

Long-term limnological research of the Bohemian Forest lakes and their recent status

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Abstract

We present an extensive review of long-term changes in chemistry and biology of all glacial lakes of the Bohemian Forest (Böhmerwald, Šumava). Owing to almost 130-year occasional hydrobiological research we are able to document significant changes in plankton composition, in particular conspicuous reduction of crustacean species in some lakes and extinction of fish as well. Major changes in lakewater chemistry were running in parallel to the changes in biota. From trends in sulphate and nitrate concentrations and from palaeolimnological evidence as well we can estimate the timing of the periods of atmospheric acidification, maximum acidity and reversal from acidity. The atmospheric acidification of all lakes started presumably since the 1950s, with certainty since the 1960s. It peaked in the late 1970s and the first half of 1980s and the pronounced reversal has taken place since the late 1980s. As a consequence of different loading with acidifying agents and with nutrients the lakes represent a fascinating set of unique freshwater bodies. At present we can categorise the Bohemian Forest lakes as follows: (i) Rachelsee, Plešné, Černé and Čertovo Lakes remain strongly acidified; (ii) Prášilské Lake and Kleiner Arbersee are moderately acidified; whereas (iii) Grosser Arbersee and Laka Lake reveal only slight acidity. The lakes represent a great potential for long-term ecological research of atmospheric quality development in Central Europe and its impact on both lake and forest ecosystems.

Key words: forested lakes, atmospheric deposition, hydrochemistry, plankton, fish, lake acidification, lake reversal, lake recovery, palaeolimnology

Introduction

More than 10,000 years ago eleven local slope glaciers shaped corries on slopes of the central summit of the Bohemian Forest (Šumava or Böhmerwald, including Bayerischer Wald, JENÍK 1996). During the postglacial era altogether eight small lakes have been preserved along a historical borderline between Czechia and Bavaria at altitudes between 900 and 1100 m – five of them (Černé, Čertovo, Plešné, Prášilské, and Laka) in Czechia and three (Rachelsee, Grosser Arbersee, and Kleiner Arbersee) in Bavaria (Table 1, VESELÝ 1994).

The first written notice mentioning Grosser Arbersee and Kleiner Arbersee was recorded in 1076 (ŠVAMBERA 1913, 1914a) though the Benedictine order settled in the adjacent region of these lakes even since the 8th century (STEINBERG & HARTMANN-ZAHN 1989). Due to an apparently easier access to the Bavarian lakes, the anthropogenic influence upon them has been manifold since the Middle Ages; the adjacent town of Bodenmais was founded in the 13th century (ARZET & al. 1986, STEINBERG & HARTMANN-ZAHN 1989). Palynological evidence (VESELÝ 1998) has suggested certain medieval land use also at some Czech lakes but historical records have shown later human impact (since the 16th century, VESELÝ 1994). Various human

Table 1. – Main characteristics of all glacial lakes in the Bohemian Forest (CN, CT, PL, LA – ŠVAMBERA 1939; PR – ZBORIL 1996; RA, GA, KA – BAYERSCHES LANDESAMT FÜR WASSERWIRTSCHAFT 1987); the lakes are ordered according to the decreasing ratio of lake volume to catchment area, which may be also considered as a rough estimate of lake retention times (in years).

name (used in English)	Lake		Location		Lake			Catchment		Lake volume: Catchment area (m ³ m ⁻²)
	Czech and German toponyms (synonyms)	code	latitude longitude	altitude (m)	surface (ha)	depth (m)	volume (10 ⁶ m ³)	area (km ²)	forest bedrock	
Černé Lake	C: Černé jezero G: Schwarzer See	CN	49°11' N 13°11' E	1008	18.4	40	2.88	1.29	Norway spruce mica-schist	2.23
Čertovo Lake	C: Čertovo jezero G: Teufelsee	CT	49°10' N 13°12' E	1028	10.3	36	1.85	0.86	Norway spruce mica-schist	2.15
Plešné Lake	C: Plešné (Plöckensteinské, Balvanité) jezero G: Plöckensteiner See	PL	48°47' N 13°52' E	1090	7.5	18	0.62	0.67	Norway spruce granit	0.93
Prášilské Lake	C: Prášilské jezero G: Stubenbacher See	PR	49°05' N 13°24' E	1079	4.2	16	0.35	0.65	Norway spruce mica-schist & granit	0.54
Rachelsee	C: Roklanské jezero G: Rachelsee	RA	48°58' N 13°24' E	1071	5.7	13	0.18	0.58	Norway spruce gneiss	0.31
Grosser Arbersee	C: Velké Javorské jezero G: Großer Arbersee	GA	49°06' N 13°07' E	935	7.7	16	0.45	2.58	Norway spruce & beech gneiss	0.17
Kleiner Arbersee	C: Malé Javorské jezero G: Kleiner Arbersee	KA	49°08' N 13°09' E	918	9.4	9	0.25	2.79	Norway spruce & beech gneiss	0.09
Laka Lake	C: jezero Laka (Pleso) G: Lakkasee (Lackasee)	LA	49°07' N 13°20' E	1096	2.8	3	0.04	1.35	Norway spruce gneiss	0.03

activities have been documented at most of Bohemian Forest lakes, such as local ore prospecting, mining and smelting, logging of the forests, glasswork, cattle grazing, forest management, dam and sluice construction (for timber transport) with consequent water level manipulation, fishing and fish introduction, etc. (for review see VESELY 1994). On the other hand, recent evaluation of archive materials (VICENA, unpubl.) has suggested that, unlike the western Bohemian Forest lakes, Plešné Lake and its forested catchment has remained less affected till this century, except for water level manipulations of the lake itself. During this century all the Bohemian Forest lakes have reached certain degree of nature protection, which has led to more or less reduction and control of any kind of land use.

While five of the Bohemian Forest lakes represent the only natural lakes in the Czech Republic, the three others account for a very minor part of the entire "lake population" in Germany. Perhaps due to this fact, more hydrobiological efforts on the lakes have been fulfilled by Czech investigators of the 19th century then by German ones. The first hydrobiological survey of all the Bohemian Forest lakes was performed almost 130 years ago by FRIC (1872, 1873). Since then occasional hydrobiological research has continued, in particular on Černé Lake (Table 2, VESELY 1994). During the last two decades limnological research of the Bohemian Forest lakes has intensified on both Bavarian side (e.g., STEINBERG & al. 1984a-c, 1985, 1988, 1991, ARZET & al. 1986, SCHAUMBURG 2000) and Czech side (e.g., FOTT & al. 1980, 1987, 1994, VESELY 1987, 1988, VESELY & MAJER 1992, VESELY & al. 1993, 1998, VRBA & al. 1996, KOPÁČEK & al. 1998a, 2000a) as a result of emerging atmospheric acidification, which has affected lakewater chemistry. As a direct consequence of these changes, unique lake ecosystems with a dominant role of microorganisms in pelagic food webs have recently developed (VRBA & al. 1996).

This study extends VESELY's (1994) review by including an overview of former research of all the Bohemian Forest lakes and presents their comparison using limnological criteria. We intend to summarise apparent trends in hydrochemistry of lake water and in plankton composition which can be gathered from early Czech and German literature and from our own experience as well. Furthermore, we intend to evaluate and estimate if the ongoing reversal of the lake water chemistry is followed by a biological recovery. Thus, the paper summarises a great potential of the Bohemian Forest lakes for long-term ecological research of atmospheric quality development in Central Europe, global climate changes, and their impacts on the lake as well as forest ecosystems.

Recent trends in water chemistry reflect those in atmospheric deposition

As the Bohemian Forest lakes are situated in rather small geologically sensitive catchments forested predominantly by Norway spruce (Table 1), first signs of lake water acidification had been observed as early as at the beginning of the 1960s (PROCHÁZKOVÁ & BLAŽKA 1999). Despite certain gaps in water chemistry data, Fig. 1 clearly demonstrates that the lake water chemistry has followed trends in emissions of sulphur and nitrogen in Central Europe. From the trends in sulphate and nitrate concentrations (Fig. 1) we can estimate the timing of the period of acidification, maximum acidity, and reversal from acidity. The atmospheric acidification started presumably since the 1950s, with certainty since the 1960s. It peaked in the late 1970s and the first half of 1980s (FOTT & al. 1980, 1987, 1994, STEINBERG & al. 1984a, ARZET & al. 1986, VESELY 1987) and the pronounced reversal has taken place since the late 1980s. Recent studies have already suggested a slight reversal from both lake acidity and high nitrogen export from the catchments (KOPÁČEK & al. 1998a, VESELY & al. 1998, SCHAUMBURG 2000).

However, the first analytical data must be considered with caution (e.g., those in WAGNER

Table 2. – Historical and recent (late summer 1999) data on Secchi depth (z_s) and some water colour characteristics (*in italic*) of the Bohemian Forest lakes (see Table 1 for their codes).

	CN	CT	PL	PR	RA	GA	KA	LA	Reference
1893–1896, z_s (m)	2.4–2.6	4.3							FRIC & VÁVRA 1898
1896, z_s (m)	3.3	2.3	2	3.5	2.8	4.1			WAGNER 1897
colour	yellow-brown	almost black	dark brown	brown	dark brown	dark brown			
(<i>ULÉ's scale</i>)	(12–13)	(15)	(14)	(13–14)	(16)	(15)			
1903–1912, z_s (m)	4.5–8.5		≤3.3	4–5		4.5–4.7	2.6	3.5–4 ¹⁾	ŠVAMBERA 1912, 1913, 1914a–c,
colour			dark brown	very dark		dark brown	dark brown		KUCHAR 1939
(<i>ULÉ's scale</i>)			(14–15)	(16)		(16)	(15)	(15)	
1936, z_s (m)	2–4							2	JIROVEC & JIROVCOVÁ 1937
colour	deep green							yellow-brown	
(<i>ULÉ's scale</i>)	(9–10)								
1947, z_s (m)	4								WEISER 1947
1960–1961, z_s (m)	8–14		1.5–1.7	3.5–8				2.5–3	PROCHÁZKOVÁ & BLAŽKA 1999
colour (mg Pt/l ¹⁾)	(5)	(<5)	(5–10)	(<5–15)				(5–25)	
1961–1962, z_s (m)			2.4–3.2						NOVÁK 1968
1964–1965, z_s (m)	15	6	1.5					2.5–3	HROUSKA 1979
1979–1986, z_s (m)	5–15.6	5.8–9.6	2.8	4				3.3 ¹⁾	FOTT & al., unpubl.
1982–1983, z_s (m)						10	5.5		ARZET & al. 1986, ARZET 1987
1986–1988, z_s (m)	8.5–9	4.3						2.6 ¹⁾	KOPÁČEK & al., unpubl.
1990–1993, z_s (m)	4.5–11		1.8–2.9	2.6–7					KOPÁČEK & al., unpubl.
1994, z_s (m)			2–3.5						HEJZLAR & al. 1998
1997–1998, z_s (m)	6.2–10	3.5–6	1.1–2.8	2.7–6.7					this study
1999, z_s (m)	4.5	2.9	1.5	2.9	7.9	4.8	3.0	2.6 ¹⁾	this study
A_{254} ²⁾	0.038	0.085	0.080	0.176	0.012	0.089	0.123	0.173	
A_{354} ²⁾	0.003	0.007	0.006	0.017	0.001	0.008	0.012	0.019	
sur. – A_{254}/DOC ³⁾	20.2	36.0	34.5	49.3	15.2	43.9	50.0	50.5	
in. – A_{354}/DOC ³⁾	43.7	41.7	54.2	62.5	46.0	53.0	55.5	60.6	

¹⁾ bottom (vegetation); ²⁾ A_{254} and A_{354} – absorbances at 254 and 400 nm (1 cm absorption path); ³⁾ A_{254}/DOC (in $m^2 mol^{-1}$) – molar absorptivities of dissolved organic matter at 254 nm, i.e. ratios of A_{254} (1 m absorption path) to DOC concentrations ($mol m^{-3}$); KOPÁČEK & HEJZLAR 1998) of surface lake water (sur.) and input waters (in., volume-weighted means of all tributaries)

1897, FRIČ & VÁVRA 1898, ŠVAMBERA 1913, 1914a). Perhaps the first most reliable and conspicuous long-term changes of water quality due to anthropogenic acidification have been recorded in colour and transparency. Table 2 summarises most of available information on water colour and Secchi depth records. At the beginning of the 20th century and earlier, visitors (e.g., GÜMBEL 1868) had referred to colour of lake water as "black", i.e. between dark brown and yellow-brown. Both WAGNER (1897) and ŠVAMBERA (1914a), however, considered information on "lake colour" as very subjective unless measured properly. Therefore, we refer to their values of the ULE's scale, which allow some inter-lake comparison of the pre-acidification status. However, these data cannot be compared with the recent ones without a comparison of historical and modern methods. Nevertheless, the historical data (Table 2) allow making the following qualitative conclusions.

First, unlike at present, all the Bohemian Forest lakes had humic dark brown water a century ago. ŠVAMBERA (1914a) considered Rachelsee as the darkest lake in the Bohemian Forest, followed by Grosser Arbersee and Čertovo Lake. The names of two other lakes came from their "black" colour. Besides Černé Lake (Schwarzer See, Table 1), also Plešné Lake was called "Černé" (Black) by local people.

Second, during the period of atmospheric acidification some lakes, in particular Černé and Čertovo Lakes, Grosser Arbersee and Rachelsee became obviously more transparent and clear, getting apparently a bluish colour. Other ones (e.g., Plešné Lake) did not change very much so far (Table 2). Such changes in water transparency and colour could reflect a reduction of chromophoric organic matter (cf. NÜRNBERG & SHAW 1998). Precipitation of humic substances followed by increasing transparency was observed in many lakes as a consequence of their atmospheric acidification (STEINBERG & KÜHNEL 1987). Sediment chemistry of Kleiner Arbersee and Grosser Arbersee revealed further evidence of the organic matter decrease in the lake water during its acidification process (STEINBERG 1991, STEINBERG & al. 1991).

Nowadays, most of the lakes have a more humic nature (brownish colour) again, except for Rachelsee, which is still clear and bluish. This different nature can be well demonstrated by comparing absorbances (A_{254} and A_{400}) and molar absorptivities ($A_{254}:\text{DOC}$, Table 2), which may be considered as certain measure of water colour (KOPÁČEK & HEJZLAR 1998). At present the darkest water has been recorded in Laka, Prášílské Lake, and Kleiner Arbersee, followed by Grosser Arbersee, Čertovo and Plešné Lakes. Unlike a century ago when Rachelsee was the most coloured lake, now it is the clearest of all the lakes. However, the tributaries supply similarly coloured humic water into all the Bohemian Forest lakes (see the bottom row in Table 2).

The first reliable data on lakewater chemistry of Černé, Čertovo, and Laka Lakes come from 1936 (JÍROVEC & JÍROVCOVÁ 1937). These data are usually considered as background values of the pre-acidification period. JÍROVEC & JÍROVCOVÁ (1937) reported almost neutral pH in the surface layers of Laka (6.6–7.2) and Černé Lakes (6.3–7.0) and pH decreasing towards the bottom (5.9–6.2). Such a pattern is common in bicarbonate lakes (WETZEL 1983). Ten years later WEISER (1947) recorded pH = 6.2 at the surface of Černé Lake. In Čertovo Lake, however, remarkably lower pH (5.4–6.9) was reported already in 1936 (JÍROVEC & JÍROVCOVÁ 1937) as well as in 1956 (pH = 4.7, LANDA & al. 1984) on the surface. According to palaeolimnological evidence (VESELÝ & al. 1993) Čertovo Lake has been acidic for several centuries.

The next sampling survey of five Czech lakes in 1959–1961 already showed first indications of atmospheric acidification (PROCHÁZKOVÁ & BLAŽKA 1999). The surface pH values varied between 5.0–6.2 but vertical pH profiles still exhibited a slight decrease towards the bottom suggesting presence of carbonate buffering system. Concentrations of nitrate (NO_3^-)

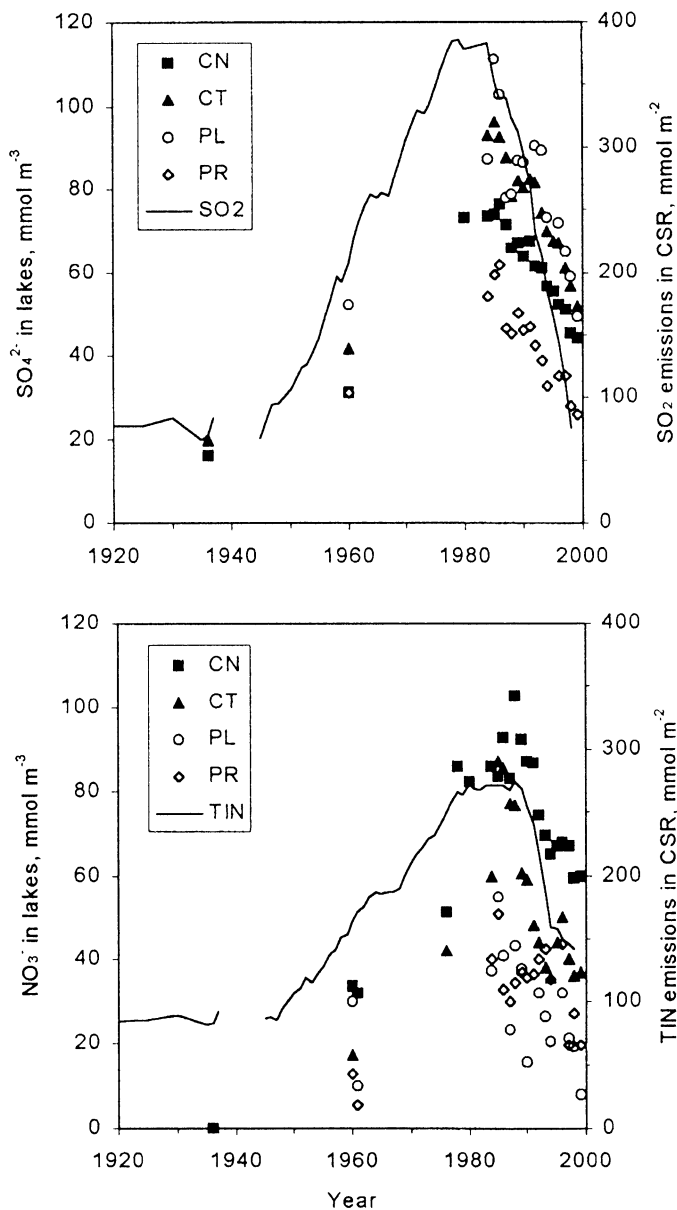


Fig. 1. – Emissions (solid lines) of SO_2 (top) and total inorganic nitrogen, $\text{TIN} = \text{NH}_3\text{-N} + \text{NO}_3\text{-N}$ (bottom), in former Czechoslovakia (CSR) and autumn concentrations of SO_4^{2-} and NO_3^- in the Bohemian Forest lakes. The Czechoslovak emission trends before 1980 for SO_2 and before 1985 for TIN were calculated from the data of the Czechoslovak Statistical Office on fossil fuel consumption, livestock production, application rate of nitrogen fertilizers, and industrial sources (KOPÁČEK & al. 1998a) according to: (i) VARHELYI (1985), SO_2 ; (ii) PACYNA & al. (1991), NO_3^- ; and (iii) and ASMAN & al. (1988), NH_3 . The emission trends of SO_2 and TIN after 1980 and 1985, respectively, are based on the emission data supplied by Czechoslovak (till 1992) and both Czech and Slovak Statistical Offices (since 1993). Concentrations of SO_4^{2-} and NO_3^- in the lakes (see codes in Table 1) come from JIROVEC & JIROVCOVÁ (1937), PROCHÁZKOVÁ & BLÁŽKA (1999), VESELY & MAJER (1992), VESELY & al. (1998), and KOPÁČEK (unpubl.).

were already elevated (Fig. 1) compared to the data of JÍROVEC & JÍROVCOVÁ (1937). Twenty years later Černé Lake was strongly acidified, with pH values as low as 4.2–4.5 in the surface layer and an increasing pattern of pH towards the bottom (FOTT & al. 1980). However, reverse pumping of river water upwards into Černé Lake, performed by a small hydroelectric power plant since 1930 to 1975, could have influenced water quality and mitigate acidification process of this lake to an unknown degree (FOTT & al. 1994). Nevertheless, the atmospheric acidification of all the Bohemian Forest lakes obviously peaked at the same time, i.e. on the turn of the 1970s and 1980s (LANDA & al. 1984, STEINBERG & al. 1984a, ARZET & al. 1986, FOTT & al. 1987, VESELÝ 1987). Both pH and acid neutralising capacity (ANC) were always higher in Laka Lake (usually: pH > 5 and positive ANC) than in the other Bohemian Forest lakes (FOTT & al. 1987, VESELÝ & al. 1998, KOPÁČEK, unpubl.). Thus only episodic acidification was recorded in Laka Lake likely due to a relatively large but not steep catchment area (Table 1) with more developed soils. In Grosser Arbersee pH usually varied around 5 during the last 15 years (WEILNER 1997, SCHAUMBURG 2000).

Both SO_4^{2-} and NO_3^- concentrations in the lake water clearly followed increasing emission trends of SO_2 and total inorganic nitrogen (TIN = $\text{NH}_3\text{-N}$ + $\text{NO}_x\text{-N}$), respectively, after the World War II (Fig. 1). They became the major anions in the lake water in the early 1980s when negative values of ANC (GRAN titration) demonstrated absence of the carbonate buffering system in the Bohemian Forest lakes. During the last 15 years SO_4^{2-} and NO_3^- concentrations in lakes declined due to ~ 80% and ~ 40% drops in the SO_2 and TIN emissions, respectively, in the region (Fig. 1, VESELÝ & al. 1998, SCHAUMBURG 2000).

Unlike sulphate, biogeochemical cycle of nitrogen is more affected by biochemical processes in soils, water, and sediments (cf. VAN MIEGROET 1994). Originally, all forms of inorganic nitrogen were close to or even below detection limits in Černé and Čertovo Lakes (JÍROVEC & JÍROVCOVÁ 1937, cf. Fig. 1) suggesting N limitation of the forest in their catchments. Then NO_3^- concentration in all lakes increased continuously (1960–1990) suggesting that atmospheric input of TIN exceeded the catchment N demand and led to an elevated terrestrial export of N. The development of the last decade has suggested a reversal from the high terrestrial losses of N (Fig. 1). This trend, however, has not been observed in Prášílské Lake and Rachelsee. In their catchments gales and bark beetle infestation caused significant damage of the forest during the last ~ 15 years (VESELÝ & al. 1998, SCHAUMBURG 2000), which drastically reduced N uptake by the forest and increased rates of N mineralisation (ANDERSON & al. 2000). These changes have resulted in the persisting higher level of NO_3^- concentrations in these lakes. The effect of in-lake processes on NO_3^- concentrations has been documented for Prášílské and Plešné Lakes (HEJZLAR & al. 1998, ANDERSON & al. 2000, KOPÁČEK & al. 2000a). More scattered and lower NO_3^- concentrations in these more productive lakes compared to oligotrophic Čertovo and Černé Lakes (Fig. 1) have been associated with higher denitrification rates in the water column.

We have no information on aluminium in the lakes before mid the 1980s, when the concentrations of total aluminium (Al_T) were ~ 1 mg l⁻¹ (except for Laka and Prášílské Lakes). Decreasing trends of Al_T in all the Bohemian Forest lakes during the last 15 years (VESELÝ & al. 1998, SCHAUMBURG 2000) obviously have reflected the rapid reversal from the lake acidity. In addition, the parallel changes toward more humic lake water (see above and Table 2) have suggested indirect evidence of a controlling role of Al on dissolved humic substances under acidified conditions described by STEINBERG & KÜHNEL (1987). Furthermore, our recent studies have revealed that Al_T loading of lakes (cf. KOPÁČEK & HEJZLAR 1998) as well as in-lake processes controlling Al speciation are the key factors determining phosphorus availability (KOPÁČEK & al. 1999, 2000a, VRBA & al., in prep.).

Table 3. – Present (late summer 1999) selected chemical parameters of input waters (in., volume-weighted means) and both surface (sur., 0.5 m depth) and bottom (bot., ~ 0.5 m above the sediment) water chemistry and plankton parameters of all the Bohemian Forest lakes (same order and codes as in Table 1; for explanation, see footnotes; for details of all chemical analyses, see KOPÁČEK & al. 2000a,b).

Lake	Depth	DO ¹⁾	pH ²⁾	ANC ³⁾	DOC ⁴⁾	TP ⁵⁾	NH ₄ ⁺ -N	NO ₃ ⁻ -N	TON ⁶⁾	R-Si ⁷⁾	Chl _a ⁸⁾	HMB ⁹⁾	SO ₄ ²⁻	Cl ⁻	Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺	Fe ₂ ¹⁰⁾	Al ¹¹⁾	Al ¹¹⁾	Al ¹¹⁾	Al ¹¹⁾	Al ¹¹⁾
	m	mg l ⁻¹		μmol l ⁻¹	mg l ⁻¹	μg l ⁻¹	μg l ⁻¹	μg l ⁻¹	μg l ⁻¹	mg l ⁻¹	μg l ⁻¹	μg C l ⁻¹	mg l ⁻¹	mg l ⁻¹	mg l ⁻¹	mg l ⁻¹	mg l ⁻¹	mg l ⁻¹	μg l ⁻¹	μg l ⁻¹	μg l ⁻¹	μg l ⁻¹	μg l ⁻¹	μg l ⁻¹
CN-in.			4.36	-50	2.84	2.4	6	817	181	2.40			5.23	0.53	0.86	0.28	0.92	0.46	42	420	358	56	6	
CN-sur.	0.5	8.75	4.78	-23	2.25	4.1	25	803	240	1.72	3.6	308	4.06	0.56	0.71	0.43	1.05	0.46	68	307	267	11	29	
CN-bot.	37	5.70	4.97	-9	1.24	3.0	157	720		1.82		53	4.16	0.63	0.79	0.57	1.03	0.50	124	254	177	8	70	
CT-in.			4.34	-57	5.16	3.6	1	368	193	2.42			4.80	0.58	0.92	0.18	0.69	0.34	157	273	171	89	14	
CT-sur.	0.5	8.58	4.50	-49	2.83	5.4	8	468	280	1.48	4.9	284	4.67	0.46	0.56	0.28	0.79	0.32	154	420	390	18	12	
CT-bot.	31.5	0.20	5.54	28	4.77	10.6	361	210		1.76	3.1	51	4.68	0.56	0.58	0.40	0.68	0.35	2363	511	60	202	250	
PL-in.			4.36	-48	5.62	18.7	53	876	200	4.98			5.59	0.34	1.29	0.41	0.99	0.18	93	669	535	135	0	
PL-sur.	0.5	9.17	5.17	-2	2.77	8.9	17	53	352	2.56	34.7	318	4.56	0.39	1.11	0.32	0.92	0.19	70	291	56	24	212	
PL-bot.	17.3	0.46	5.84	70	5.58	26.6	949	23		3.03	8.4	162	4.15	0.43	1.01	0.40	0.95	0.16	829	502	11	283	209	
PR-in.			4.89	-20	4.27	4.3	28	451	142	2.34			1.91	0.66	0.99	0.23	0.59	0.28	182	148	47	97	4	
PR-sur.	0.5	8.56	5.08	-11	4.29	5.5	32	209	283	1.31	6.7	103	2.41	0.46	0.63	0.26	0.59	0.28	101	198	49	74	76	
PR-bot.	1.5	0.40	5.70	80	6.38	23.5	497	6		2.12	4.8	139	2.55	0.54	0.65	0.47	0.75	0.36	2108	424	64	155	206	
RA-in.			4.37	-52	3.49	2.1	52	1507	192	2.47			4.04	0.48	0.79	0.44	0.79	0.51	45	555	454	101	5	
RA-sur.	0.5	8.20	4.97	-20	0.91	2.7	41	657	182	1.66	1.7	167	3.00	0.41	0.60	0.38	0.69	0.34	58	261	104	5	153	
RA-bot.	12.5	0.10	5.93	151	3.21	11.3	912	13		2.45	13.3	240	2.02	0.51	0.67	0.39	0.80	0.40	1960	354	32	116	207	
GA-in.			5.54	15	2.47	3.2	3	430	146	3.11			2.73	0.50	1.05	0.18	0.83	0.36	50	100	20	64	16	
GA-sur.	0.5	8.20	5.91	14	2.43	6.2	21	309	235	2.06	3.8	126	3.24	0.35	0.81	0.24	1.12	0.36	75	113	14	44	55	
GA-bot.	15.5	0.50	6.17	205	3.63	24.2	483	0		3.21		78	2.58	0.56	1.04	0.53	2.76	0.58	3274	382	23	169	191	
KA-in.			4.88	-13	2.65	4.6	0	365	172	2.49			3.58	0.53	0.92	0.13	0.67	0.31	64	163	72	79	12	
KA-sur.	0.5	8.26	5.51	-1	2.95	7.2	21	178	255	1.34	3.2	62	3.08	0.41	0.78	0.17	0.56	0.26	160	135	30	75	31	
KA-bot.	8	0.54	5.48	30	2.45	12.0	373	197		1.65		35	3.09	0.37	0.59	0.31	0.67	0.24	973	250	14	29	207	
LA-in.			5.65	16	2.45	2.3	5	790	165	3.25			1.55	0.64	1.16	0.33	0.85	0.43	79	68	12	51	5	
LA-sur.	0.5	8.96	5.81	16	4.10	6.4	18	409	352	1.73	5.0	127	1.63	0.59	1.00	0.29	0.73	0.37	195	109	6	57	47	
LA-bot.	2.5	9.12	5.92	21	3.64	7.2	22	411		1.17	7.7	83	1.56	0.56	1.00	0.26	0.80	0.40	347	115	7	74	35	

¹⁾ DO – dissolved oxygen (DataSonde 4, Hydrolab); ²⁾ in laboratory; ³⁾ ANC – acid neutralising capacity (GRAN titration); ⁴⁾ DOC – dissolved organic carbon (LiquiTOC, Foss/Heraeus); ⁵⁾ TP – total phosphorus (molybdate method after perchloric acid digestion); ⁶⁾ TON – total organic nitrogen (Kjeldahl digestion and distillation); ⁷⁾ R-Si – reactive silica (molybdate method); ⁸⁾ Chl_a – chlorophyll *a* (determined on Whatman GF/C filters after acetone extraction, spectrophotometrically, uncorrected); ⁹⁾ HMB – heterotrophic microbial biomass (see Fig. 3 for details); ¹⁰⁾ Fe₂ – total iron (thiocyanate method after perchloric acid digestion); ¹¹⁾ Al_{tot}, Al_{org}, Al_{part}, Al_{part}, Al_{part}, Al_{part} – total, particulate, dissolved organic, and ionic aluminium forms, respectively (for Al speciation, see KOPÁČEK & al. 2000a).

Recent status of the lakes and their comparison

In order to assess the present status of the Bohemian Forest lakes in a comparable way, we observed all the lakes with the same sampling strategy in the 1999 late summer (August 31–September 9). The lakes were sampled from an inflatable boat at the points of their maximum depth; all tributaries of each lake were sampled according to KOPÁČEK & al. (2000b). Complete methods of chemical analyses (see also footnotes in Table 3), data processing and statistics are described in KOPÁČEK & al. (2000a,b)

Table 3 shows main results of chemical and plankton analyses of both surface and bottom water, as well as volume-weighted mean chemical composition of all surface tributaries. The lakes revealed, besides some common features, conspicuous inter-lake differences. Except of the shallow Laka Lake the seven other lakes were stratified. Concentrations of dissolved oxygen (DO) followed clinograde distributions with more or less pronounced oxygen deficit at the bottom, except for Černé and Laka Lakes (see bottom values of DO in Table 3). However, the data in Table 3 are based on samples from 0.5–1 m above the bottom, whereas anoxia was found closer to the bottom of the six lakes. The oxygen depletion was accompanied by reduction of NO_3^- (in all lakes but Laka) and SO_4^{2-} (only in Rachelsee, Grosser Arbersee, and Plešné L.) above the bottom. These processes contributed importantly to the in-lake alkalinity (ANC) generation (Table 3), which partly mitigated the lake acidity (cf. KOPÁČEK & al. 1999, 2000a). Grosser Arbersee showed the highest pH among all the lakes, whereas it was acidified in the 1980s (cf. ARZET & al. 1986, WEILNER 1997). In addition, the exceptionally high calcium concentration (2.76 mg l^{-1}) above the bottom (Table 3) suggested different chemistry in this lake. To our opinion, this difference can be explained by a liming in the Grosser Arbersee catchment. However, we have not yet been able to find out any confirmation of such a treatment.

Table 4 summarises the chemistry of both tributaries and surface lake water given in Table 3 with respect to the most relevant factors for the acidity and/or trophic status of the lakes; parameters of phytoplankton biomass (chlorophyll *a* (Chl_a) concentration) and heterotrophic microbial biomass (HMB) are compared as well. Except for Grosser Arbersee and Laka Lake, the tributaries of other lakes showed signs of the atmospheric acidification like low pH and ANC, and high concentrations of Al forms, SO_4^{2-} , and NO_3^- .

We could clearly distinguish a group of four lakes (Rachelsee, Plešné, Černé and Čertovo), which were strongly acidified at present and reflected higher loading of acidifying compounds (input: pH < 4.4, ANC ~ $-50 \mu\text{mol l}^{-1}$, Table 3). Čertovo Lake received and even retained the most acid water (lowest pH and ANC), while Plešné Lake was subjected to the highest input of Al, SO_4^{2-} , and DOC (Table 4, KOPÁČEK & HEJZLAR 1998). On the other hand, Rachelsee was exposed to two- to three-times higher NO_3^- loading than any other Bohemian Forest lake, which most likely reflected the reduced NO_3^- bioconsumption in the Rachelsee catchment due to current dying out of bark-beetle invaded spruce trees. In Rachelsee and Plešné Lake, biochemical reduction of NO_3^- and SO_4^{2-} increased both alkalinity and pH above the bottom. Enhanced consumption of N by the very high plankton biomass (Chl_a and HMB) contributed to the remarkable NO_3^- depletion in the epilimnion of Plešné Lake as well (compare the differences between NO_3^- concentration in the input and lake water, Table 3). These in-lake alkalinity generating processes led to the changes in Al speciation and production of particulate Al (Al_{part}). Consequently the highest Al_{part} concentrations were observed in Plešné Lake and Rachelsee (Table 4).

Prášílské Lake and Kleiner Arbersee formed a group of moderately acidified lakes (input: pH > 4.8, ANC = $-20 \mu\text{mol l}^{-1}$, Table 3). Their common feature was a lower Al loading (Al_T , ~ $150 \mu\text{g l}^{-1}$) with predominance of organically bound Al (Al_{org} , Table 3) compared to the

Table 4. – An inter-lake comparison of selected parameters relevant for recent acidity (upper part) and/or trophic (lower part) status of all Bohemian Forest lakes (late summer 1999). The lakes (see codes in Table 1) were ordered according to increasing or decreasing values of particular parameters (minimum and maximum given in parentheses, see also Table 3); in. – input water, sur. – surface lake water; see text for further explanation.

Parameter			strong	← acidification effects →	weak
pH	in.		(4.34)	CT < CN = PL < RA < KA < PR < GA < LA	(5.65)
	sur.		(4.50)	CT < CN < RA < PR < PL < KA < LA < GA	(5.91)
ANC	in.	($\mu\text{mol l}^{-1}$)	(-57)	CT < RA < CN < PL < PR < KA < GA < LA	(16)
	sur.	($\mu\text{mol l}^{-1}$)	(-49)	CT < CN < RA < PR < PL < KA < GA < LA	(16)
Al _T	in.	($\mu\text{g l}^{-1}$)	(669)	PL > RA > CN > CT > KA > PR > GA > LA	(68)
	sur.	($\mu\text{g l}^{-1}$)	(420)	CT > CN > PL > RA > PR > KA > GA > LA	(109)
Al _i	in.	($\mu\text{g l}^{-1}$)	(535)	PL > RA > CN > CT > KA > PR > GA > LA	(12)
	sur.	($\mu\text{g l}^{-1}$)	(390)	CT > CN > RA > PL > PR > KA > GA > LA	(6)
Al _{part}	sur.	($\mu\text{g l}^{-1}$)	(12)	CT < CN < KA < LA < GA < PR < RA < PL	(212)
SO ₄ ²⁻	in.	(mg l ⁻¹)	(5.59)	PL > CN > CT > RA > KA > GA > PR > LA	(1.55)
	sur.	(mg l ⁻¹)	(4.67)	CT > PL > CN > GA > KA > RA > PR > LA	(1.56)
NO ₃ -N	in.	(mg l ⁻¹)	(1.51)	RA > PL > CN > LA > PR > GA > CT > KA	(0.37)
	sur.	(mg l ⁻¹)	(0.80)	CN > RA > CT > LA > GA > PR > KA > PL	(0.05)
Parameter			oligo-	← trophic status →	meso-
DOC	in.	(mg l ⁻¹)	(2.45)	LA < GA < KA < CN < RA < PR < CT < PL	(5.62)
	sur.	(mg l ⁻¹)	(0.91)	RA < CN < GA < PL < CT < KA < LA < PR	(4.27)
HMB	sur.	($\mu\text{g l}^{-1}$)	(62)	KA < PR < GA < LA < RA < CT < CN < PL	(318)
Chla	sur.	($\mu\text{g l}^{-1}$)	(1.68)	RA < KA < CN < GA < CT < LA < PR « PL	(34.7)
TP	in.	($\mu\text{g l}^{-1}$)	(2.1)	RA < LA < CN < GA < CT < PR < KA « PL	(18.7)
	sur.	($\mu\text{g l}^{-1}$)	(2.7)	RA < CN < CT < PR < GA < LA < KA < PL	(8.9)
DOP ¹⁾	in.	($\mu\text{g l}^{-1}$)	(2.2)	CT = PR = KA > CN > LA > PL > GA > RA	(< 0.5)
	sur.	($\mu\text{g l}^{-1}$)	(4.4)	GA > KA > CT > PR = LA > CN > PL = RA	(< 0.5)
DRP ¹⁾	in.	($\mu\text{g l}^{-1}$)	(< 1)	CN = CT < RA < LA < PR = KA < GA « PL	(16.1)

¹⁾ DOP, DRP – dissolved organic and dissolved reactive phosphorus

former group. Forr & al. (1994) have suggested that permanently lower Al_T as well as little proportion of ionic Al forms (Al_i) in Prášílské Lake (cf. Tables 3 and 4) has allowed the better survival of crustacean zooplankton in this lake.

Grosser Arbersee and Laka Lake formed the third group of lakes slightly affected by the acidification at present (input: pH > 5.5, ANC > 0 $\mu\text{mol l}^{-1}$, Al_T = 100 $\mu\text{g l}^{-1}$, Table 3). Despite the positive ANC, the vertical pH profile of Grosser Arbersee still revealed a slight increase of pH towards the bottom like in acidified lakes.

The Bohemian Forest lakes differed remarkably in P cycling. While most of the lakes received low total P (TP) with negligible proportion of dissolved reactive P (DRP), Plešné Lake received one order of magnitude higher TP concentrations, which was formed predominantly by DRP (Table 4). However, DRP in the Plešné Lake epilimnion was below the detection limit as in any other lake. The enhanced DRP loading obviously favoured the phytoplankton growth in Plešné Lake (Fig. 2).

For the inter-lake comparison Chla concentrations were used to characterise roughly the

phytoplankton biomass and its vertical distribution. The Chl *a* concentrations were < 10 µg l⁻¹ in most of the lakes, though its vertical distribution in Rachelsee and Plešné Lake showed conspicuous peaks (~ 40 µg l⁻¹, Fig. 2). While the surface value in Rachelsee was the lowest among the lakes (Table 3), Chl *a* was 42 µg l⁻¹ in the 11-m depth of this clear water lake. This surprisingly high value was similar to the metalimnetic Chl *a* maximum of mesotrophic Plešné Lake (Fig. 2) and obviously represented some phytoplankton adaptation to lower light intensities in the corresponding depths (see transparencies in Table 2). Generally, more or less pronounced Chl *a* peaks in deeper layers have been a typical pattern of the phytoplankton vertical distribution in most of the lakes.

Bacterioplankton in the Bohemian Forest lakes were dominated by very long (> 100 µm) filamentous microorganisms. These microorganisms contributed on average for more than 80% of the total HMB in all but two lakes in the late summer of 1999 (Fig. 3). Lower proportion of filaments used to be typical for anoxic conditions above the bottom, while the highest biomass of filaments (96–98% of HMB) was found in the epilimnion of most lakes (Rachelsee, Černé, Čertovo, Plešné, and Prášilské Lakes). Most likely the high epilimnetic HMB could utilise allochthonous DOC causing thus more or less pronounced reduction of its concentration in some lakes (Fig. 3). Moreover, cleavage of the allochthonous DOC by UV-B radiation probably may release some additional substrate for bacterial growth.

Long-term changes in zooplankton, benthos, and fish

Since the first FRIČ's (1872, 1873) survey of all the Bohemian Forest lakes 130 years ago crustacean zooplankton have remained in a focus of interest of any further hydrobiologist visiting the lakes. We can guess at least three reasons of the interest: (1) A plankton net has remained the basic sampling tool over a century. (2) The number of species has never been excessively high which has made the insight on their presence/absence or dominance easier. (3) Crustacean zooplankton of the Bohemian Forest lakes have differed on both geographical and time scales, which posed a challenge to make hypotheses.

Some twenty years after the first survey FRIČ & VÁVRA (1898) observed significant changes in both abundance and composition of the zooplankton of Černé Lake. They supposed them to be caused by a changed fish stock (see below). Their explanation indeed was probably the first mention of a possible influence of fish predation upon zooplankton, an idea widely accepted nowadays as an important factor in recent freshwater ecology (WETZEL 1983).

In his paper concerning zooplankton of the Černé Lake ŠRÁMEK-HUŠEK (1942) reported on a continuing reduction in species richness of pelagic Crustacea. He concluded that *Holopedium gibberum*, *Daphnia longispina*, *Bosmina longispina* and *Acanthodiptomus denticornis* became extinct in the lake, the only two species remaining then were *Cyclops abyssorum* and *Ceriodaphnia quadrangula* (all names according to the present nomenclature). After a temporary comeback of *Holopedium gibberum* (WEISER 1947) the reduction proceeded further until the state where *Cyclops abyssorum* disappeared either and the population of *Ceriodaphnia quadrangula* was surviving in extremely low numbers. The only regular components of summer zooplankton were two rotifer species, *Microcodon clavus* and *Polyarthra remata*. The final impoverishment of zooplankton was attributed to the ongoing acidification of the lake (FOTT & al. 1994). The later increase in abundance of *Ceriodaphnia quadrangula* (since 1997) may be one of the first signs of recovery in the open water community from the acid stress (FOTT & al., in prep.).

SOLDÁN & al. (1999) also documented a decrease of mayfly diversity but not abundance in Prášilské Lake during its acidification period: while three species were recorded there in the

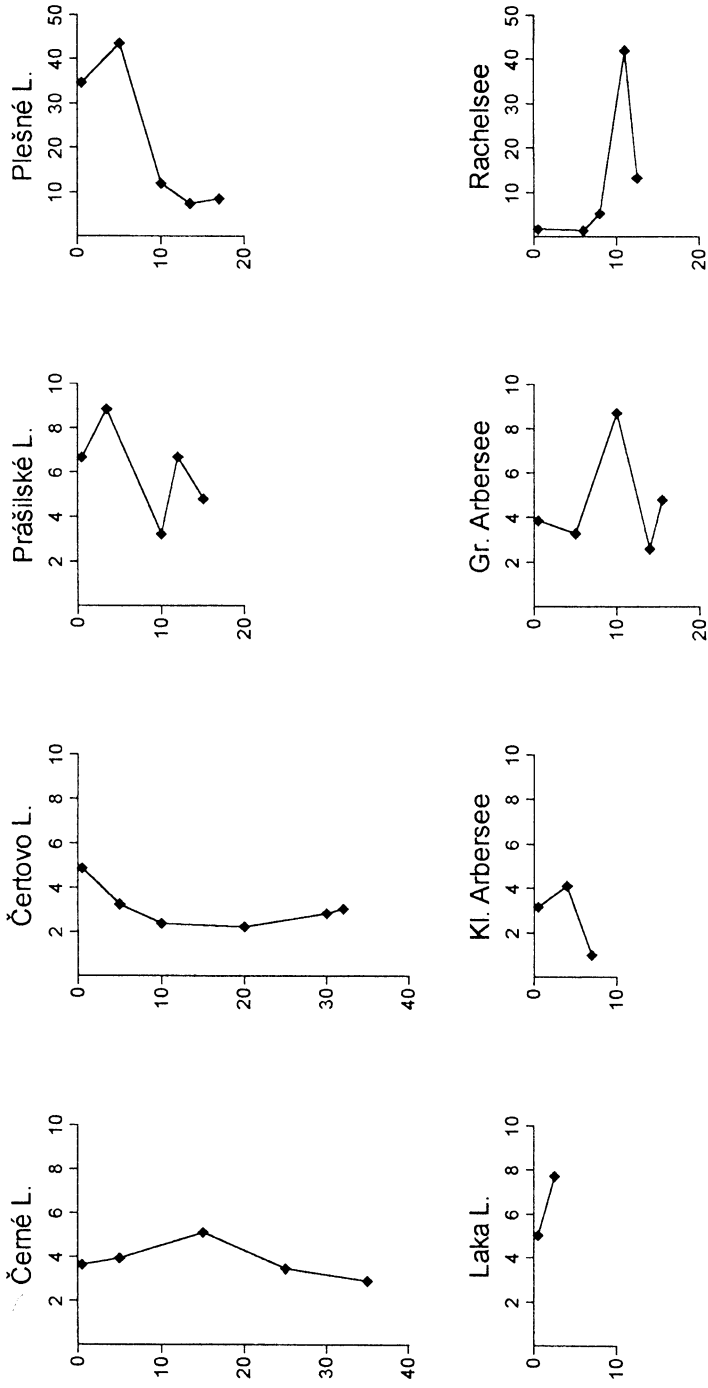


Fig. 2. – Vertical profiles of Chl *a* (in $\mu\text{g l}^{-1}$, note different scales for Plešné L. and Rachelsee) in the Bohemian Forest lakes (late summer 1999).

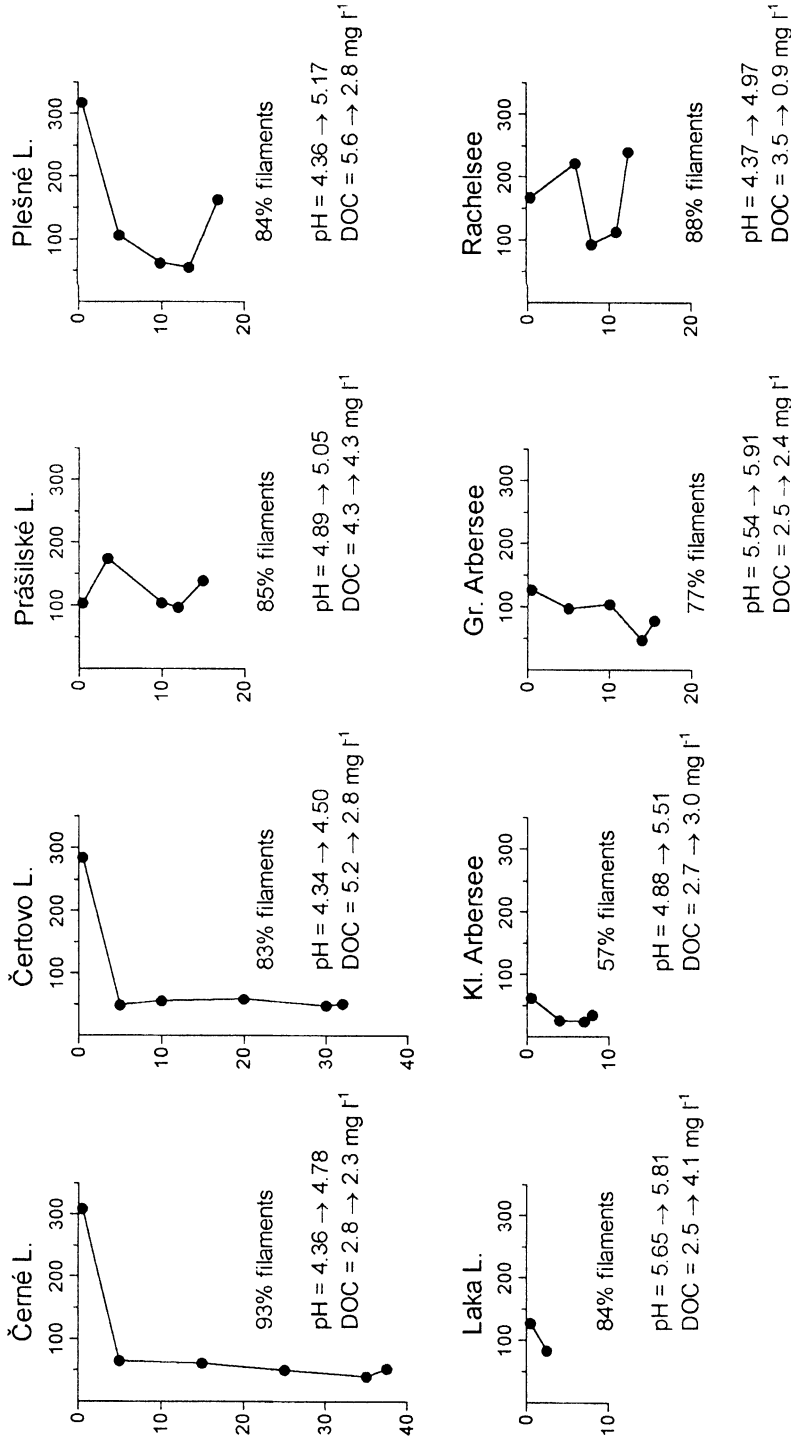


Fig. 3. – Vertical profiles of total HMB (in $\mu\text{g C l}^{-1}$) in the Bohemian Forest lakes (late summer 1999); average proportion of filaments in the total HMB as well as changes in pH and DOC concentrations (in mg l^{-1}) from inflow to surface lake water (\rightarrow) are given for each lake. A line intercept method was used for quantification of the total length of all heterotrophic filaments (NĚDOMA & al., in press), which was converted to carbon biomass using the following formula: $B_F = L \times D^2 \times L_F \times f_c$, where B_F is the biomass, L_T is the total length of filaments per litre of a sample, D_F is an average diameter of filaments, and f_c is a conversion factor; the factor was derived from the NORLAND'S (1993) allometric relationship between bacterial cell volume (a hypothetical 2- μm bacterial rod with the particular D_F) and carbon content. The total HMB represent the sum of B_F and carbon biomass of unicellular bacterioplankton (estimated according to STRASK-RABOVÁ & al. 1999).

1940s and 1950s, only one acid tolerant species, *Leptophlebia vespertina* was found since the late 1970s. However, its abundance increased twofold in the 1990s compared to the 1970s as well as exceeded that total mayfly abundance observed in the 1940s and 1950s. At present we can only speculate if the rising abundance of benthic organisms reflects the ongoing reversal. Thus some continuation of this unique long-term research will be highly appreciated.

VESELÝ (1994) has reviewed the history of fish occurrence, their introduction and extinction in the Bohemian Forest lakes. The presence or absence of fish in the lakes, however, still remains a puzzle to a certain degree. As far as we can infer from both archive records (VICE-NA, unpubl.) and early literature (GRUEBER & MÜLLER 1846, FRAUENFELD 1866, GÜMBEL 1868, see also VESELÝ 1994) some lakes (in particular Rachelsee, Plešné and Prášílské) were naturally fishless. Among other reasons a difficult access might have disabled fish from invading the lakes via outflow. Artificial stocking of brown trout (Rachelsee and Laka: WAGNER 1897, ŠVAMBERA 1914c) changed this situation. Other cases of stocking, either in the early times (ČERNÝ 1910) or later ones are difficult to trace out. Large lake forms of brown trout (*Salmo trutta* "morpha lacustris") are documented from Černé, Čertovo and Plešné Lakes (FRÍČ & VÁVRA 1898, ČERNÝ 1910).

Historical data indicated that Grosser Arbersee and Kleiner Arbersee had been used for fishing since the 16th century (WINKLER 1981 in ARZET & al. 1986). Original populations of brown trout (*Salmo trutta*) were later replaced by introducing the geographically foreign rainbow trout (*Oncorhynchus mykiss*). As a consequence of atmospheric acidification the fish populations disappeared from the both lakes since the late 1950s or early 1960s and stocking attempts in 1965 failed (STEINBERG al. 1984b, ARZET & al. 1986).

Large-scale introduction of the geographically foreign brook trout (*Salvelinus fontinalis*) into Černé Lake after 1890 led to a significant reduction of the population of brown trout. The growth of brook trout was extremely good after its introduction to the lake and it was still good in 1950 (FRÍČ & VÁVRA 1898, LOHNISKÝ 1963). A successful acclimatisation of brook trout to the lake, its higher fitness, even resistance to parasites, and more efficient competition for food resources resulted in a miserable existence of the indigenous species (DYK 1992). The more efficient predation of the newcomer upon zooplankton may explain at least some changes in zooplankton mentioned already by FRÍČ & VÁVRA (1898). The exact time of extinction of brown trout in the lakes is not known but it certainly could not have survived the onset of acidification in the 1960's. The acid tolerant brook trout survived in the lake Černé until the mid-1970s (KRUPAUER & VOSTRADOVSKÝ 1972, VESELÝ 1994). The early attempt of introduction of a pelagic whitefish *Coregonus wartmani* was unsuccessful (FRÍČ & VÁVRA 1898).

As far as we know, any fish return has not been documented yet into any Bohemian Forest lake. On the other hand, the absence of fish has been proved in Prášílské Lake recently (KUBEČKA & al. 2000). Also presence of invertebrate predators, like *Chaoborus* sp. in Laka Lake, rather contradicts the fish recovery. In the near future, a special attention should be paid to any signal of fish presence in the lakes; any uncontrolled fish stocking should be avoided.

Can we observe any long-term changes in the phytoplankton?

Similarly to other acidified lakes, the phytoplankton of the Bohemian Forest lakes have been dominated by phytoflagellates (typically *Dinophyceae*, *Chrysophyceae*, and *Cryptophyceae*; FOTT & al. 1980, LUKAVSKÝ in WEILNER 1997, NEDBALOVÁ & VRTIŠKA 2000, SCHAUMBURG 2000). The only exception has been the phytoplankton of Plešné Lake with dominance of *Monoraphidium* cf. *dybowskii* and filamentous cyanobacteria (*Pseudanabaena* sp. and *Limnothrix* sp.; HEJZLAR & al. 1998, NEDBALOVÁ & VRTIŠKA 2000). Nevertheless, species compo-

sition of the phytoplankton of four Czech lakes (Černé, Čertovo, Prášilské, and Plešné) was actually similar. All recently present species of these lakes were observed in Černé Lake as early as in 1936 (B. FORT, unpubl.); the only species of his list which was not found at present is *Cyclotella* sp. (found also in sediment cores of Černé Lake, SCHMIDT & al. 1993). Thus the comparison of the present state with the old records proved that many phytoplankton species of acid-sensitive oligotrophic lakes were able to survive when the lakes became acidic (FORT & al. 1994).

Changes in biomass and shifts in composition of phytoplankton have been usually reported from anthropogenically acidified lakes in some lake districts of the Northern Hemisphere (see SCHINDLER 1994 for his critical review). While changes in crustacean zooplankton seem to indicate the changing lakewater quality, such information cannot be inferred from few reports on phytoplankton of any Bohemian Forest lake. One reason is methodological. The former algologists (except B. FORT) did not concentrate their samples by centrifugation, sedimentation or filtration. Another reason concerns a sampling strategy. Recent extensive phytoplankton studies have shown that distributions of phytoplankton species differ both in space and time (NEDBALOVÁ & VRTÍŠKA 2000). Moreover, as the particular species can differ also in their specific content of chlorophyll *a* (Chl_a), phytoplankton biovolume and Chl_a maxima coincided neither spatially nor temporally (NEDBALOVÁ 2000; cf. FELIP & CATALAN 2000). Therefore, widely used estimation of phytoplankton biomass by Chl_a does not allow an adequate comparison unless sampling vertical Chl_a profiles on a seasonal basis.

Due to the above reasons we can hardly track any phytoplankton changes using rather scarce past data of either Chl_a concentration or taxonomic composition available from the Bohemian Forest lakes. On the other hand, microscopical evaluation of the biomass is too laborious and time-consuming to be recommended for a routine monitoring of the phytoplankton changes. Perhaps regular monitoring of mullomonadacean species composition in early spring (cf. STEINBERG & HARTMANN 1986) may be used for indication of the possible recovery of phytoplankton in the future.

Invasion of *Sphagnum*-mosses and other macrophytes into littoral zone has been usually reported as another consequence of atmospheric lake acidification (SCHINDLER 1994). Among the Bohemian Forest lakes such changes were documented only for Grosser Arbersee and Kleiner Arbersee (MELZER & ROTHMEYER 1983) so far.

Phytoplankton of the Bohemian Forest lakes have been apparently always phosphorus limited. TP concentrations have been comparable to those in the early 1960s (PROCHÁZKOVÁ & BLAŽKA 1999) in the Czech lakes also throughout the last two decades, whereas DRP concentrations have been usually below the detection limit (VRBA & al. 1996, HEJZLAR & al. 1998, KOPÁČEK & al. 2000a, unpubl.). Both bedrock and soil composition governs trophic status of the lakes (KOPÁČEK & al. 1998b). Moreover, biogeochemical cycle of P in these acidified catchment-lake ecosystems has been affected by Al which reduced in-lake P availability both in the water column (KOPÁČEK & al. 2000a, VRBA & al., in prep.) and sediments (BOROVEC 2000). Most likely the in-lake P availability has been changing due to both acidity progress and reversal, whereas TP loading of any particular lake has not changed within the last 40 years.

We hypothesise that the actual phytoplankton biomass in the acidified Bohemian Forest lakes is probably determined by the level of Al_T loading into a lake and by in-lake processes controlling speciation of Al (VRBA & al., in prep.). Despite the highest P input to Plešné Lake (Table 4), the immobilisation of P by Al probably disabled full availability of P for plankton growth. Thus, the total biomass (sum of phytoplankton and HMB) in Plešné Lake averaged only about twice higher compared to Čertovo and Prášilské Lakes during the 1998 summer (VRBA & al., in prep.). This seasonal inter-lake comparison suggested that different algal spe-

cies dominated the phytoplankton of Plešné Lake when compared with the other ones. While the higher P input apparently favoured occurrence of small green algae and filamentous cyanobacteria in Plešné Lake, dinoflagellates and chrysophytes dominated the phytoplankton of the other two lakes, in spite of almost identical species list of all the three lakes (NEDBALOVÁ & VRTIŠKA 2000). The phytoplankton and HMB averaged 78% and 21%, respectively of the total epilimnetic biomass in Plešné Lake. On the contrary, much higher proportion of HMB (63%) in Čertovo Lake clearly demonstrated higher bacterial efficiency in P acquisition under low TP and negligible DRP input. In Prášílské Lake, HMB (in particular filaments) dropped temporarily during the summer from 37% to 11% as a consequence of increasing cladoceran grazing (VRBA & al., in prep.). On the other hand, phagotrophy on bacterioplankton might compensate the lack of P in some mixotrophic algae, e.g., *Dinobryon* (ZNACHOR & HRUBÝ 2000).

Unlike most of freshwater lakes, the remarkable filamentous microorganisms have been present in bacterioplankton of the Bohemian Forest lakes during the last two decades (not quantified – cf. FOTT & al. 1980, RŮŽIČKA & al. 1981, VRBA & al. 1996). At present they are usually longer than 100 µm and belong mostly to *Eubacteria* (RÁČKOVÁ, unpubl.), however, aquatic micromycetes (forming typical branched mycelia) occur in plankton in some periods as well. On the other hand, similar counts of unicellular bacteria, i.e. 10⁶ per ml (Plešné Lake) and 10⁵ per ml (other Czech lakes) were found in the early 1960 (PROCHÁZKOVÁ & BLAŽKA 1999) as well as after 1979 (RŮŽIČKA & al. 1981, VRBA & al. 1996, HEJZLAR & al. 1998, this study).

Palaeolimnological analyses of lake sediments

During last two decades, palaeolimnological analyses of sediment cores have been performed at most of the Bohemian Forest lakes (see VESELY 1994 for review, FOTT & PRAŽÁKOVÁ 1994, VESELY 1998, 2000). Generally, evaluation of diatom, chrysophyte and/or chydorid remains, i.e. pH inferred from their occurrence throughout a sediment profile, revealed clear evidence of the strong atmospheric acidification of the lakes during the second half of this century (STEINBERG & al. 1984a, ARZET & al. 1986, SCHMIDT & al. 1993, VESELY & al. 1993). However, the inferred pH suggested different "starting points" of this atmospheric acidification among the lakes. VESELY & al. (1993) documented that the inferred pH remained below 5 in Čertovo Lake at least during the past two centuries. All three Bavarian lakes also revealed slightly acidic conditions (pH < 6) for several centuries ago. In Grosser Arbersee a continuous natural acidification could be documented since ~ 9,000 B.P. (STEINBERG & al. 1991, STEINBERG 1991).

Sediments of Rachelsee and Grosser Arbersee indicated a temporary pH decrease below 5 already in the 19th century. This pH drop together with parallel increase of some heavy metal concentrations in the sediment were interpreted as local effects of human activities, e.g. ore mining and smelting, glasswork, etc. (STEINBERG & al. 1984c, 1985). Emissions from the local industry in Bodenmais obviously caused periodical acidification of Grosser Arbersee in the past (STEINBERG & al. 1984c). That local air pollution indeed did not affect the neighbouring Kleiner Arbersee, which was apparently protected by its geographic location (ARZET & al. 1986). On the other hand, concentrations of some heavy metals in the lake sediment, in particular peaks of lead, indicated also certain historical remote pollution of the Bohemian Forest lakes (VESELY 1998, 2000). Characteristic fingerprints of polycyclic aromatic hydrocarbons (STEINBERG & HARTMANN-ZAHN 1989) or various chlorinated organic compounds (JÜTTNER & al. 1997) could help to distinguish different emission sources.

Pollen analyses of sediment cores were performed from the following lakes: Grosser Ar-

bersee, Prášílské, Čertovo, Černé, and Rachelsee (STEINBERG & HARTMANN-ZAHN 1989, SCHMIDT & al. 1993, VESELÝ & al. 1993, VESELÝ 1998, MICHLER, unpubl., respectively). They reflected changes in vegetation cover around the lakes and indicated human impacts on the forest composition, e.g., certain decline of beech since the Middle Ages. VESELÝ (1998) also documented repeated periods of a forest retreat recorded in the sediment of Černé Lake. However, further palynological research, in particular on the other lakes, is necessary and may help to distinguish between local impacts and more general trends in the vegetation development in the Bohemian Forest.

Consequently, another question should be addressed to possible oscillations of natural acidification of the lakes, which might be related to different uptake of base cations during certain growth phases of coniferous forests. Several times higher uptake rate of base cations has been estimated by young Norway spruce forests (from ~ 10 to 60–70 years of age) compared to the older forests in Sweden (MOLDAN & al. 1999). Thus thorough evaluation of available documents on forestry practice may also help in interpretation of sediment chemistry of the Bohemian Forest lakes (HRUŠKA & al. 2000). Furthermore it may help to recognise and/or separate possible impacts of climate changes.

Conclusions

The almost 130 years of limnological research of the Bohemian Forest lakes as well as our present results show an importance of these ecosystems for further research from several aspects:

1. They are softwater lakes located in the catchments geologically sensitive to atmospheric deposition of pollutants and thus representing sensitive indicators of environmental changes.
2. They are situated in the vicinity of important European emission centres of S and N and thus they are valuable sensors of both acidification and recovery from acidity.
3. Pronounced differences among the lakes in their trophic status, acidity, and microbial composition make possible to study biological processes and biodiversity in these unique ecosystems.
4. Whole ecosystem studies involving atmospheric deposition, transport of ions, soil and water compositions enable to investigate present status of nutrient availability for both terrestrial and aquatic biota and to predict their future development.
5. Moreover, multidisciplinary sediment analyses enable to extend this research back to the past and to distinguish between natural (e.g., temperature variations) and anthropogenic impacts in the forest composition and health.
6. Evaluation of both long-term data and sediment analyses also make possible better understanding of processes causing both natural and anthropogenic acidification and to distinguish between their impact on catchment soils and lake water.

Acknowledgements. We thank to the authorities of both NP Šumava and NP Bayerischer Wald for their permission to study the unique lake ecosystems as well as to the Grant Agency of the Czech Republic for the financial support (projects 206/97/0072, 206/98/0727, and 206/00/0063). We appreciate kind assistance of German colleagues from the NP Bayerischer Wald and WWA Regensburg, Deggendorf, and Passau in sampling three Bavarian lakes. We also thank to many colleagues from HBI and several students of both USB and Charles University for their field and lab assistance during this research. C. Steinberg reviewed an earlier version of the manuscript.

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