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Long-term studies (1871–2000) on acidification and recovery of lakes in the Bohemian Forest (central Europe)

Jaroslav Vrba[a,b,*], Jiří Kopáček[a,b], Jan Fott[c], Leoš Kohout[c], Linda Nedbalová[c], Miroslava Pražáková[c], Tomáš Soldán[b,d], Jochen Schaumburg[e]

[a]Hydrobiological Institute AS CR, Na Sádkách 7, CZ-37005 České Budějovice, Czech Republic
[b]University of South Bohemia, Branišovská 31, CZ-37005 České Budějovice, Czech Republic
[c]Department of Hydrobiology, Faculty of Science, Charles University, Viničná 7, CZ-12844 Prague 2, Czech Republic
[d]Institute of Entomology AS CR, Branišovská 31, CZ-37005 České Budějovice, Czech Republic
[e]Bavarian State Office for Water Management, Lazarettstr. 67, D-80636 Munich, Germany

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Abstract

This paper evaluates long-term changes in the atmospheric depositions of S and N compounds, lake water quality, and biodiversity at eight glacial lakes in the Bohemian Forest over the past 130 years. This time interval covers (i) the 'background' pre-acidification status of the lakes, (ii) a period of changes in the communities that can be partly explained by introduction of fish, (iii) a period of strong lake acidification with its adverse impacts on the communities, (iv) the lake reversal from acidity, which includes the recent status of the lakes. The lake water chemistry has followed—with a characteristic hysteresis—both the sharp increase and decline in the deposition trends of strong anions. Remarkable changes in biota have mirrored the changing water quality. Fish became extinct and most species of zooplankton (Crustacea) and benthos (Ephemeroptera and Plecoptera) retreated due to the lake water acidification. Independent of ongoing chemical reversal, microorganisms remain dominant in the recent plankton biomass as well as in controlling the pelagic food webs. The first signs of the forthcoming biological recovery have already been evidenced in some lakes, such as the population of *Ceriodaphnia quadrangula* (Cladocera) returning into the pelagial of one lake or the increase in both phytoplankton biomass and rotifer numbers in another lake.

Keywords: Mountain lakes; Acid deposition; Water chemistry; Biodiversity; Phytoplankton; Zooplankton; Benthos; Fish

1. Introduction

Eight small glacial lakes are situated on forested slopes of the central summit of the Bohemian Forest (Böhmerwald, Šumava) along the historical border between Bavaria and Bohemia. The lakes have been fascinating for explorers for more than 100 years. Owing to the 130-year occasional hydrobiological research and palaeolimnological studies, we are now able to document the significant changes in the lake water chemistry and the consequent changes in the plankton and benthos composition (in particular, the conspicuous reduction in crustacean and/or insect species in some lakes) as well as the extinction of fish (e.g. Veselý,

*Corresponding author. Tel.: +420-38777-5872; fax: +420-38531-0248.
E-mail address: vrba@hbu.cas.cz (J. Vrba).

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1994; Vrba et al., 2000). Therefore, the Bohemian Forest lakes represent excellent sites for further long-term ecological research.

Like the whole region of Central Europe, the Bohemian Forest was exposed to heavy atmospheric pollution during the last century. Regional emissions of S and N compounds reached up to ~280 mmol m^{-2} $year^{-1}$ from World War II to the 1980s, and then declined by ~80% and ~35%, respectively, during the 1990s (Kopáček et al., 2001, 2002). Owing to small and geologically sensitive catchments, any changes in acid deposition were reflected in the lake water composition and biota (Vrba et al., 2000; Kopáček et al., 2001). Here, we summarise all available long-term data on the acidity-derived changes in biodiversity of the Bohemian Forest lakes in the context of chemical changes, and present the recent status as a start-point of the forthcoming biological recovery.

2. Material and methods

2.1. Site description

We have studied eight glacial lakes in the Bohemian Forest (the Hercynian crystalline mountain massive, the Šumava Mts. and Bayerischer Wald; 48°47′–49°11′N, 13°07′–13°52′E), five lakes on the Czech side (Černé, Čertovo, Plešné, Prášilské, and Laka), and three on the German side (Rachelsee, Grosser Arbersee, and Kleiner Arbersee). All the lakes are of a small size (areas: 2.8–18.4 ha; volumes: $0.04–2.88 \times 10^6$ m^3; maximum depths: 3–40 m), situated in geologically sensitive catchments (bedrock of gneiss, mica-schist or granite), at altitudes between 918 and 1096 m a.s.l. Their small catchment areas (0.58–2.79 km^2) are mainly covered by Norway spruce and, more sparsely, by beech and fir (Veselý, 1994; Schaumburg, 2000).

2.2. Lake sampling and analyses

Samples of lake water were taken at the deepest point of each lake, primarily in September–October and occasionally in July–August. A comparative sampling of all the eight lakes was conducted within 10 days in early September 1999. The samples for chemical analyses were immediately filtered through a 200-μm polyamide sieve. The samples for analyses of microorganisms were fixed with either formaldehyde (for bacteria) or acid Lugol's solution (for phytoplankton). Large zooplankton were sampled by several vertical hauls with a quantitative net (200-μm mesh size) of the Apstein type, and small zooplankton were sampled with a Van Dorn sampler from the specific depths and concentrated by a plankton net (40-μm mesh size); both samples were preserved by formaldehyde.

The data on hydrochemistry came from the sources referred by Kopáček et al. (2001, 2002). The plankton samples were processed according to Straškrabová et al. (1999) with the exception of filamentous microorganisms (Nedoma et al., 2001). The total zooplankton (crustacea + rotifers), phytoplankton (algae + cyanobacterial filaments), and heterotrophic microbial biomass (bacteria + heterotrophic filaments) were expressed as organic carbon (μg C l^{-1}; Straškrabová et al., 1999).

Benthos (mostly Ephemeroptera and Plecoptera) of the five Czech lakes were sampled 12 times between 1956 and 1995 in all seasons. The samples were collected by using metal cups or sampling nets for 10–15 min mostly by means of the 'kicking technique' according to Kershaw and Frost (1978), i.e. by digging in the stony and sandy bottoms. At the same time, the attention was also paid to submerged aquatic plants and to the surface of larger stones in the littoral zone.

2.3. Historical data

This paper combines the historical data on the occurrence of species and water quality of the Bohemian Forest lakes summarised by Veselý (1994), Schaumburg (2000), Vrba et al. (2000) and all further available data on zooplankton and macrozoobenthos (e.g. Ošmera, 1971; Procházková and Blažka, 1999; including unpublished data of Fott et al.). The first survey of crustacean zooplankton of all Bohemian Forest lakes was performed by Frič (1872, 1873). The recent biodiversity of crustacean zooplankton was compared to these 130-year-old observations, considered as a representative of the pre-acidification status. Moreover, the past occurrence of cladoceran species in the lakes was independently verified by the palaeolimnological analyses of the sediment cores taken from the lakes (Pražáková and Fott, 1994; Pražáková and Fott, unpublished data). All available information concerning the fishes in the Bohemian Forest lakes, summarised by Vrba et al. (2000), was evaluated to track their original presence, historical stocking, and extinction.

The deposition trends in S and total inorganic nitrogen ($TIN = NO_3 + NH_4$) in the Bohemian Forest were derived from Kopáček et al. (2001). These trends are based on estimated data (1860–1991) and measured values (since 1992; Hruška et al., 2000). The estimated deposition was based on the historical central European emission trends, the long-term Czech deposition trends, and the measured deposition of S and TIN in the Bohemian Forest. The uncertainty associated with the estimate was less than $\pm 30\%$ (Kopáček et al., 2001).

3. Results and discussion

3.1. Long-term changes at Černé Lake

Černé Lake, with the most detailed set of historical data on lake water quality and biodiversity, provides a characteristic example of the changing Bohemian Forest environment (Fig. 1). The changes in the rate of atmospheric deposition of acidifying pollutants were the principal driving force of all the documented changes. Under the relatively stable deposition trends in S and TIN at the beginning of the Industrial Revolution, the lake water chemistry remained apparently unaffected until the mid-1940s. The first reliable chemical analyses from 1936 showed that the epilimnetic pH was almost neutral (6.9–7.0 throughout summer), the concentrations of sulphate were low and nitrate was below the detection limit (Jírovec and Jírovcová, 1937). This implies that the forest vegetation in the catchment was still nitrogen limited. Due to the sharply increasing TIN deposition between 1950 and 1980, the nitrogen saturation of soils in the catchment became likely (already in the early 1960s) and consequently, the lake concentrations of NO_3 increased in parallel with the TIN deposition, similarly to SO_4 (Fig. 1).

During the 1960s and 1970s, the massive input of acidifying compounds caused a strong acidification of the Černé Lake resulting in a drop of 2 pH units. The lake water became remarkably clear (see transparency of Secchi depths in Fig. 1). Both the deposition and the lake acidification peaked in the 1980s. During this period, the in-lake concentrations of aluminium (Al) were ~ 1 mg l^{-1}, which was significantly above the toxic levels for fish and most zooplankton (Veselý et al., 1998b). The present decreasing trend in the Al concentrations in Černé Lake obviously reflects the decline in the concentrations of strong acid anions (Fig. 1) and is—beside a constant rise in pH—the most important symptom of the lake water reversal from the acid stress. However, the decline in the lake water concentrations of SO_4^{2-} and NO_3^- is not as rapid as the reduction of S and N emissions, and their present concentrations are higher than they were in the past for comparable emission rates during the increase in acidification (Kopáček et al., 2002).

The acidification-driven changes in the lake water quality were accompanied by a drastic reduction of biodiversity (Fig. 1). However, the first imbalance in the lake ecosystem was likely caused by introduction of brook trout in the 1890s and its repeated stocking (Vrba et al., 2000) and resulted in the first reduction in species richness of pelagic Crustacea. Brook trout probably reduced the number of zooplankton species (extinction of *Holopedium gibberum*, *Daphnia longispina*, *Bosmina longispina*, and *Acanthodiaptomus denticornis*; Šrámek-Hušek, 1942), thereby suppressing the indigenous population of brown trout within half a century (Fig. 1). The stock of brook trout exhibited good condition and population parameters in contrast with the bad condition of a single specimen of the native brown trout caught in 1962 (Dyk, 1992). While the original species of brown trout was not observed in the lake after 1962, the brook trout (more resistant to acidification) survived under the increasing acid stress until the mid-1970s (Vrba et al., 2000). Besides the fish species, the acidification of Černé Lake obviously caused the extinction of most species of crustacean

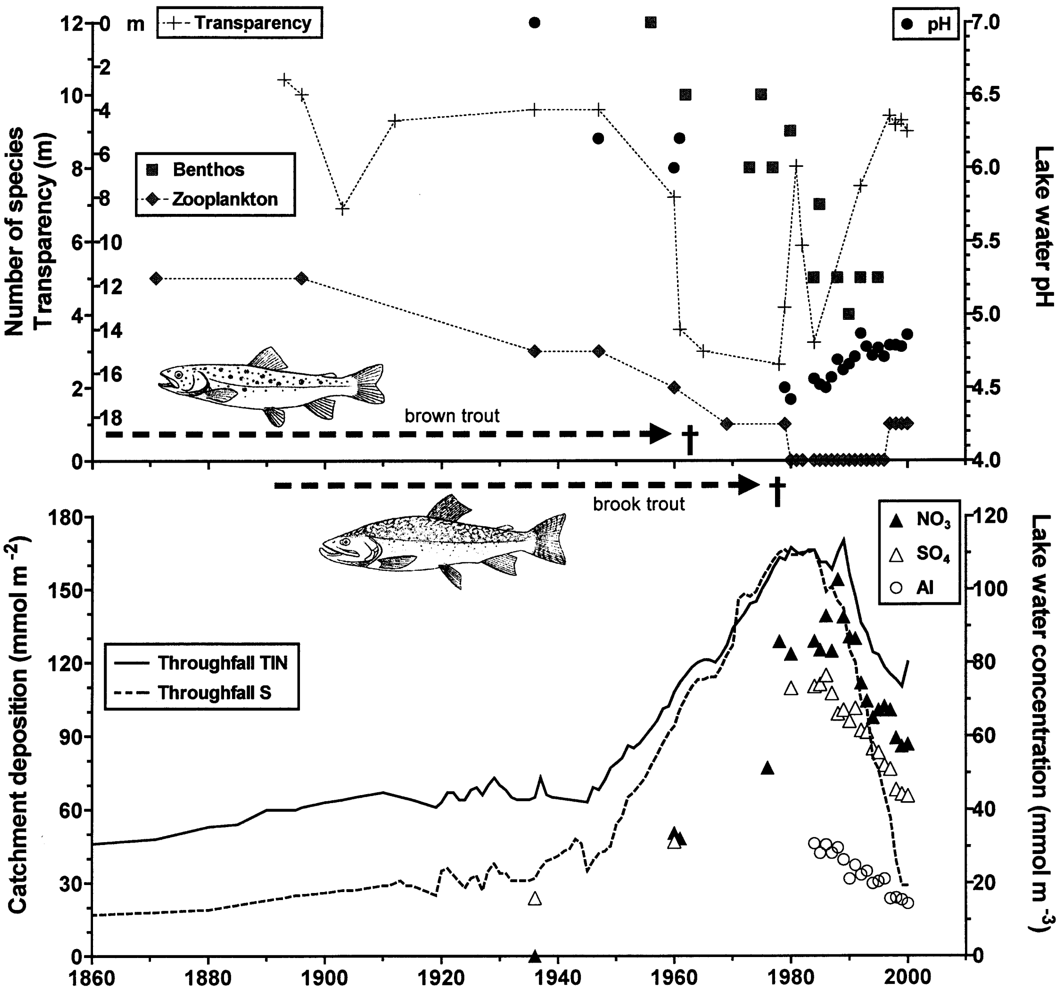

Fig. 1. Long-term limnological data on Černé Lake, 1871–2000 (from different sources): number of conspicuous zooplankton (Crustacea caught by plankton nets in the pelagial) and benthos (Ephemeroptera and Plecoptera) species (top left axis, left scale); lake water transparency as Secchi depths (top left axis, right scale), pH (top right axis), and concentrations of sulphate (SO_4), nitrate (NO_3), and aluminium (Al) (bottom right axis); estimated atmospheric deposition trends for sulfur (S) and total inorganic nitrogen (TIN) on the catchment (bottom left axis).

zooplankton and littoral macrozoobethos after the 1950s/1960s (Fig. 1, Tables 2 and 3). Finally, around 1970, the only regular components of summer zooplankton were *Ceriodaphnia quadrangula*, which survived in extremely low numbers, and two rotifer species (*Microcodon clavus* and *Polyarthra remata*). The final impoverishment of zooplankton later in the 1980s was attributed to the further acidification of the lake (Fott et al., 1994). The population of *C. quadrangula* probably survived the period of the highest acidity in the rocky littoral (though not found in the littoral samples between 1982 and 1992 either) and reappeared in the pelagial in 1997, after approximately one decade of the lake water reversal from acidification (see Fig. 1).

Similar, but not so drastic changes were also observed in the composition of benthic communities in Černé Lake. The total number of mayfly (Ephemeroptera) and stonefly (Plecoptera) species

Table 1
Historical occurrence of fish in the Bohemian Forest lakes (CN, Černé; CT, Čertovo, PL, Plešné; PR, Prášilské; RA, Rachelsee; GA, Grosser Arbersee; KA, Kleiner Arbersee; LA, Laka)

Species	CN	CT	RA	PL	KA	PR	GA	LA
Indigenous species (present before 1870):								
Salmo trutta L.—brown trout	E	E	A?	A?	E	A?	E	E
Stocked species (before acidification):								
Salmo trutta L.—brown trout			E	E		E		E
Oncorhynchus mykiss (Walbaum)—rainbow trout					E		E	
Salvelinus fontinalis (Mitchill)—brook trout	E			[E]		[E]		[E]

A, the species is absent in a lake; E, the species was present, stocked or introduced in a lake but is extinct nowadays (for details see Vrba et al., 2000). [E] means a stocking took place according to oral information, which cannot be confirmed with certainty; the lakes are fishless at present. The only documented fish, which occurred in early times in most of the lakes, was brown trout; however, three lakes seem to have been naturally fishless in the long past (A?).

dropped to one third between 1956 and 1990 (from 12 to four species; see Table 3, Fig. 1). Only the acidotolerant *Leptophlebia vespertina* (Ephemeroptera) and four acidotolerant species of stonefly were found in Černé Lake during the last sampling in 1995 (see Table 3).

3.2. Atmospheric acidification reduced biodiversity in all the lakes

The example of Černé Lake (Fig. 1) comprehensively describes the causes and consequences of the strong atmospheric acidification in central Europe. The value of this site for detecting environmental changes can be increased by obtaining similar data from the other Bohemian Forest lakes. Despite the less frequent historical sampling than that of Černé Lake, the available data cover all milestones of the acidification process in most Czech lakes (Vrba et al., 2000). Moreover, sampling of all the eight lakes covered not only the situation 130 years ago (Frič, 1872, 1873), but also the last two decades (Veselý et al., 1998a,b; Schaumburg, 2000; Vrba et al., 2000). The major changes in the lake water chemistry were running in parallel in seven dimictic lakes. The trends in lake water concentrations of SO_4 and NO_3 (e.g. Kopáček et al., 2002) as well as the palaeolimnological evidence (e.g. Arzet et al., 1986), provide us with the basis we can use to estimate the timing of individual periods of acidification with a sharp increase in the acidity during the late 1950s to the 1970s, maximum acidity (the late 1970s to ~1985), and reversal from acidity (since the late 1980s). Similarly to the other acidified regions of the Northern Hemisphere (e.g. Schindler, 1988, 1994; Stenson et al., 1993), the Bohemian Forest lakes have revealed both characteristic changes in the lake water chemistry and a significant reduction in biodiversity. The shallow Laka Lake (of the largest catchment area and the lowest retention time) probably represents a certain exception among the lakes under the study because it was acidified only temporarily (in spring), without any clear trends in the water chemistry (Vrba et al., 2000) but with some changes in biota.

Despite some uncertainty regarding the original presence of fish in three of the lakes and despite all attempts at stocking fishes during the last century, we are sure that fish became extinct in all Bohemian Forest lakes between the 1960s and 1970s (Table 1, Vrba et al., 2000). The disappearance of rainbow trout from both Kleiner Arbersee and Grosser Arbersee in the 1950s/1960s and the failure to stock this species were indeed the first indicators of ecosystem changes, which initiated the palaeolimnological research of the three lakes on the Bavarian side (e.g. Arzet et al., 1986).

Table 2 compares the present status of seven conspicuous species of Crustacea in the Bohemian Forest lakes with the situation 130 years ago (Frič, 1872, 1873). Most of the species became extinct or diminished due to the strong acidification of the lakes 20 years ago. Even at that time, two species, *Daphnia longispina* and *Cyclops abyssorum* persisted in Prášilské Lake and the latter

Table 2
Historical occurrence of the conspicuous species of crustacean zooplankton (typical littoral species not included) in the Bohemian Forest lakes (see key in Table 1)

Species	CN	CT	RA	PL	KA	PR	GA	LA
Cladocera (total number of species in the past):	4	4	1	1	2	3	4	2
Bosmina longispina Leydig	E	E	A	A	A	E	E	A
Ceriodaphnia quadrangula (O.F.M.)	**S**[*]	E	A	A	**S**	E	**S**	**S**
Daphnia longispina (O.F.M.)[**]	E	E	E	E	A	**S**	E	**S**
Holopedium gibberum Zaddach	E	E	A	A	E	A	**S**	A
Copepoda (total number of species in the past):	2	2	2	3	1	2	2	0
Acanthodiaptomus denticornis (Wierz.)	E	E	A	E	E	E	E	A
Cyclops abyssorum Sars	E	E	E	E	A	**S**[**]	**S**	A
Heterocope saliens (Lillj.)	A	A	E	**S**	A	A	A	A
Crustacea (total number of surviving species):	1	0	0	1	1	2	3	2

[*] In Černé lake, *C. quadrangula* was not observed in 1871 (presumably overlooked) but it was quoted from the 1890s (Frič and Vávra, 1898, under name *C. pulchella*).

[**] According to recent molecular analyses (Petrusek, unpublished results), the *Daphnia* population from Prášilské Lake is identical with *Daphnia rosea* Sars sensu Schwenk et al. (2000).

A, the species apparently absent in a lake at any time; the remains never found in the sediment. E, the species is extinct in a lake now, but it was present 130 years ago (Frič, 1872, 1873) or the remains of Cladocera were found in the sediment. S, the surviving species have persisted the acidification of a lake.

species also in Grosser Arbersee, most likely due to the far lower Al concentrations in both lakes compared with the Al concentrations in the rest of the lakes (Fott et al., 1994; Schaumburg, 2000; Vrba et al., 2000). At present, all the species listed in Table 2, which were found by Frič, are absent in Čertovo Lake and Rachelsee, whereas only *Heterocope saliens* has survived in Plešné Lake and *Ceriodaphnia quadrangula* in Černé Lake (Table 2). The latter species has survived also in Grosser Arbersee, Kleiner Arbersee, and Laka Lake, but surprisingly, it has never been found in Prášilské Lake during the 20th century and up to the present day. In conclusion, two of the eight conspicuous species (i.e. *Bosmina longispina* and *Acanthodiaptomus denticornis*) became virtually extinct in all the lakes during the last century, and two others (*Holopedium gibberum* and *Heterocope saliens*) have survived up to the present in one lake only (Table 2).

In addition to this general retreat of the crustacean zooplankton in all the lakes, we can expect a similar reduction of other invertebrate species, although it cannot be documented appropriately. We can document such a retreat of rotifers only for Plešné Lake. Frič (1872, 1873) observed a *Conochilus* species in Grosser Arbersee and Plešné Lake that (according to the present knowledge) was most probably *Conochilus unicornis* Rousselet 1892. No *Conochilus* (an unmistakable pelagic colonial form, the live sample of which is distinguishable by eye) has been found in any Bohemian Forest lake later on. Černy (1910) found non-acidophilic species (according to Berzinš and Pejler, 1987), e.g., *Keratella quadrata* (Müll.), *K. testudo* (Ehr.), *Lecane luna* (Müll.), and *Monostyla cornuta* (Müll.) (all the names are according to the present nomenclature), which have not been observed in Plešné Lake after the acidification either.

The first information on macrozoobenthos were published already by Frič and Vávra (1898) who mentioned a mass occurrence of *Glenocorisa propinqua propinqua* (Heteroptera) in Černé and Čertovo Lake. This species was not mentioned to be present in both lakes in the late 1950s (last records by Roubal, 1957) but surviving populations was observed in Plešné and Prášilské Lake during the 1990s. However, we assume that its retreat is not directly dependent on acidification (because this species is relatively acidotolerant, Soldán et al., 1996) but more likely it is a consequence of

Table 3
Historical occurrence of the mayfly and stonefly larvae in the five Czech lakes in the Bohemian Forest (see key in Table 1)

Species	CN	CT	PL	PR	LA
Ephemeroptera (total number of species in the 1950s):	4	3	4	4	5
Siphlonurus lacustris (Eaton)	E	E	E	E	S
Siphlonurus alternatus (Say)	E	A	E	E	E
Ameletus inopinatus Eaton	E	E	E	E	E
Cloeon dipterum (L.)	A	A	A	A	E
Leptophlebia vespertina (L.)	**S**	**S**	**S**	**S**	**S**
Plecoptera (total number of species in the 1950s):	8	6	10	10	9
Amphinemura triangularis (Ris)	**S**	A	**S**	E	**S**
Protonemura auberti Illies	E	E	E	E	E
Protonemura montana Kimmins + *P. hrabei* Raušer	**S**	**S**	**S**	E	**S**
Nemoura cinerea (Retzius)	E	E	E	E	E
Nemurella picteti Klapálek	A	E	E	E	E
Leuctra aurita Navás	**S**	A	**S**	E	S
Leuctra autumnalis Aubert	A	A	E	E	A
Leuctra digitata Kempny	**S**	**S**	**S**	**S**	**S**
Leuctra fusca (L.)	E	A	A	E	E
Leuctra handlirschi Kempny	A	E	E	A	A
Leuctra nigra (Olivier)	E	A	E	E	E
Insect larvae (total number of surviving species):	5	3	5	2	6

A, the species has been apparently absent in the lake during the last 50 years. E, the species is extinct in the lake now, but it was present in the 1950s. S, the surviving species have persisted the acidification of a lake.

significant changes in available food sources (Papáček and Soldán, 1995). This assumption can be documented by the occurrence of *G. p. propinqua* in Prášilské Lake with the cladoceran population (Kubecka et al., 2000; Kohout and Fott, 2000). Also some species with the arcto-alpine disjunction, e.g. *Molanna nigra* (Trichoptera) has survived in Prášilské Lake till the present. In general, however, benthos of the Bohemian Forest lakes still remains poorly understood.

Table 3 shows long-term changes in mayflies (Ephemeroptera) and stoneflies (Plecoptera), the only macrozoobenthos groups observed in detail in five Czech lakes since the early 1950s (e.g. Soldán et al. 1998). Total number of species has been gradually (>50%) reduced till the 1990s and the most pronounced species reduction was observed at Prášilské Lake (from 14 original to two recent species). However, the changes in the species composition did not correlate directly with the density. Within all the lakes, the mayfly *Leptophlebia vespertina* exhibits a key role. This mayfly is probably the most acidotolerant species within these groups, showing pH tolerance limits of approximately 4.0 (Egblom and Lindell, 1983). This north European species (otherwise solitary or even rare in central Europe in general) has survived in all studied lakes; however, its population was apparently stressed by the acidification process here. This can be documented by significantly lower fecundity of females collected in 1975 and 1982. Recently, *L. vespertina* increased its population densities in all five lakes considerably, at least twice (Čertovo) or even more than 10 times (Laka).

3.3. Recent status of the lakes and their potential for recovery

Besides several common features of the acidified lakes studied, they showed remarkable differences in some chemical and plankton parameters (Vrba et al., 2000; Kopáček et al., 2001). On the basis of the chemistry of both tributaries and surface lake water, we have categorised the lakes as follows: (i) Rachelsee, Plešné, Černé, and Čertovo remain strongly acidified; (ii) Prášilské and Kleiner Arbersee are moderately acidified but still with a depleted carbonate buffering system; whereas (iii) Grosser Arbersee and Laka have low bicarbonate alkalinity (Vrba et al., 2000). Accordingly, the less acidified lakes (with lower Al concentrations) show higher numbers (2–3) of surviving species (Table 2) and a higher biodiversity of rotifers and Crustacea (Table 4).

In consequence of different loading with acidifying agents and nutrients (Vrba et al., 2000), the lakes represent a fascinating set of unique freshwater bodies, which differ in particular aspects from those found at acidified lakes elsewhere (cf. Stenson et al., 1993). Both plankton biomass and pelagic food webs became dominated by microorganisms because of the reduction of biodiversity and thus of absence of the higher trophic levels. There is observed a characteristic and extremely high heterotrophic microbial biomass with an extreme proportion of filaments, which is usually as high as phytoplankton biomass (Fig. 2). The only exception represents the plankton of Plešné Lake, where phytoplankton accounts for ~80% of the total biomass due to the higher inflow concentration of phosphorus compared with the other lakes (Vrba et al., 2000; cf. Fig. 2). The summer zooplankton biomass mostly accounted for <1% of the total biomass (Fig. 2). Tables 4 and 5 summarise most invertebrate (except for insects) and phytoplankton taxa, respectively, recently found in the Bohemian Forest lakes.

The recent phytoplankton composition of seven dimictic lakes is surprisingly similar (two filamentous Cyanobacteria and 20–23 algae commonly found in the preserved samples), whereas a lower number of algal taxa (13) has been found in Laka Lake (Table 5). However, the actual number of algal species in the lakes might be higher if sampled repeatedly (cf. presence of *Cryptomonas* spp. in Čertovo and Plešné Lake, Table 5). Schaumburg (2000) reported as many as 39 and 63 phytoplankton species present in Grosser Arbersee and Kleiner Arbersee, respectively, (but just 22 items in Rachelsee) during longer observation periods. Although the species composition is similar, the phytoplankton biomass in Plešné Lake is usually dominated by non-motile species (*Monoraphidium dybowskii* and Cyanobacteria), whereas phytoflagellates dominate the phytoplankton biomass in all other lakes studied (cf. Table 5; Nedbalová and Vrtiška, 2000). All recently present species at these lakes were observed in Černé Lake as early as in 1936 (B. Fott, unpublished); the only species of his list which was not found at present is *Cyclotella* sp. (Vrba et al., 2000). Thus, the comparison of the present status with the old records suggests that many phytoplankton species of acid-sensitive oligotrophic lakes were able to survive when the lakes became acidic (Fott et al., 1994).

On the other hand, owing to lack of detailed phytoplankton data in the past, we can hardly prove a phytoplankton recovery in these lakes, except for an almost 50% increase in the chlorophyll *a* concentration in Plešné Lake between 1994 and 1998 (Vrba, unpublished data). While the total phosphorus concentrations remained unchanged during this period, the increase in phytoplankton biomass was likely a consequence of less phosphorus immobilisation by Al (Kopáček et al., 2000) due to the decreasing trend in the Al concentration in the lake (up to now ~50% reduction compared with the maximum values ~15 years ago; Veselý et al., 1998b). Therefore, this ongoing Al decrease seems to be the key factor of any possible biological recovery of the lake ecosystems studied. First, the current Al concentrations are less impoverishing the phosphorus availability for phytoplankton (Bittl et al., 2001; Vrba et al., unpublished) and second, any toxic effects of Al on the aquatic biota decreased significantly during the chemical reversal of the lakes.

Unlike the recovery of Černé Lake, which is indicated by the increase in the cladoceran population (*C. qudrangula*), the beginning of zooplankton recovery in Plešné Lake seems to be manifested by the increase in pelagic rotifers. While their mean numbers were almost negligible (30–180 ind. m^{-3}) in summer 1990–1992, the numbers increased by 2–3 orders of magnitude (11 000–37 000 ind. m^{-3}) in summer 1997–1999. Because the acidotolerant species of rotifers (cf. Table 4; Berzinš and Pejler, 1987) are generally dominant in the plankton, the increase in their abundance apparently resulted from the increase in

Table 4
Recent list of all rotifer and crustacean taxa (common open-water species in bold) in the Bohemian Forest lakes, 1997–2000 (see key in Table 1)

Species	CN	CT	RA	PL	KA*	PR	GA*	LA*
Rotatoria (only pelagic samples):								
Bdelloidea g. sp.	x	x	x	x	x	x	–	–
Brachionus sericus* Rouss.*	**(x)**	**–**	**–**	**x**	**–**	**–**	**–**	**–**
Collotheca pelagica* (Rouss.)*	**x**	**x**	**(x)**	**x**	**–**	**x**	**–**	**–**
Colurella sp.	(x)	–	–	–	–	–	–	–
Erignatha clastopis (Gosse)	–	–	–	x	–	x	–	–
Euchlanis dilatata (Ehr.)	–	–	–	–	(x)	–	(x)	(x)
Keratella serrulata* (Ehr.)*	**x**	**x**	**x**	**xx**	**x**	**x**	**(x)**	**(x)**
Keratella ticinensis* (Call.)*	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**x**
Lecane ligona (Dunl.)	–	(x)	x	(x)	–	(x)	–	–
Lecane mira (Murr.)	–	–	–	–	(x)	–	–	–
Lecane stichaea Harr.	x	x	–	x	x	x	(x)	x
Lepadella acuminata (Ehr.)	(x)	(x)	–	x	(x)	–	–	–
Microcodon clavus* Ehr.**	**xx**	**xx**	**x**	**x**	**–**	**x**	**–**	**x**
Monommata sp.	–	–	–	–	–	(x)	–	–
Monostyla lunaris (Ehr.)	x	x	x	x	x	x	x	(x)
Monostyla pyriformis (Dad.)	–	–	–	–	–	x	–	–
Polyarthra major* Burckh.*	**–**	**–**	**–**	**–**	**x**	**–**	**x**	**xx**
Polyarthra remata* Skor.*	**xx**	**xx**	**–**	**–**	**xx**	**xx**	**x**	**xx**
Synchaeta oblonga* Ehr.*	**xx**	**x**	**–**	**xx**	**x**	**xx**	**(x)**	**–**
Synchaeta pectinata* Ehr.*	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**x**
Trichocerca spp.	(x)	(x)	(x)	(x)	–	x	–	(x)
Trichotria tetractis (Ehr.)	–	–	–	–	–	x	–	–
Cladocera (both pelagic and littoral samples):								
Acantholeberis curvirostris (O.F.M.)	x	x	x	–	x	x	x	x
Acroperus harpae Baird	x	x	x	x	x	x	x	x
Alona affinis (Leydig)	(x)	x	x	x	x	x	(x)	x
Alona guttata Sars	x	x	–	x	x	x	–	(x)
Alona quadrangularis (O.F.M.)	–	–	–	–	x	–	–	x
Alonella excisa (Fisch.)	x	x	(x)	x	x	x	x	x
Alonella nana (Baird)	–	–	–	–	(x)	–	–	–
Alonopsis elongata (Sars)	x	x	–	–	x	(x)	x	x
Ceriodaphnia quadrangula* (O.F.M.)**	**xx**	**–**	**–**	**–**	**xx**	**–**	**x**	**x**
Chydorus sphaericus (O.F.M.)***	–	–	–	–	x	–	–	–
Daphnia longispina* (O.F.M.)*	**–**	**–**	**–**	**–**	**–**	**xx**	**–**	**x**
Eurycercus lamellatus O.F.M.	–	–	–	–	x	–	x	x
Graptoleberis testudinaria (Fisch.)	–	–	–	–	–	–	–	(x)
Holopedium gibberum* Zaddach*	**–**	**–**	**–**	**–**	**–**	**–**	**x**	**–**
Iliocryptus sordius (Liévin)	(x)	–	–	–	–	–	–	–
Peracantha truncata (Müller)	–	–	–	–	–	–	x	x
Polyphemus pediculus L.	–	–	–	–	x	x	x	x
Sida crystallina (O.F.M.)	–	–	–	–	x	–	x	–
Simocephalus vetulus (O.F.M.)	–	–	–	–	–	–	–	x
Copepoda (both pelagic and littoral samples):								
Acanthocyclops vernalis* (Fisch.)**	**–**	**xx**	**–**	**xx**	**x**	**–**	**–**	**x**
Cyclops abyssorum* Sars*	**–**	**–**	**–**	**–**	**–**	**xx**	**xx**	**–**
Diacyclops nanus (Sars)	x	x	(x)	x	–	x	x	–
Eucyclops serrulatus (Fisch.)	x	–	–	x	(x)	(x)	(x)	(x)
Heterocope saliens* (Lillj.)**	**–**	**–**	**–**	**xx**	**–**	**–**	**–**	**–**
Macrocyclops fuscus (Jur.)	x	x	(x)	–	x	x	x	x
Paracyclops fimbriatus (Fisch.)	–	–	–	(x)	–	–	–	–
Total number of present taxa:	23	20	13	21	26	26	22	27

* We sampled the lake only in September 1999.
** A typical pelagic species.
*** A littoral-pelagic (tychoplanktic) species.
x, present species; (x), only 1–2 specimens in some samples; xx, important component of zooplankton biomass; –, absent species.

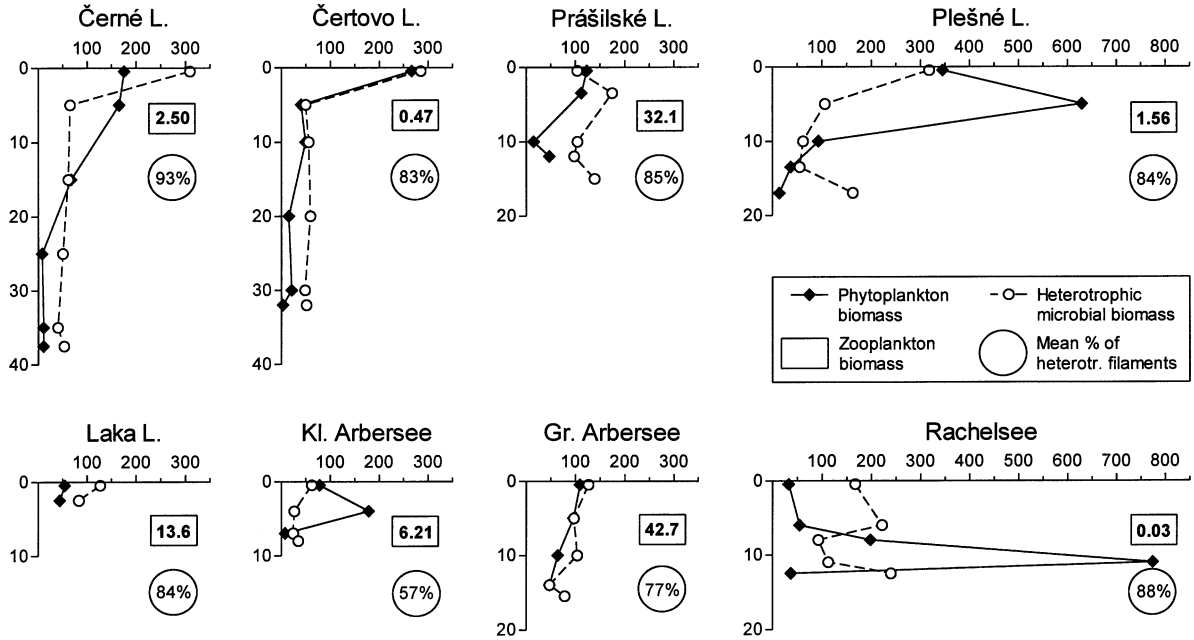

Fig. 2. A comparison of plankton biomass (in μg C l^{-1}) in the Bohemian Forest lakes in September 1999: volume weighted means of zooplankton biomass (bold numbers, in rectangles) and vertical profiles of phytoplankton and heterotrophic microbial biomass (average proportion of filaments in per cent of the heterotrophic microbial biomass in each lake, in circles).

food resources in Plešné Lake rather than from a direct effect of the chemical reversal.

As far as some groups of aquatic insect are concerned, we have not yet noticed any remarkable recovery trends in the original fauna. The present samples exhibit the same total numbers species or higher by 1–2 species of macrozoobentos compared with those in the early 1990s (cf. Fig. 1). However, the total number of specimens and their densities are evidently increasing in the littoral zone of all the lakes studied. Besides the 10-fold increase in mayfly density (*L. vespertina*), the recent regular occurrence of planktonic larvae of *Chaoborus obscuripes* van der Wulp (Diptera) is typical for the shallow Laka Lake with a large biomass of submerged vegetation. This invertebrate predator likely controls the zooplankton community. Unlike in the other lakes with crustacean zooplankton (cf. Table 4 and Fig. 2), rotifers are dominant in zooplankton biomass in Laka Lake, whereas both *D. longispina* and *C. quadrangula* occur at low numbers. Such a dominance of invertebrate predators and rotifers in the absence of fish were described as the first period of plankton recovery of the acidified Swedish lakes treated by liming. No further recolonisation of those lakes by dense cladoceran populations (e.g. *D. longispina*, *H. gibberum*, and *C. quadrangula*) followed unless the introduced fish eliminated the invertebrate predators (Stenson et al., 1993).

As far as we know, no return of fish has been documented in any Bohemian Forest lake as yet. It is typical that the decrease in the lake water concentration of SO_4 drags behind the drop in atmospheric S depositions (Fig. 1) and that the consequent hysteresis in the chemical reversal of lakes from acidification further delays any biological recovery (Kopáček et al., 2002). The recent survey of all the lakes presents the first comprehensive background data for a more detailed study and evaluation of the process of biological recovery of the lakes. The set of long-term data reviewed in this paper shows that the Bohemian Forest lakes represent a unique opportunity to study the natural biological recovery processes in lake ecosystems damaged from an extremely strong acid stress.

Table 5
Recent list of common phytoplankton taxa in the Bohemian Forest lakes, survey of September 1999 (see key in Table 1)

Species	CN	CT	RA	PL	KA	PR	GA	LA
Cyanobacteria:								
Limnothrix sp.	x	x	x	xx	x	x	x	x
Pseudanabaena sp.	x	x	x	xx	x	x	x	x
Dinophyceae:								
Gymnodinium uberrimum (Allman) Kofoid et Sweezy	xx	xx	xx	–	xx	xx	xx	–
Gymnodinium sp.	x	x	x	x	x	x	x	x
Katodinium bohemicum (Fott) Litvinenko	x	x	x	x	x	x	x	x
Katodinium planum (Fott) Loeblich III	x	–	x	x	–	–	–	–
Peridinium umbonatum Stein	xx	xx	xx	xx	xx	xx	xx	xx
Cryptophyceae:								
Cryptomonas erosa Ehrenberg	x	x	x	x	x	xx	x	x
Cryptomonas gracilis Skuja	–	x*	–	x*	x	x	x	–
Cryptomonas marssonii Skuja	–	x*	x	x	xx	x	xx	–
Cryptomonas reflexa Skuja	–	–	–	–	xx	–	xx	xx
Chrysophyceae:								
Bitrichia ollula (Fott) Bourrelly	x	x	x	x	x	x	x	x
Dinobryon spp.	xx	xx	xx	xx	x	xx	x	xx
Mallomonas sp.	x	x	–	x	x	x	x	–
Ochromonas sp. (large)	x	x	x	x	x	x	x	x
Ochromonas sp. (small)	–	x	–	x	–	x	–	–
Spiniferomonas sp.	x	x	x	x	x	x	xx	x
Synura echinulata Korschikov	x	x	x	x	xx	x	x	x
Xanthophyceae:								
Isthmochloron trispinatum (W. et G.S. West) Skuja	x	x	x	x	x	x	x	–
Chlorophyta:								
Arthrodesmus incus (Bréb.) Hass.	–	–	–	–	x	–	–	–
Carteria multifilis (Fres.) Dill + *C. radiosa* Korschikov	x	x	xx	x	x	x	x	–
Chlamydomonas sp.	x	x	x	x	x	x	x	x
Chlorogonium fusiforme Matwienko	x	x	x	x	x	x	x	–
Chloromonas angustissima (Ettl) Gerl. et Ettl	x	x	x	x	x	x	x	x
Koliella corcontica Hind.	x	x	x	x	x	x	x	x
Monoraphidium dybowskii (Wolosz.) Hind. et Kom.-Legn.	x	x	x	xx	x	x	x	–
Tetraedron minimum (A. Br.) Hansg.	x	x	x	–	x	–	x	–
Phytoplankton (total number of common taxa):	22	24	22	23	25	23	24	15

* Absent *Cryptomonas* species in samples from the survey of September 1999, but commonly present in the lake phytoplankton during 1997–1998 (Nedbalová and Vrtiška, 2000).

x, present species; xx, important component of total phytoplankton biomass; –, absent species.

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