0.50	

Table 3. – Long-term changes of mayfly diversity at the locality Vchýnický canal, Srní (C)

species found/ collection period	1946–1950		1955–1960		1975–1980		1990–1995	
	N	%	N	%	N	%	N	%
Ameletus inopinatus	-		-		1	3.13	-	
Siphlonurus lacustris	-		-		5	15.63	7	21.21
Baetis alpinus	8	50.00	27	64.29	15	46.88	19	57.58
Baetis rhodani	3	18.75	-		6	18.75	5	15.15
Baetis vernus	-		11	26.19	3	9.38	-	
Ecdyonurus venosus	-		1	2.38	-		-	
Epeorus sylvicola	-		3	7.14	-		2	6.06
Rhithrogena iridina	1	6.25	-		-		-	
Ephemerella ignita	4	25.00	-		2	6.25	-	
No. of species (S)	4		4		6		4	
No. of individuals (N)	16		42		32		33	
Species richness (Margalef)	2.49		1.85		3.32		1.98	
Dominance (Simpson)	0.35		0.49		0.29		0.40	
Species diversity (Shannon)	1.70		1.32		2.11		1.59	
Species diversity (Brillouin)	-1.40		-2.88		-1.88		-2.33	
Evenness (Sheldon)	0.81		0.62		0.72		0.75	

Table 4. – Long-term changes of mayfly diversity at the locality Prášilský brook, Prášily (D)

species found/ collection period	1946–1950		1955–1960		1975–1980		1990–1995	
	N	%	N	%	N	%	N	%
Ameletus inopinatus	-		-		2	2.41	5	3.25
Siphlonurus lacustris	-		-		-		3	1.95
Baetis alpinus	29	85.29	19	67.86	56	67.47	121	78.57
Baetis rhodani	2	5.88	5	17.86	15	18.07	12	7.79
Baetis vernus	-		-		3	3.61	9	5.84
Ecdyonurus venosus	1	2.94	3	10.71	5	6.02	-	
Epeorus sylvicola	2	5.88	-		-		4	2.60
Rhithrogena iridina	-		1	3.57	2	2.41	-	
No. of species (S)	4		4		6		6	
No. of individuals (N)	34		28		83		154	
Species richness (Margalef)	1.96		2.07		2.61		2.29	
Dominance (Simpson)	0.74		0.51		0.49		0.63	
Species diversity (Shannon)	0.83		1.34		1.51		1.21	
Species diversity (Brillouin)	-3.08		-2.37		-3.62		-4.73	
Evenness (Sheldon)	0.44		0.63		0.47		0.38	

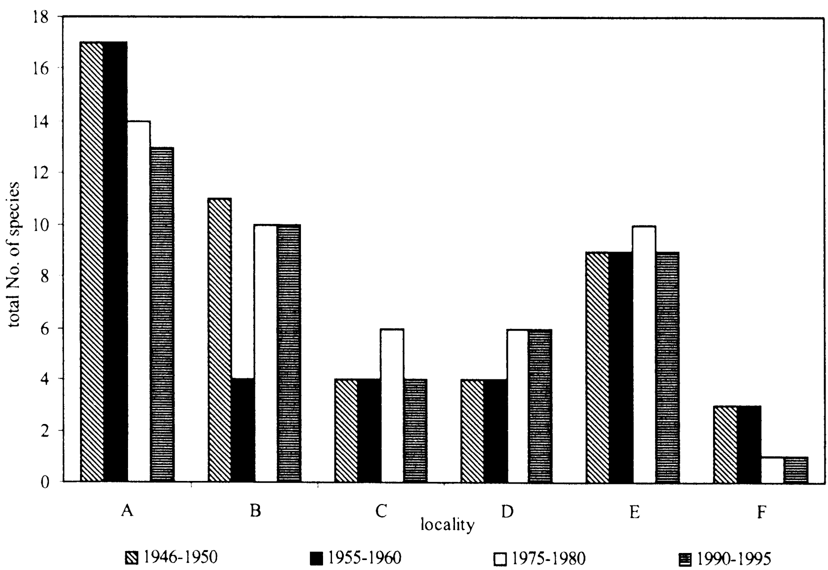


Fig. 1. – Numbers of species at localities A-F in individual collection periods. For species composition at individual localities see Tables 1-6. A - Křemelná river, Čeňkova Pila; B - Křemelná river, Vysoké Lávky; C - Vchýnický canal, Srní; D - Prášilský brook, Prášily; E - Slatinný brook, Gerlova Huť; F - Prášilské lake, Prášily.

Table 5. – Long-term changes of mayfly diversity at the locality Slatinný brook, Gerlova Huť (E)

species found/ collection period	1946–1950		1955–1960		1975–1980		1990–1995	
	N	%	N	%	N	%	N	%
Ameletus inopinatus	-		12	8.45	28	18.67	9	5.17
Siphlonurus lacustris	3	2.73	-		5	3.33	11	6.32
Baetis alpinus	19	17.27	32	22.54	23	15.33	55	31.61
Baetis rhodani	14	12.73	19	13.38	9	6.00	21	12.07
Baetis vernus	6	5.45	25	17.61	32	21.33	14	8.05
Ecdyonurus forcipula	-		-		2	1.33	-	
Ecdyonurus venosus	6	5.45	2	1.41	-		-	
Ecdyonurus austriacus	28	25.45	32	22.54	19	12.67	44	25.29
Epeorus sylvicola	7	6.36	18	12.68	29	19.33	15	8.62
Rhithrogena hercynia	-		1	0.70	2	1.33	1	0.57
Rhithrogena iridina	19	17.27	-		-		-	
Rhithrogena loyolaea	8	7.27	-		-		-	
Leptophlebia vespertina	-		1	0.70	-		4	2.30
Ephemerella mucronata	-		-		1	0.67	-	
No. of species (S)	9		9		10		9	
No. of individuals (N)	110		142		150		174	
Species richness (Margalef)	3.92		3.72		4.14		3.57	
Dominance (Simpson)	0.16		0.17		0.16		0.20	
Species diversity (Shannon)	2.88		2.66		2.88		2.63	
Species diversity (Brillouin)	-2.70		-3.23		-3.18		-3.53	
Evenness (Sheldon)	0.82		0.70		0.70		0.69	

Table 6. – Long-term changes of mayfly diversity at the locality Prášilské lake, Prášily (F)

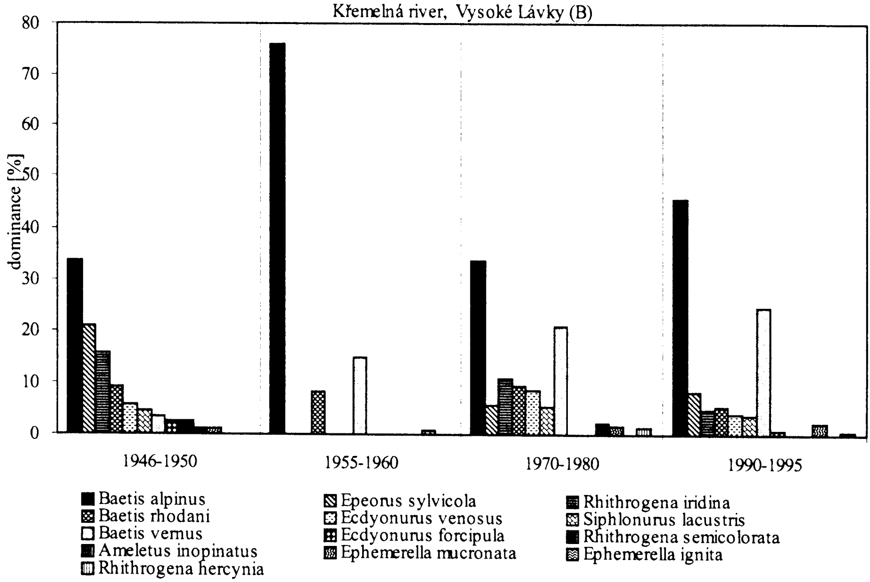
species found/ collection period	1946–1950		1955–1960		1975–1980		1990–1995	
	N	%	N	%	N	%	N	%
Ameletus inopinatus	4	9.52	-		-		-	
Siphlonurus alternatus	-		1	6.67	-		-	
Siphlonurus lacustris	15	35.71	2	13.33	-		-	
Leptophlebia vespertina	23	54.76	12	80.00	28	100.00	56	100.00
No. of species (S)	3		3		1		1	
No. of individuals (N)	42		15		28		56	
Species richness (Margalef)	1.23		1.70		0.00		0.00	
Dominance (Simpson)	0.44		0.66		1.00		1.00	
Species diversity (Shannon)	1.33		0.91		0.00		0.00	
Species diversity (Brillouin)	-2.84		-1.99		-3.50		-4.44	
Evenness (Sheldon)	0.84		0.62		1.00		1.00	

Table 7. – Divisive hierarchic classification (TWINSPAN) of localities A-F in collection period 1-4, coenological table

locality	C	D	D	A	B	A	A	B	B	A	C	D	E	E	E	E	D	C	B	C	F	F	F	F		
collection period	1	2	3	2	1	3	4	3	4	1	2	1	1	2	3	4	4	4	2	3	1	2	3	4		
species																									species group	
Electrogena lateralis	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
Rhithrogena carpatoalpina	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
Rhithrogena hybrida	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
Habrophlebia lauta	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
Caenis macrura	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
Baetis fuscatus	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
Ecdyonurus submontanus	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
Rhithrogena semicolorata	-	-	-	3	3	3	2	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
Ephemera vulgata	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
Ephemerella mucronata	-	-	-	-	2	2	3	2	3	4	-	-	-	-	1	-	-	-	-	-	-	-	-	-	0	0
Rhithrogena iridina	4	3	3	1	5	5	4	5	3	5	-	-	5	-	-	-	-	-	-	-	-	-	-	-	0	0
Ecdyonurus forcipula	-	-	-	-	3	1	-	-	1	2	-	-	-	-	2	-	-	-	-	-	-	-	-	-	0	0
Rhithrogena hercynia	-	-	-	3	-	3	2	2	1	1	-	-	-	1	2	1	-	-	-	-	-	-	-	-	0	0
Ephemerella ignita	5	-	-	4	-	3	3	-	-	3	-	-	-	-	-	-	-	-	1	4	-	-	-	-	0	0
Ecdyonurus venosus	-	5	4	5	4	3	4	4	3	4	3	3	4	2	-	-	-	-	-	-	-	-	-	-	0	0
Baetis alpinus	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	-	-	-	-	0	0
Baetis rhodani	5	5	5	5	4	4	5	4	4	2	-	4	5	5	4	5	4	5	4	5	-	-	-	-	0	0
Baetis vernus	-	-	3	4	3	5	5	5	5	5	5	-	4	5	5	4	4	-	5	4	-	-	-	-	0	0
Epeorus sylvicola	-	-	-	5	5	4	4	4	4	5	4	4	4	5	5	4	3	4	-	-	-	-	-	-	0	0
Rhithrogena loyolaea	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	0	0
Ecdyonurus austriacus	-	-	-	-	-	-	-	-	-	-	-	-	5	5	5	5	-	-	-	-	-	-	-	-	0	0
Ameletus inopinatus	-	-	3	4	2	3	2	3	-	4	-	-	-	4	5	4	3	-	-	3	4	-	-	-	0	1
Siphlonurus lacustris	-	-	-	3	3	1	3	4	3	3	-	-	3	-	3	4	2	5	-	5	5	5	-	-	1	0
Leptophlebia vespertina	-	-	-	2	-	-	1	-	-	3	-	-	-	1	-	3	-	-	-	-	5	5	5	5	1	1
Siphlonurus alternatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	1	1
group of localities	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1		
	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1		
	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1						

remaining localities (i.e. Vchynický canal, C and Prášilský brook, Prášily, D) are evidently scattered within different quadrants even occupying all of the in the former case (Fig. 4). The same phenomenon is apparent from the ordination plot of localities with projection of the TWINSPAN sample classes envelopes showing both position of envelopes in individual quadrants and their overlap (Fig. 5).

On the other hand, ordination plot of individual sampling period does not seem to show any clear definable distribution within the ordination space (Fig. 6). Sampling period 1 (and/or its respective envelope) evidently occupies the largest ordination space being distributed in all quadrants. The same is true concerning the sampling period 2 although in a lesser extent. On the contrary, sampling periods 3 and 4 are more concentrated in the centre (Fig. 6) indicating more homogeneous samples.



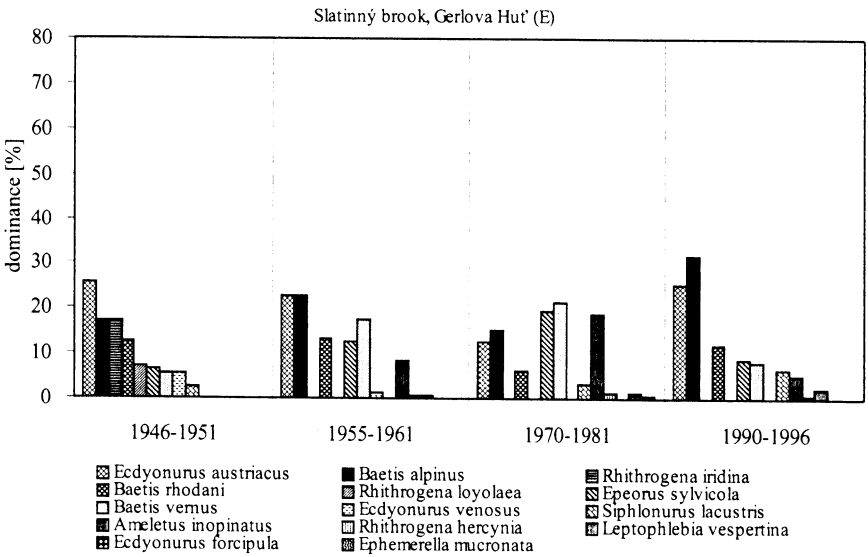


Fig. 2. – Changes of dominance of individual species at the localities Křemelná river, Vysoké Lávky (B) and Slatinný brook, Gerlova Huť (E)

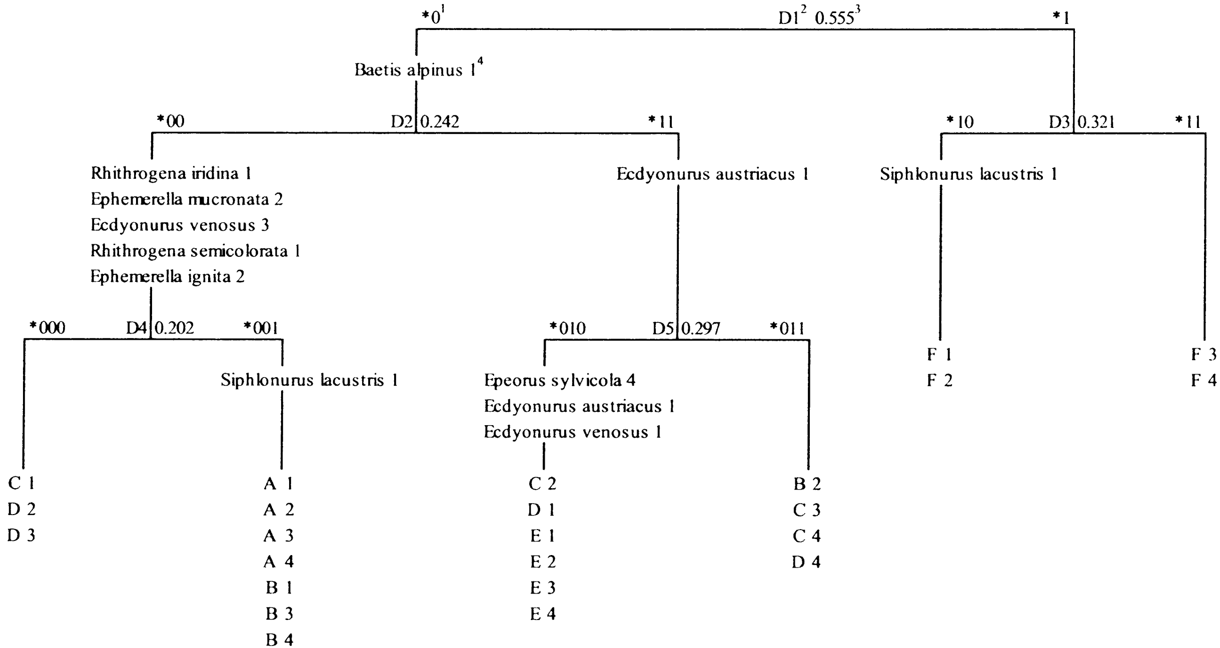


Fig. 3. – Divisive hierarchic classification (TWINSPAN) of localities A-F in collection period 1-4, dendrogram with depicted main indicator species
[1]TWINSPAN group, [2]No. of division, [3]eigenvalue, [4]pseudospecies level

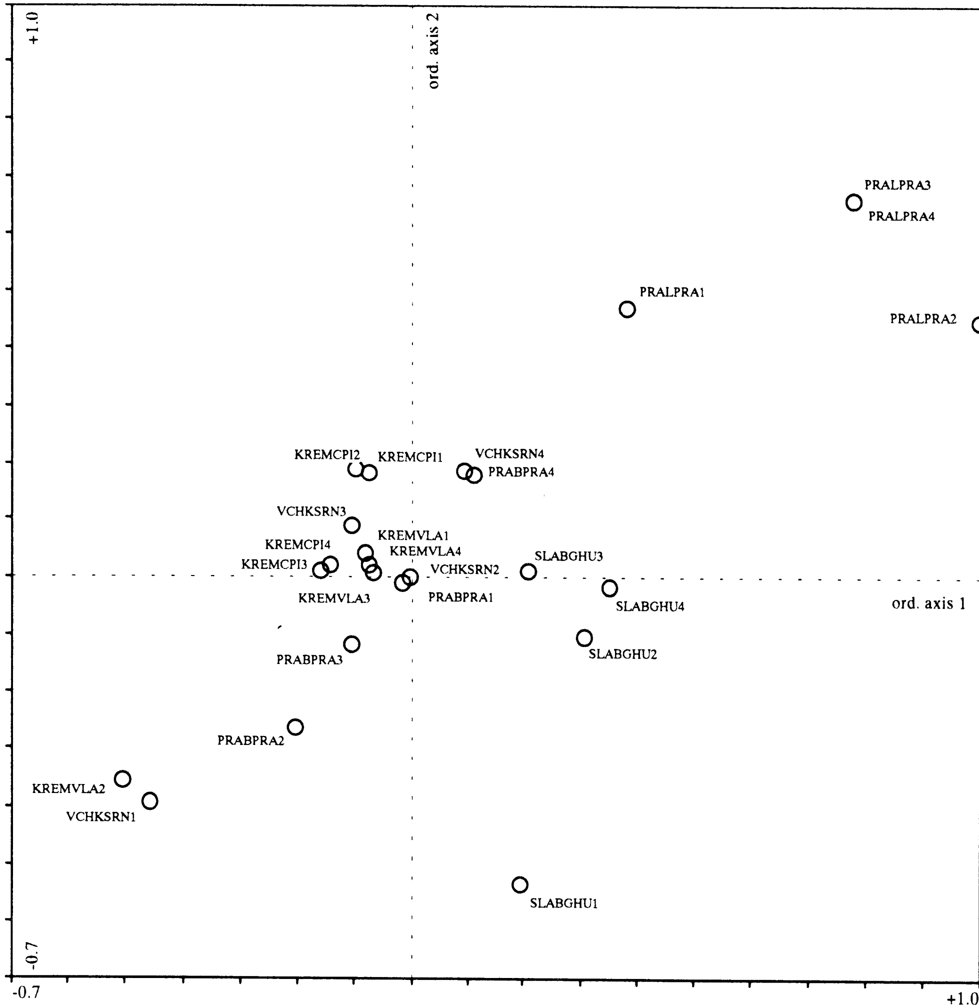


Fig. 4. – Detrended correspondence analysis, ordination plot of localities in individual collection period according to first two ordination axes. KREMCPI - Křemelná river, Čeňkova Pila; KREMVLA - Křemelná river, Vysoké Lávky; VCHKSRN - Vchýnický canal, Srní; PRABPRA - Prášilský brook, Prášily; SLABGHU - Slatinný brook, Gerlova Huť; PRALPRA - Prášilské lake, Prášily.

Ordination plot of species found (Fig. 7) shows two principal groups of species: one cumulated in the centre of diagram and the other, consisting of rarely found species placed at a considerable distance from the beginning in quadrants II–IV. The latter species include *Leptophlebia vespertina* and *Siphlonurus alternatus* in quadrant II found only at the Prášilské lake (6), *Ecdyonurus austriacus* and *Rhithrogena loyolaea* characteristic for epirhithral locality Slatinný brook, Gerlova Huť (E) and *Ephemerella ignita*, a species not typical at montane habitats but otherwise common at lower altitudes. As to other species (Fig. 7), this group comprises those currently occurring at the localities investigated. The most common of them (e.g. *Baetis alpinus, B. vernus* and *Ecdyonurus venosus*) inhabiting running waters only are situat-

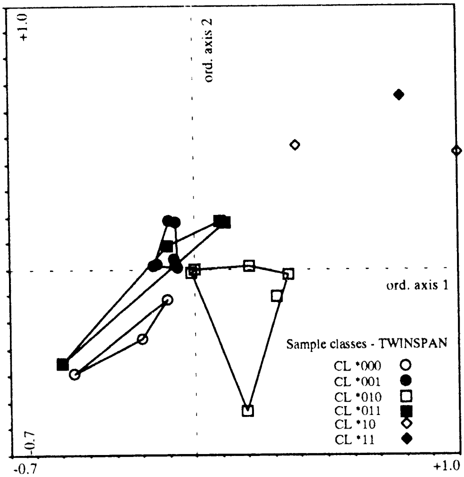


Fig. 5. – Detrended correspondence analysis, ordination plot of localities in individual collection period according to first two ordination axes with projection of TWINSPAN samples envelopes. See Fig. 4 for identification of localities position in individual collection periods and Fig. 3 for definition of sample classes.

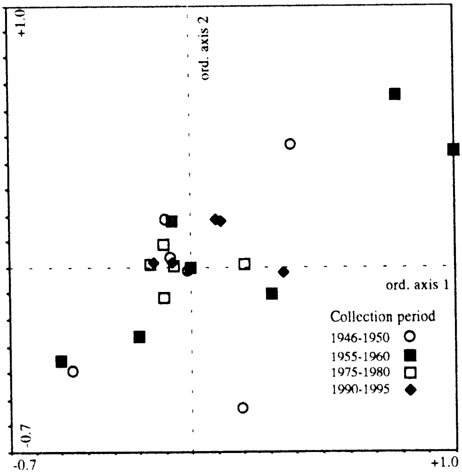


Fig. 6. – Detrended correspondence analysis, ordination plot of localities in individual collection period according to first two ordination axes with respect to collection period. See Fig. 4 for identification of localities position.

ed in quadrant IV, species inhabiting both lotic and lenitic habitats (*Ameletus inopinatus* and *Siphlonurus lacustris*) are placed in quadrant II. Remaining species occupies a place in quadrant I (Fig. 7). Those occurring only at the locality Křemelná, Čeňkova Pila (A) (e.g. *Ephemera danica*, *Habrophlebia lauta* and *Caenis macrura*) are found at the largest distance from the beginning while typical montane species (e.g. *Ecdyonurus forcipula* and *Ephemerella mucronata* are closer to it (Fig. 7).

Discussion and conclusions

As to the number of species, that of the Křemelná basin (Tables 1–6, Figs. 1–2) deserves a particular attention showing this area very important from the protection of biodiversity point of view. Total number of mayfly species so far recorded from the whole Šumava Mts. reached as many as 61 that represented 51 % of species known from Central Europe (Soldán & al. 1996). Of these, 17 species occurred at localities investigated and further 9 species (*Alainites muticus, Cloeon dipterum, Baetis scambus, Nigrobaetis niger, Arthroplea congener* – „red“ species of autochtonous fauna with boreomontane area disjunction for details see e.g. Soldán 1992, *Electrogena affinis, Habroleptoides confusa, Leptophlebia marginata,* and *Ephemerella notata*) were found at other localities of the Křemelná basin (Landa & Soldán, unpubl.). These 28 species thus reach about a half of species number of the mountains. Moreover, most species occur in a relatively very high abundance. Taking into account the elevation of the Křemelná basin and generally decreasing diversity in montane altitudes, this number undoubtedly represents natural state of diversity. Species number is about twice high in comparison with that of other Hercynian mountains of Central Europe (Landa & Soldán 1981). Consequently, the area deserves particular protection since the situation is similar as far as other aquatic macroinvertebrates are concerned (cf. Landa & Soldán 1982, Soldán 1996, Růžičková 1998). Water quality of lotic habitats is very high, reaching, according to diversity of

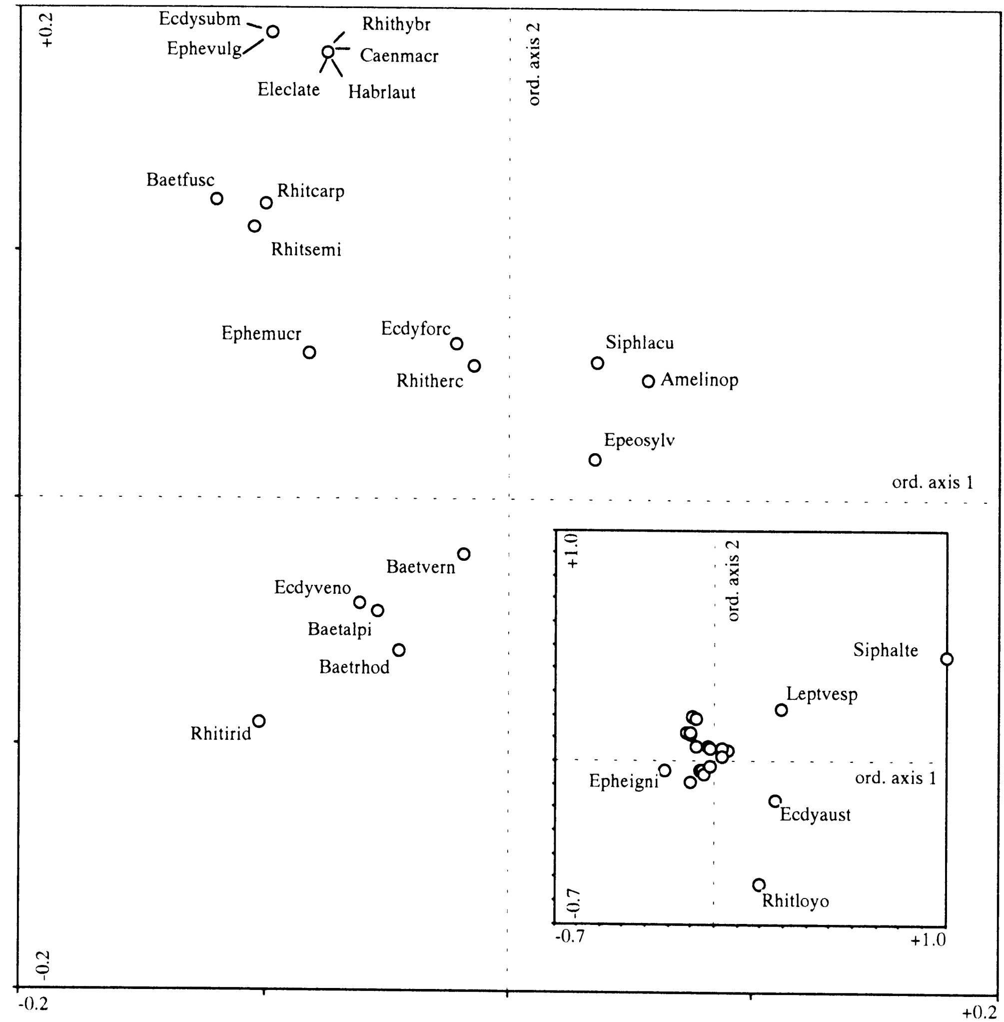


Fig. 7. – Detrended correspondence analysis, ordination plot of species according to first two ordination axes, central part of diagram magnified. See Tables 1–6 for abbreviations of species names.

mayflies, permanently very low values of index of saprobity in the rank of oligosaprobity category (0.91, 0.62 and 0.75 in the Křemelná in sampling periods 2, 3 and 4, respectively – LANDA & SOLDÁN 1989, SOLDÁN & al. 1998).

A comparison of our results with data by RŮŽIČKOVÁ & BENEŠOVÁ (1996) and RŮŽIČKOVÁ (1997, 1998) shows great differences in indexes of diversity (only Shannon-Weaver one can be compared) although approximately the same localities were sampled at the same years (1994–1996, our sampling period 4). Generally, our indexes are much higher (Tables 1–6) reaching even 3.58 at the locality Křemelná, Čeňkova Pila (A). According to our opinion this contradiction is caused by two main circumstances: Samples were determined only to the generic level by the above authors and mostly taken only in spring-summer and summer-autumn season. These facts decrease Shannon-Weaver index rapidly since number of species is strongly reduced. For instance, instead of 6 species of the genus *Rhithrogena* living at the above locality, only a single taxon (*Rhithrogena* sp.) is taken into account.

On the other hand, results of the above authors showing higher diversity in natural biotopes of the Křemelná river basis in comparison with other parts of the mountains (mainly the basin of the upper Vltava river) are in a good agreement with our long-term data. Růžičková (1998) showed the former localities to belong to group characterized by lesser acidification but comparable or slightly higher conductivity. Water pH (often even slightly alkaline in the Křemelná) being clearly higher than average pH range in Central Europe (4.0–7.4) and evidently higher than acidification limits value of 5.5 (Raddum & Skjelkvale 1995) seems to be the main factor responsible for relatively high and stable diversity. The Křemelná basin seems to possess, possibly due to geological conditions, natural buffering capacity responsible for elimination of the effects of naturally dystrophic water and air-borne acid deposits. While pH values at 150 localities of the Labe basin mostly ranged between 5.8–7.5 in the late 1950's and decreased in general by 0.5–1.3 units (Landa & Soldán 1989) the decrease of these value was evidently lower in the Otava river basin although statistically significant (Landa & al. 1984). Acidification „disasters" – enormous and sudden drops of pH sometimes occurring in the Otava basin (Veselý 1996) exert to have no fatal effect to mayfly larvae survival or population recovery (cf. Soldán & al. 1998). This probably concerns also some lotic artificial habitats (e.g. our locality of Vchynický canal, Srní – C) but definitively not lenitic habitats of glacial lakes (see discussion below) even if combined with increased content of nutrient in water sources (Veselý & Majer 1999).

Other environmental variables, like nitrogen and phosphorus content (and/or higher conductivity) do not play such serious role at lotic localities investigated in the Křemelná basin as far as mayflies are concerned. Some other factors, like alkalinity, total hardness or extremely high sulphate hardness in this area (Veselý 1992) seem to have negligible effects on mayfly populations, and moreover, there are nearly no dissolved oxygen deficits also due to relatively low maximal summer temperatures reaching only 9.5–11.5 °C in the montane habitats of the whole mountains (Landa & Soldán 1989), or 10–11 °C directly in the Křemelná basin (Růžičková 1998). The values of lotic localities of the Křemelná river basin never drop below 6–10 mg $O_2.l^{-1}$. On the other hand, as seen at the locality of Vchynický canal (C) and the Křemelná river, Vysoké Lávky (B, sampling period 2, see discussion below), factors like reduced and increased flow, seasonal flow constancy, short-time fluctuation (cf. Ward 1992) and substrate roughness (and periphyton) changes, sedimentation and scouring (cf. Brittain & Saltveit 1989) considerably change and/or affect diversity of mayflies.

Based on diversity indexes and multicriterial analysis method used long-term changes of mayfly diversity at our six selected localities can be characterized as follows: The locality A (Křemelná, Čeňkova Pila) exhibits the highest diversity of mayflies of all the localities investigated (Table 1). As seen from the total number of species found within individual sampling periods (17–13), diversity seems to be relatively stable although this number slowly but regularly decreased during the past 50 years (Fig. 1). Taking into account the TWINSPAN classification relative stability is documented by classification in the same final group in all sampling periods (group *001 with indicator species *Siphlonurus lacustris*, see Fig. 3). Similarly, DCA placed all sampling periods to the same quadrant (I) at position near the beginning and clearly defined, stable diversity is apparent from relatively small respective envelope (Fig. 5). This means, as documented also by ordination of species (Fig. 7), that this locality hosts mostly not specialized abundant species, like e. g. *B. vernus* and *Baetis alpinus* which reach very high degree of dominance, up to nearly 39 % in the latter case (Table 1). However, high diversity at this locality is confined to findings of some non typical species of foothills and the coline zone like *Ephemera vulgata, Caenis macrura, Ecdyonurus submontanus,* *Habrophlebia lauta,* and *Electrogena lateralis* not occurring at higher altitudes at all. Species ordination of DCA placed this species into a compact group situated in quadrant I at the place relatively far from the beginning (Fig. 7). Some very common eurytopic species (*Ephemerella ignita*) are present at this locality, too, but their occurrence seem to represent pessimum of their area lying most in the coline zone or even in lowlands. On the other hand, typical montane species (*Siphlonurus lacustris, Ameletus inopinatus* and *Epeorus sylvicola*) are present at this locality as well being situated in quadrant II near the central part of species ordination space (Fig. 7). To conclude, this situation shows this locality to have stable high water quality and long-term ability to eliminate upstream unfavourable man-induced environmental effects.

The locality Křemelná river, Vysoké Lávky (B) exhibits similar species diversity, however, naturally lower owing to higher elevation. However, this type of relatively stable and high diversity is apparent only in sampling periods 1, 3 and 4 (Fig. 1) while number of species conspicuously decreased in the sampling period 2 (Table 2). This is documented by shift of this sampling period to quite different final group in TWINSPAN classification (Fig. 3). Within this period, the total number of species considerably decreased by more than 50 % and only 4 species, namely *Baetis alpinus, B. rhodani, B. vernus,* and *Ephemerella ignita* were collected, the latter one in negligible abundance (Table 2). These species represent very resistant and eurytopic mayflies able to survive at considerably polluted or disturbed habitats (cf. SOLDÁN & al. 1998). Larvae of these species evidently occupies ecological niches released by more sensitive species (i. e. those having narrower ecological range) mostly of the family *Heptageniidae* (mainly species of the genera *Rhithrogena* and *Ecdyonurus*) and reached extreme abundance as documented in *Baetis alpinus* and *B. rhodani*, showing quantitative presentation of 76.14 or 14.75 %, respectively (Table 2, Fig. 2). The considerable decrease of diversity in the sampling period two can be explained by severe regulation of stream bed at this locality performed in the first half of the 1950's in connection with military activities (construction of new stream chanel and removing the meanders in about 3 km long upstream river segment). However, the original diversity apparently at least partly recovered during following sampling periods although the quantitative presentation of *B. alpinus* and *B. rhodani* remained very high reaching up to nearly 25 % in the former species. This situation seems to be usual in mayfly taxocoene changes followed the stream regulation as well as organic pollution (BRITTAIN & SALTVEIT 1989, WARD 1992, SOLDÁN et al. 1998).

The locality of Vchynický canal exhibits rather not well understood changes of diversity as documented by TWINSPAN classification. Individual sampling periods are classified even within 3 final groups (Fig. 3) and ordination of localities shows this locality situated in 3 quadrants (Fig. 4). Evidently, long-term tendency in diversity development is characterized by a great faunistic exchange. Although only 4–6 species were found in each sampling period, the quantitative composition of this taxocoene differed considerably. With the period 1 species of the *Baetidae* (*Baetis alpinus* and *B. vernus*) were dominant with a great percentage of *Ephemerella ignita* (Table 3). However, within the following periods the quantitative presentation of the Heptageniidae and then Siphlonuridae and Ameletidae (*Siphlonurus lacustris* and *Ameletus inopinatus*) increased (Table 3). These diversity changes (and low mayfly diversity in general) most probably depends on strong discharge fluctuation at this locality and irregular water level manipulation.

As far as the number of species is concerned, similar diversity has been found at the locality Prášilský brook, Prášily (Table 4). Contrary to streams of similar type in different river basins, e.g. in the Vltava river ones, this locality is inhabited by surprisingly low number of species of mayflies (cf. LANDA & SOLDÁN 1989, SOLDÁN & al. 1998). *Baetis alpinus* is the only dominating species and species of the Heptageniidae are found very rarely and only several specimens of typical montane species, *Siphlonurus lacustris* and *Ameletus inopinatus* were colleced here (Table 4). According to the TWINSPAN classification coenological conditions are even similar to those of the locality of an artificial habitat (Vchynický canal, C). Ordination of localities (Fig. 4) shows sampling periods of this place to be scattered in three quadrants in various distance from the beginning. Low mayfly diversity might be explained by the effects of organic pollution since it is situated below the village of Prášily. However, evidently more sensitive stonefly species are present here, some of them (e.g. *Brachyptera seticornis* and some species of the genus *Leuctra*) in relatively very high abundances.

On the other hand, the locality of Slatinný brook, Gerlova Huť (E) shows stable and not very fluctuating diversity of mayflies within the past 50 years. The taxocoene is well characterized by the occurrence of typical montane species, like e. g. *Epeorus sylvicola, Ecdyonurus forcipula, E. austriacus, Rhithrogena loyolaea* and *Leptophlebia vespertina*, most of them being good indicators for respective groups of TWINSPAN classification (Fig. 3). All four sampling periods are classified within the same final group. Although some changes of quantitative presentation of individual species are apparent, no clear tendency perhaps except for those to increase the numbers of *Baetis alpinus* in sampling period 3 and 4 can be defined (Fig. 2) and almost all sampling periods are classified in the same quadrant in ordination plot of localities (Fig. 4) although the respective TWINSPAN samples envelope is larger than that of localities the Křemelná river (Figs. 5, 6). Moreover, rare and local montane species (*Rhithrogena loyolaea*) or species endemic to the Alps and the Šumava Mts. (*Ecdyonurus austriacus*) are being frequently found at this locality.

The locality of the Prášilské lake (F) exhibits the smallest diversity of mayflies of all the localities investigated in the Křemelná river basin. Altogether 4 species (Table 4) have been found here within the past 50 years but since the 1960's the only species, *Leptophlebia vespertina*, has been collecting at this place. Owing to this extremely low diversity even diminished during the last two sampling period this locality is classified as an isolated one, separated by the first TWINSPAN division and naturally further divided with respect to indicator species *Leptophlebia vespertina* (Fig. 3). Contrary to the above localities, mayfly diversity changes caused by acidification process can be clearly defined in this case. Acidification process of the Šumava Mts. glacial lakes is relatively well understood (see. e.g. review by Veselý 1994) as well as the process of mayfly diversity reduction. The *Heptageniidae* are gradually replaced by relatively tolerant species of the family *Baetidae* and these are, in final stage replaced by species of the genera *Siphlonurus* and *Leptophlebia* as seen not only in Scandinavian lakes (Harmanen 1980) but also in some Hercynian mountains in Central Europe (Landa & Soldán 1989, Soldán & al. 1998). Since *L. vespertina* represents the most tolerant mayfly species to acidification with tolerance limits round pH of 4.0 (Egblom & Lingdell 1983) it is naturally the only species inhabiting glacial lakes in the Šumava Mts. at present. Like in some Scandinavian lakes this species seems to increase its quantitative presentation in connection with the processes of acidification and recent recovery (cf. Raddum & Fjellheim 1995).

Acknowledgements. Our thank are due to the Grant Agency of Czech Republic for the support of this study by grant No. 206/99/0405. We would like to thank Dr. J. Matěna of the Institute of Hydrobiology, České Budějovice who offered valuable comments to the manuscript.

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