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Phytoplankton in acidified lakes: structure, function and response to ecosystem recovery

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Ph.D. thesis

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Annotation: Key factors and mechanisms influencing species composition and structure of plankton biomass with an emphasis on phytoplankton were studied in two acidified lake districts (Bohemian Forest and Tatra Mountains). Current progress in their biological recovery from acidification was assessed.

I declare that for publications submitted as a part of this Ph.D. thesis, Linda Nedbalová was an important member of the team, and significantly contributed to data collection, biological analyses and to manuscript preparation.

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I declare that neither this thesis, nor any of the publications attached within, have been submitted for the purpose of obtaining the title of Ph.D. or any other title at another institution.

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C O N T E N T

1. INTRODUCTION

This thesis is based on five publications dealing with plankton assemblages of lakes in two heavily acidified mountain areas in Central Europe, the Bohemian Forest and the High Tatra Mountains. As both lake districts are the object of long-term systematic ecological research, a unique set of complex limnological data was gathered, enabling a comparison with other affected regions throughout the world and also some attempts at generalisation. My role in the team consisted chiefly in the study of phytoplankton as the key component of the food web. I was mainly concerned with the structure, seasonal development and function of the phytoplankton assemblages, and I also focused on the evaluation of general biological response to the current chemical recovery of the lakes from acidification.

The main questions addressed in this thesis with an emphasis on phytoplankton assemblages are the following:

- What is the recent progress in chemical and biological recovery of the Bohemian Forest lakes from acidification?

- What are the key factors and mechanisms influencing species composition and structure of plankton biomass in the Bohemian Forest lakes?

- What is the role of episodic acidification in shaping both phytoplankton abundance and biomass in a non-acidified high mountain seepage lake (Ľadové Lake, High Tatra Mountains)? Are there any changes associated with the decrease of acid deposition?

2. BACKGROUND OF THE STUDY

2.1. Anthropogenic acidification of lake ecosystems: the case of the Bohemian Forest and Tatra Mountains

In the 1970s and 1980s, anthropogenic acidification of lakes, streams and soils due to atmospheric deposition of sulphur and nitrogen compounds was one of the major environmental threats in large regions of Europe and North America which received high loads of acidifying pollutants (e.g. HENRIKSEN 1980, SCHINDLER 1988, JOHNSON & LINDBERG 1991). Acid sensitive lakes are generally found in catchments with weathering-resistant bedrock, such as granite and quartzite, and poorly developed soils (WRIGHT & HENRIKSEN 1978, WRIGHT & al. 1980). The key role of toxic aluminium in biological damage was widely accepted (HÖRNSTRÖM & al. 1984, DRISCOLL 1985), and current studies have suggested a more complex role of aluminium in ecosystem functioning (e.g. KOPÁČEK & al. 2000a, PUHE & ULRICH 2001). In many lake districts, acidification has caused a drastic reduction of biodiversity followed by the disruption of food web structures (e.g. SCHINDLER 1988).

The mountain lakes in the Bohemian Forest and High Tatra Mountains are situated within ~ 200 km of the German-Polish-Czech border area, known for its large coal resources and numerous power plants as the „Black Triangle". The emissions of SO_2 in this region were the highest in Europe, reaching up to ~ 800 mmol.m^{-2}.year^{-1} during the peak in the late 1980s (BARRETT & al. 1995). Since both lake districts lie on a geologically sensitive bedrock, they were seriously affected by acidification (FOTT & al. 1994).

In the Bohemian Forest, the impact of acid rain on lake water chemistry and biology has been quite well documented, especially in the case of the Černé Lake. The lowest pH (~ 4.5) was observed in the middle of the 1980s, and this pH decline resulted in the disappearance of fish and planktonic cladoceran species from the lake (FOTT & al. 1994, VESELÝ 1994). Concentrations of aluminium in the Bohemian Forest lakes peaked at higher values in comparison with other acidified lake districts, reaching nearly 1 mg.l^{-1} in Čertovo Lake with the dominant proportion being in the labile fraction (FOTT & al. 1994). According to their acidification status, the lakes were divided into three categories: (i) strongly acidified lakes (Černé Lake, Čertovo Lake, Rachelsee, Plešné Lake), (ii) moderately acidified lakes (Prášilské Lake, Kleiner Arbersee) and (iii) slightly acidified lakes (Grosser Arbersee, Laka) (VRBA & al. 2000). Crustacean zooplankton survived the period of the most severe acidification only in the latter two lake groups, and fish are extinct in all lakes (FOTT & al. 1994, VESELÝ 1994, SCHAUMBURG 2000). Therefore, the pelagic zone of the lakes is

characterised by simplified food webs with dominance of microbial interactions and by an important proportion of heterotrophic filaments in the plankton biomass (VRBA & al. 1996).

In contrast to the Bohemian Forest, there are fewer direct reports on the beginning of acidification derived changes of lake water chemistry in the High Tatra Mountains (KOPÁČEK & al. 1998). The first data on sulphate and nitrate concentrations in lake water come from 1937 (STANGENBERG 1938), and these background levels increased until the 1980s when the acidification peak was reached, roughly at the same time as in the Bohemian Forest lake district (KOPÁČEK & al. 1998, KOPÁČEK & al. 2004a). Repeated synoptic samplings carried out from 1980–1983 revealed profound changes in the water chemistry of sensitive lakes. Acidified lakes above timberline were characterised by extremely low chlorophyll-*a* concentrations (< 0.2 μg.l^{-1}), and by the disappearance of crustacean zooplankton (STUCHLÍK & al. 1985). The sensitivity of particular lakes to acidification and the degree of impact was shown to be determined by the concentration of calcium and magnesium (FOTT & al. 1992), and nitrogen was shown to contribute significantly to decreases in lake water pH (KOPÁČEK & STUCHLÍK 1994). Overall, major factors governing lake water chemistry were bedrock composition and the amount of soils and vegetation in their catchments (KOPÁČEK & al. 2006). With respect to zooplankton status, in comparison with pre-acidification data (e.g. MINKIEWICZ 1914), naturally fishless lakes above timberline were divided into three groups: (i) non-acidified lakes with zooplankton composition unchanged, (ii) acidified lakes, where planktonic crustacean zooplankton disappeared and (iii) strongly acidified lakes, where only the acid-tolerant littoral species *Chydorus sphaericus* (Cladocera) survived. These groups were delimited using the arbitrary limits of an acid neutralising capacity of 25 and 0 μeq.l^{-1}. The toxicity of aluminium and food starvation due to acidification-induced oligotrophication were identified as key factors limiting the distribution of zooplankton species (FOTT & al. 1994, HOŘICKÁ & al. 2006). The acidification status of lakes was also reflected in a different structure of epilithic diatom assemblages (ŠTEFKOVÁ 2006).

2.2. Phytoplankton in acidified lakes

The phytoplankton is one of the first biological communities to be affected by acidification (SCHINDLER 1987). Changing chemical composition of lake water is reflected in shifts in species composition and biomass (FINDLAY & al. 1999, HÖRNSTRÖM 2002, ANDERSON & al. 2005).

2.2.1. Species composition

The effects of acidification on the diversity and structure of phytoplankton assemblages have been well documented. In general, the deficiency of plankton species biodiversity is one of the most important consequences of the anthropogenic acidification of lake water (ALMER & al. 1978). The phytoplankton of the most acidified oligotrophic lakes is typically represented by a low number of slowly growing flagellates. By means of vertical migration, these species are probably able to facilitate their nutrient supply, which is a more important factor driving taxonomic composition in comparison with acidity as such (HÖRNSTRÖM & al. 1984).

The phytoplankton of circumneutral oligotrophic lakes is typically dominated by nanoplanktonic flagellates from the Chrysophyceae, Chlorophyceae and Bacillariophyceae. In contrast, Dinophyceae and sometimes Cryptophyceae become more important in acidified lakes (DIXIT & SMOL, 1989). One of the most striking changes in affected communities is the disappearance of planktonic diatoms and desmids from lakes (ALMER & al. 1978, HÖRNSTRÖM & al. 1984). The common presence of *Peridinium umbonatum, Gymnodinium uberrimum, Dinobryon pediforme*, and other small naked dinoflagellates and chrysophycean flagellates are often recorded (ROSÉN 1981). Other species frequently occurring in acidified oligotrophic waters include *Bitrichia ollula* (Chrysophyceae), *Mallomonas* spp., S*ynura echinulata* (Synurophyceae) or *Isthmochloron trispinatum* (Xanthophyceae) (HÖRNSTRÖM, 2002).

Large dinoflagellates are typical K-selected species with low growth rates and the ability to exploit low nutrient concentrations (REYNOLDS, 1984). Namely *Peridinium umbonatum* is considered to be characteristic for strongly acidified lakes elsewhere (e.g. ALMER & al. 1974, ALMER & al. 1978, HÖRNSTRÖM & al. 1999, FINDLAY 2003). *Peridinium umbonatum* is known to be very tolerant to high concentrations of toxic aluminium, and in addition it is a superior competitor for nutrients in ultraoligotrophic conditions (YAN 1979). High abundance of *Peridinium umbonatum* is often found in acidified lakes, where crustacean

zooplankton is absent or highly reduced. Selective herbivory thus probably does not play an important role in the common dominance of this species in strongly affected lakes (HAVENS & DECOSTA 1985, FOTT & al. 1994). In another large dinoflagellate, *Gymnodinium uberrimum*, tolerance to conditions at low lake water pH can be enhanced by the presence of a thick gelatinous sheath (FINDLAY & KASIAN 1986).

Green algae (Chlorophyta) and cyanobacteria are usually highly reduced in conditions of low pH (ROSÉN 1981, DIXIT & SMOL 1989). However, the green coccal alga *Monoraphidium dybowskii*, for example, is known to be tolerant to high levels of toxic aluminium species, similarly to *Peridinium umbonatum*. In laboratory experiments, the growth of *Monoraphidium dybowskii* was unaffected up to a concentration of 1000 $\mu g.l^{-1}$ with a dominant proportion of labile monomeric aluminium (HÖRNSTRÖM & al. 1985). An extensive lake survey in Sweden revealed that this species is quite common in acidified lakes characterized by higher nutrient levels, and its occurrence is often recorded together with the colonial cyanobacterium *Merismopedia tenuissima* (ROSÉN 1981).

Overall, observed shifts in phytoplankton structure in lakes affected by anthropogenic acidification are the results of an interplay between high acidity, nutrient depletion and aluminium toxicity. However, the increased concentration of toxic aluminium species is considered to be mainly responsible for the disappearance of some phytoplankton species or even groups (HÖRNSTRÖM & al. 1984). The effect of aluminium is sometimes manifested not only by growth reduction, but also by disturbance of cell shape and content, as has been demonstrated by HÖRNSTRÖM & al. (1984) in *Monoraphidium griffithii* and *Synedra* cf. *nana*.

Even a considerable drop in pH together with associated changes in lake water chemistry sometimes does not result in a significant effect on the diversity and taxonomic composition of phytoplankton. In ultraoligotrophic acid-sensitive mountain lakes, severe growth conditions in the preacidification period have selected species, which are apparently able to survive when the lake become acidic. For example, the species composition of the strongly acidified Černé Lake in the Bohemian Forest has remained almost unchanged in comparison with data from 1935–1936 collected by B. Fott (FOTT & al. 1994). The only exception is the disappearance of *Cyclotella* sp. from the lake, which is in agreement with the generally accepted sensitivity of planktonic diatoms to acidification (ALMER & al. 1978). Unfortunately, long-term data on species composition allowing such comparisons are often lacking.

The presence of flagella has been recognised as crucial feature of phytoplankton in mountain lakes, enabling algae to maintain an optimal depth in the water column with regard to light conditions, nutrient concentration and temperature requirements (PECHLANER 1971).

Flagellates thus most frequently represent the dominating fraction of phytoplankton in mountain lakes, irrespective of pH (ROTT 1988, PUGNETTI & BETTINETTI, 1999, TOLOTTI & al. 2003). Due to the lack of nutrients as the result of natural oligotrophy, sometimes combined with oligotrophication caused by acidification (see below), mixotrophy seems to be a succesful life strategy for phytoplankton in mountain lakes characterised by low nutrient input (FELIP & al. 1999, PUGNETTI & BETTINETTI 1999, SIMONA & al. 1999). The ability of mixotrophic nutrition has been demonstrated for several dinoflagellates, chrysophytes and cryptophytes (e.g. PORTER 1988, NYGAARD & TOBIESEN 1993, ISAKSSON 1998). A good example is the genus *Dinobryon* (Chrysophyceae), covering its phosphorus demand by phagotrophy on the single-celled bacterioplankton (BIRD & KALFF 1987). This grazing by *Dinobryon* has a potentially important effect on both the size and structure of bacterial populations (ZNACHOR & HRUBÝ 2000).

2.2.2. Oligotrophication during acidification and phytoplankton biomass

Acidification influences not only the chemical composition of lake water, but also lake trophic status. Oligotrophication is characterised by a drop in nutrient supply and availability, and the precipitation of phosphorus by aluminium has been proposed as one possible mechanism (DICKSON 1980). Contradicting hypotheses concerning oligotrophication during acidification were reviewed by OLSSON & PETTERSSON (1993). JANSSON & al. (1986) suggested that low phosphorus level in acidified lakes is caused by reduced input from the watershed, possibly due to the efficient fixation of phosphorus to aluminium complexes in soils. The internal phosphorus cycle and availability is apparently disrupted as a result of acidification (KOPÁČEK & al. 2000a, BITTL & al. 2001). Due to the natural inactivation of available phosphorus by aluminium in water bodies with elevated aluminium input and a pH gradient between its inlet and outlet (KOPÁČEK & al. 2001, KOPÁČEK & al. 2004b), acidified lakes are generally characterised by low phytoplankton biomass and consequently high transparency (ALMER & al. 1974). However, many acid-sensitive lakes were probably already oligotrophic before the onset of acidification (OLSSON & PETTERSSON 1993).

On the other hand, a whole-lake experimental acidification did not result in decreases in phosphate and phytoplankton biomass (SCHINDLER 1980). Moreover, long-term observations of phytoplankton during acid rain induced acidification have sometimes revealed increases in biomass (HAVENS & DE COSTA 1984, FINDLAY & al. 1999). One explanation of this effect could be the replacement of small species by large ones (FINDLAY & KASIAN 1986), and the

dominance of large forms can thus be one of the reasons for high transparency (ALMER & al. 1978). In strongly acidified lakes, however, the reduced ability of aluminium to precipitate reactive phosphorus and resulting increase in nutrient availability was shown to be key mechanism resulting in high phytoplankton biomass (DICKSON 1980). Accordingly, the highest amount of phytoplankton in southern Sweden was recorded in lakes with pH below 4.5 (ALMER & al. 1974). In the period of maximal acid deposition, acidified lakes in the High Tatra Mountains were characterised by extremely low chlorophyll-*a* concentrations, whereas higher values were found both in non-acidified and especially in the strongly acidified lakes (HOŘICKÁ & al. 2006). This distribution of chlorophyll-*a* concentrations (similar to Almer´s U-curve for Swedish lakes, ALMER & al. 1974) corresponded to the values of total phosphorus (VYHNÁLEK & al. 1994, KOPÁČEK & al. 2000b).

An extremely high activity of extracellular phosphatases is often observed in acidified lakes (JANSSON & al. 1986, VRBA & al. 1996). Elevated concentrations of aluminium, which act as a competitive inhibitor, were suggested as the reason for this phenomenon (JANSSON 1981). However, BITTL & al. (2001) showed that the inhibitory effect of aluminium could not fully explain the extreme activities of phosphatases in the Bohemian Forest lakes, and suggested that phosphorus immobilization by particulate aluminium could be the complementary cause. Direct microscopic detection of extracellular phosphatases with a fluorogenic substrate (ELFP) showed that their activity is not evenly distributed within the phytoplankton community, and mirror the nutritional status of individual cells. Moreover, the production of phosphatases is very rare in groups with mixotrophic capacities (ŠTROJSOVÁ & VRBA 2006).

2.2.3. Phytoplankton of lakes in the Bohemian Forest and Tatra Mountains

The Bohemian Forest and the Tatra Mountains are the only two regions in the Czech and Slovac Republics where lakes of natural origin occur. These remote lakes have fascinated explorers for more than a century. In the Bohemian Forest, the pioneering limnological study was done by FRIČ & VÁVRA (1898). Detailed phycological investigations of the Černé Lake plankton was carried out by B. Fott, who even described three new species there, *Bitrichia ollula* (Chrysophyceae), *Katodinium planum* and *Katodinium bohemicum* (Dinophyceae) (FOTT 1937, 1938). In 1978, studies of acidification were started by a team from Charles University in Prague, but they focused at the beginning mainly on the chemistry of lake water and zooplankton composition in relation to acid rain driven changes (e.g. FOTT & al. 1980).

FOTT & al. (1994) compared actual data on phytoplankton species composition with that from the pre-acidification period, and came to the conclusion that phytoplankton structure has remained surprisingly stable in spite of drastic changes in lake water chemistry. However, no quantitative study was performed. Further data on phytoplankon including chlorophyll-*a* concentrations were published e.g. in VRBA & al. (1996, 2000) and HEJZLAR & al. (1998). NEDBALOVÁ & VRTIŠKA (2000) investigated the seasonal development and vertical distribution of phytoplankton in four lakes. Species richness of cyanobacteria and algae in selected lakes was also studied (LUKAVSKÝ in WEILNER 1997), and a new species of *Coelastrum* was described from the littoral zone of Černé Lake, Grosser Arbersee and Kleiner Arbersee (LUKAVSKÝ 2006). Other studies focused in detail on interesting interactions and mechanisms, e.g. ZNACHOR & HRUBÝ (2000) on *Dinobryon* grazing on bacteria, ŠTROJSOVÁ & VRBA (2006) on the seasonal and vertical distribution of the phosphatase activity of *Monoraphidium dybowskii* in Plešné Lake or NEDOMA & NEDBALOVÁ (2006) on the chlorophyll content of Plešné Lake phytoplankton.

Although algological investigations of lakes in the Tatra Mountains have a shorter history, the area can be considered as well explored (HINDÁK & KOVÁČIK 1993, HINDÁK 1994). The first mention about phytoplankton can be found in MINKIEWICZ (1914); more detailed data concerning several lakes were included in ERTL & al. (1965) and JURIŠ & al. (1965). An extensive survey was done by JURIŠ & KOVÁČIK (1987), who published a list of species in a large set of lakes. LUKAVSKÝ (1994) observed a decrease in phytoplankton species richness with increasing altitude and decreasing pH. Due to their difficult accessibility, lake research was mostly limited to single observations. The only two studies focusing on the seasonal development of phytoplankton were presented by DARGOCKÁ & al. (1997) and FOTT & al. (1999). In DARGOCKÁ & al. (1997), the influence of spring episodic acidification on the species composition and biomass of phytoplankton in a non-acidified lake was also discussed. VYHNÁLEK & al. (1994) studied chlorophyll and phosphorus concentrations of lake water, which were shown to be related to the acidification status of the lakes. Data on chlorophyll-*a* concentrations in the surface layer of a representative set of lakes were included in the monitoring, and form an integral part of numerous publications dealing both with period of the acidification peak and lake district recovery (e.g. STUCHLÍK & al. 1985, FOTT & al. 1994, KOPÁČEK & al. 2006, STUCHLÍK & al. 2006). Due to very the low trophic status of most lakes, a sensitive fluorometric method was introduced for the determination of chlorophyll-*a* in the framework of regular regional surveys (STRAŠKRABOVÁ & al. 1999).

2.3. Recovery of lakes from acidification

As ecosystems are naturally changing both through internal processes and global changes, the recovery from acidification cannot be simply judged as a return to a state before disturbance (GUNN & SANDØY 2003). According to the European Water Framework Directive, the goal in restoring ecosystems is to obtain "the biological community which is expected in conditions of minimal anthropogenic impact" (EUROPEAN COMMISSION 2000). Other definitions stress the return of key species (e.g. DISE & al. 1994).

The evidence of widespread biological damage both in Europe and Northern America has forced authorities to implement regulations, which have resulted in substantial reductions in the deposition of acidifying compounds (HEDIN & al. 1987, JENKINS 1999), and in a partial recovery of surface waters from anthropogenic acidification (STODDARD & al. 2000, WRIGHT & al. 2005). However, the biological recovery of affected lakes is often delayed or uncertain (KOPÁČEK & al. 2002, JEFFRIES & al. 2003, SKJELKVÅLE & al. 2003).

In the context of current chemical recovery, phytoplankton species, as probably the most sensitive plankton organisms, are likely to react very quickly due to their rapid turnover times (SCHINDLER 1987, FINDLAY 2003). The recovery of phytoplankton species diversity and a shift towards circumneutral assemblages has been observed both in Europe and Northern America (HÖRNSTRÖM 1999, FINDLAY 2003). In Sweden, extensive liming activities led to the restoration of original phytoplankton species composition, with the exception of several species of cyanobacteria and desmids, in lakes, which were previously strongly acidified (HÖRNSTRÖM 2002). Concerning zooplankton, a massive return of *Daphnia longispina* (Cladocera) by hatching from sediment egg-banks was observed in lakes in southern Norway (NILSSEN & WÆRVÅGEN 2002). In acid-stressed lakes near Sudbury (Canada), evidence for relatively rapid biological recovery was reported for plankton, mobile species of benthic invertebrates and some fish populations (KELLER & al. 1992, YAN & al. 1996). However, the restoration of aquatic communities can not be adequately predicted, especially in the case of isolated mountain headwater lakes. The natural dispersal of metazoan fauna is a stochastic process, and the successful establishment of a new population depends on the size of inoculum and both abiotic and biotic factors (CÁCERES & SOLUK 2002). Furthermore, ecosystem resistance due to the presence of invertebrate predators in acidified lakes without fish may prevent rapid biological recovery (NILSSEN & WÆRVÅGEN 2003, WÆRVÅGEN & NILSSEN 2003).

In the Bohemian Forest and Tatra Mountains, the partial reversal in hydrochemistry of acidified lakes due to political and economical changes in postcommunist countries since 1989 has also been observed (KOPÁČEK & al. 1998), but changes in lake water chemistry followed the decreases in nitrogen and sulphur emissions with a certain hysteresis (KOPÁČEK & al. 2002). One significant change in the chemistry of the lakes has been a rapid decrease in concentrations of aluminium (VESELÝ & al. 1998, KOPÁČEK & al. 2006). However, even the full implementation of the Gothenburg Protocol will not be sufficient for the full recovery of the most sensitive lakes (KOPÁČEK & al. 2004a).

Similarly as in other acidified lake districts, biological recovery of mountain lakes in Central Europe has been shown to be significantly lagging behind the reversal in lake water chemistry. In the Bohemian Forest, the first sign of a biotic response has been observed in Černé Lake, where *Ceriodaphnia quadrangula* (Cladocera) reappeared in the open water in the late 1990s (KOPÁČEK & al. 2002). The return of this species was probably possible only due to its survival in the littoral zone during the peak of acidification (FOTT & al. 1994). Recently, the survival of *Daphnia longispina* (Cladocera), which disappeared from several Bohemian Forest lakes a result of acidification, was tested in a bioassay, and the best results were obtained with the water from Plešné Lake. Subsequently, a large scale experiment was conducted by transferring two indigenous crustacean plankton species into this lake. The reintroduction of *Cyclops abyssorum* (Copepoda) was confirmed to be successful after one year, though that of *Daphnia longispina* was not (KOHOUT & FOTT 2006).

In the Tatra Mountains, a significant increase in chlorophyll-*a* concentrations in lake water was observed in 2004 in comparison with 1994 data, which might be due to better phosphorus bioavailability following increases in pH (KOPÁČEK & al. 2006). Concerning zooplankton, the first signs of biological recovery were recorded in the early 2000s, when several extinct species of crustacean reappeared in some acidified lakes. However, acidification still remains the most important factor driving the zooplankton composition in lakes (HOŘICKÁ & al. 2006). The return of most previously extinct littoral Cladocera has also been detected, within ten years of the beginnining of chemical recovery (SACHEROVÁ & al. 2006).

4. SUMMARY AND CONCLUSIONS

This thesis deals chiefly with various aspects of plankton ecology in mountain lakes recovering from anthropogenic acidification. A brief summary of attached publications and general conclusions with an emphasis on phytoplankton assemblages follow.

Biological recovery of the Bohemian Forest lakes from acidification
(NEDBALOVÁ & al. 2006a)

Based on data collected in autumn 2003, this study of eight Bohemian Forest lakes focused in detail on an evaluation of the current progress in their chemical and biological recovery from acidification. In comparison with a 1999 survey, four lakes (Kleiner Arbersee, Prášilské Lake, Grosser Arbersee and Laka) have recovered their carbonate buffering system. However, the other four lakes (Černé Lake, Čertovo Lake, Rachelsee and Plešné Lake) still remain chronically acidified. The composition and amount of volume-weighted plankton biomass reflected differences in the acidification status and nutrient loading to particular lakes. While bacterioplankton was the main component in acidified lakes except for Plešné Lake, phytoplankton and zooplankton co-dominated the plankton biomass in the recovering lakes. A dominance of phytoplankton was characteristic for mesotrophic Plešné Lake, because of higher phosphorus input to this lake. Overall, the species composition and amount of phytoplankton biomass reflected differences in acidification status, nutrient availability and zooplankton status among the lakes. For example, grazing pressure of filtering zooplankton seems to be the cause for the high proportion of the large dinoflagellate *Gymnodinium uberrimum* in the phytoplankton biomass of some lakes. Concerning newly observed signs of biological recovery, we documented an increase in zooplankton biomass in the recovering lakes and a two-order-of-magnitude increase in rotifer abundance in acidified Plešné Lake. Moreover, this survey is the first evidence of the return of some macrozoobenthos species that were extinct during acidification (in particular from the Ephemeroptera and Plecoptera).

Phytoplankton of a high mountain lake (Ľadové pleso, the Tatra Mountains, Slovakia): seasonal development and first indications of a response
to decreased acid deposition (NEDBALOVÁ & al. 2006b)

In this one-year study, we examined the seasonal and vertical distribution of phytoplankton in a non-acidified high mountain lake (Ľadové Lake, High Tatra Mts) with an emphasis on the effect of the currently less-pronounced episodic acidification of surface layers during melting periods. Unicellular flagellates, namely from the Cryptophyceae and Chrysophyceae

dominated the phytoplankton, and different seasonal and depth distributions of important species (*Plagioselmis lacustris*, *Crypptomonas* cf. *erosa*, *Ochromonas* spp. and *Mallomonas akrokomos*) indicated differences in their ecological requirements. Total phytoplankton biomass did not exceed values typical for oligotrophic lakes, and showed a marked seasonal development with two high peaks in the deeper layers: one in December under thin clear ice and one just after the improvement of growth conditions due to melting of the winter cover. The specific content of chlorophyll-*a* showed clear patterns in both seasonal and vertical distribution. Concerning long-term trends in the lake water chemistry from 1980–2004, a significant increase in surface pH and acid neutralising capacity was observed, and the extent of episodic acidification has diminished both in time and space. We suppose that the shift in species composition, as well as the increase in phytoplankton abundances in comparison with a 1990–1991 study can be considered as the first sign of a biological response to decreased acid deposition.

Long term studies (1871–2000) on acidification and recovery of lakes in the Bohemian Forest (Central Europe) (VRBA & al. 2003a)

In this paper, we documented long-term changes in acid deposition, lake water chemistry and biodiversity of eight Bohemian Forest lakes. Due to a 130-year research tradition, we were able to cover the pre-acidification period, the period of strong acidification as well as the period of reversal from acidity, especially in the case of the most extensively studied Černé Lake. During the 1960s and 1970s, heavy acid deposition caused a drop of 2 pH units in this lake. The shift in lake water chemistry was accompanied by a drastic reduction in biodiversity, which included the extinction of most species of crustacean zooplankton, littoral macrozoobenthos (Ephemeroptera, Plecoptera) and fish. Acidification resulted in reduced biodiversity in all lakes, and pelagic food webs became dominated by microorganisms. Concerning phytoplankton, the 1999 survey documented the presence of 20–23 species in the seven dimictic lakes. Due to scarce historical records, we could not evaluate acidification-driven changes in phytoplankton species composition and biomass in detail. However, a comparison of the 1999 survey with older data suggested that many phytoplankton species were able to survive when the lakes became acidic. As regards signs of potential biological recovery from acidification, we observed an almost 50 % increase in chlorophyll-*a* concentrations in Plešné Lake between 1994 and 1998, which was likely a consequence of reduced phosphorus immobilisation by aluminium. Moreover, the population of *Ceriodaphnia*

quadrangula returned to the pelagial of Černé Lake and the number of rotifers started to increase in Plešné Lake.

A key role of aluminium in phosphorus availability, food web structure, and plankton dynamics in strongly acidified lakes (Vʀʙᴀ & al. 2006)

This study focused on the evaluation of aluminium as a key factor driving plankton structure in four acidified lakes in the Bohemian Forest. The highest proportion of ionic aluminium was found in the most acid Čertovo Lake; on the other hand, the highest phosphorus input was characteristic for Plešné Lake. Phytoplankton in all lakes was apparently phosphorus limited, which was demonstrated both by elevated carbon to phosphorus ratios and the extremely high activity of acid extracellular phosphatases. The changes in lake water chemistry (pH and aluminium speciation) between 1998 and 2003 resulted in a significant increase in phytoplankton biomass. We suggested that both ionic and particulate aluminium may govern phosphorus availability namely through direct toxicity, inhibition of extracellular phosphatase activity and phosphorus inactivation. In lakes with lower concentrations of phosphorus, flagellates probably dominate the phytoplankton biomass due to their capacity for active migration. Moreover, mixotrophic species (e.g. frequent *Dinobryon* spp.) can partially satisfy their phosphorus demand by grazing on unicellular bacteria. Non-motile species (e.g. *Monoraphidium dybowskii*) likely take advantage of the higher phosphorus input to Plešné Lake. The dominance of this species in Plešné Lake can be further supported by its tolerance to high levels of toxic aluminium species. Hence, a unique set of specific food webs dominated by microorganisms have developed in the pelagic zone of particular lakes as the result of differences in aluminium and phosphorus input and acidification status.

Massive occurrence of heterotrophic filaments in acidified lakes: seasonal dynamics and composition (Vʀʙᴀ & al. 2003b)

We documented the massive presence of extremely long (> 100 μm) heterotrophic filaments in the plankton of acidified lakes in the Bohemian Forest. Our aim was to evaluate possible reasons for their seasonal development patterns and their high proportion in the plankton biomass in particular lakes. The main factors influencing filament dynamics were identified as both grazing of mixotrophic flagellates from the genus *Dinobryon* (Chrysophyceae) on unicellular bacteria and filtration of *Daphnia longispina*, which occassionally reduced protistan grazers as well as the filaments. In both oligotrophic lakes (Čertovo and Prášilské), *Dinobryon pediforme* was often the most abundant phytoplankton species, taking advantage

of mixotrophic growth in conditions of severe phosphorus limitation. On the other hand, *Dinobryon sociale* var. *americana* occurred in mesotrophic Plešné Lake usually in low abundace, and autotrophic phytoplankton species dominated in this lake due to the elevated nutrient supply. The plankton composition and dynamics in the lakes clearly showed the influence of both protistan grazing and the top-down control of cladoceran grazing on shaping the structure of pelagic assemblages.

Overall, we tried to determine key factors and mechanisms influencing actual species composition and structure of plankton biomass in acidified lakes under study. Through the effects of direct toxicity, phosphorus immobilisation and inhibition of extracellular phosphatases, aluminium was shown to shape the specific structure of pelagic food webs in particular Bohemian Forest lakes. The amount of total plankton biomass was apparently the result of a complex interplay between pH and phosphorus and aluminium concentrations in tributaries and lake water. In addition, protistan grazing by *Dinobryon* spp. was identified as the reason for an unusually high proportion of heterotrophic filaments in the plankton biomass. Concerning phytoplankton, higher nutrient input seems to favour the occurrence of non-motile forms. On the other hand, flagellates often with the ability of mixotrophic nutrition dominate in the lakes with lower nutrient input, as it is typical for oligotrophic mountain lakes elsewhere.

Furthermore, the results of an extensive limnological survey have demonstrated in detail that the beginning of biological recovery of the lakes from acidification has been significantly delayed after the chemical reversal. However, a significant progress was recorded in comparison with previous studies. Due to the harsh growth conditions in the lakes already during the pre-acidification period, the response of phytoplankton communities was manifested chiefly through increases in biomass as a result of reduced phosphorus immobilisation by aluminium in conditions of higher pH. However, we have documented a shift in phytoplankton species composition in a lake characterised by diminishing extent of episodic acidification. Most likely, further reversal in lake water chemistry in both lake districts will be reflected in changes in biomass and relative proportion of species due to the varying importance of bottom-up and top-down control. In general, we suppose that namely the ecosystem resistance may prevent full biological recovery of the lakes.

5. REFERENCES

ALMER, B., DICKSON, W., EKSTRÖM, C., HÖRNSTRÖM, E. & MILLER, U. (1974): Effects of acidification on Swedish Lakes. *Ambio* **3:** 30–36.

ALMER, B., DICKSON, W., EKSTRÖM, C. & HÖRNSTRÖM, E. (1978): Sulphur pollution and the aquatic ecosystems. In: NRIAGU, J. O. (ed.): *Sulphur in the environement, part II. Ecological impacts.* Wiley, New York, 271–311.

ANDERSON, N. J., JEPPESEN, E. & SONDERGAARD, M. (2005): Ecological effects of reduced nutrient loading (oligotrophication) on lakes: an introduction. *Freshwater Biology* **50:** 1589–1593.

BARRETT, K. & al. (1995): European transboundary acidifying air pollution. EMEP/MSC-W Report 1/95, Norwegian Meteorological Institute, Oslo.

BIRD, D. F. & KALFF, J. (1987): Algal phagotrophy: Regulating factors and importance relative to photosynthesis in *Dinobryon* (Chrysophyceae). *Limnol. Oceanogr.* **32(2):** 277–284.

BITTL, T., VRBA, J., NEDOMA, J. & KOPÁČEK, J. (2001): Impact of ionic aluminium on extracellular phosphatases in acidified lakes. *Environmental Microbiology* **3(9):** 578–587.

CÁCERES, C. E. & SOLUK, D. A. (2002): Blowing in the wind: a field test of overland dispersal and colonisation by aquatic invertebrates. *Oecologia* **131:** 402–408.

DARGOCKÁ, J., KNESLOVÁ, P. & STUCHLÍK, E. (1997): Fytoplanktón niektorých rôzne acidifikovaných plies Vysokých Tatier. *Štúdie o TANAPe* **2(35):** 41–62.

DICKSON, W. (1980): Properties of acidified waters. *Proc. Int. Conf. Ecol. Impact Acid Precip., SNSF-project*: 75–83.

DISE, N., AHLF, W., BRAHMER, G., COSBY, B. J., FOTT, J., HAUHS, M., JUTTNER, I., KREUTZER, K., RADDUM, G. G. & WRIGHT, R. F. (1994): Group report: Are chemical and biological changes reversible? In: STEINBERG, C. E. W. & WRIGHT, R. F. (eds.): *Acidification of freshwater ecosystems, implications for the future.* John Wiley and sons, Chichester, UK, pp. 375–391.

DIXIT, S. S. & SMOL, J. P. (1989): Algal assemblages in acid-stressed lakes with particular emphasis on diatoms and chrysophytes. In: RAO, S. S. (ed.): *Acid stress and aquatic microbial interactions.* CRS Press Inc., Boca Raton, Fla., 176 p.

DRISCOLL, C. T. (1985): Aluminium in acidic surface waters: chemistry, transport and effects. *Environ. Health Perspectives* **63:** 93–104.

ERTL, M., JURIŠ, Š. & VRANOVSKÝ, M. (1965): K poznaniu planktónu Veľkého a Malého Hincovho pleas. *Zborník prác o TANAPe* **8:** 57–69.

EUROPEAN COMMISSION (2000): Directive 2000/60/EC of the European Parliament and the Council of 23 October 2000 establishing a framework for community action in the field of water policy. *Official Journal* **L327** of **22**, **12**, **2000**, pl.

FELIP, M., BARTUMEUS, F., HALAC, S. & CATALAN, J. (1999): Microbial plankton assemblages, composition and biomass, during two ice-free periods in a deep high mountain lake (Estany Redó, Pyrenees). *J. Limnol.* **58(2):** 193–202.

FINDLAY, D. L. & KASIAN, S. E. M. (1986): Phytoplankton community responses to acidification of Lake 223, Experimental Lake Area, northeastern Ontario. *Water Air Soil Pollut.* **30:** 719–726.

FINDLAY, D. L., KASIAN, S. E. M., TURNER, M. T. & STAINTON, M. P. (1999): Responses of phytoplankton and epilithon during acidification and early recovery of a lake. *Freshwater Biol.* **42:** 159–175.

FINDLAY, D. L. (2003): Response of phytoplankton communities to acidification and recovery in Killarney Park and the experimental lakes area, Ontario. *Ambio* **32(3):** 190–195.

FOTT, B. (1937): Dva nové druhy rodu *Diceras* Reverdin. *Věstník Královské České Společnosti nauk* Tř. **II:** 1–7.

FOTT, B. (1938): Eine neue *Gymnodinium*- und *Massartia*-Art. *Studia Botanica Čechoslovaca* **1:** 100–104.

FOTT, J. (1980): Předběžná zpráva o současném stavu acidifikace Černého jezera. In : *Zborník referátov celoštátneho seminára Voda - životné prostredie - problematika vody v podhorských oblastiach.* ZP SVTS, Tatranská Lomnica 1980, 214–224 (Diel I.).

FOTT, J., STUCHLÍK, E., STUCHLÍKOVÁ, Z., STRAŠKRABOVÁ, V., KOPÁČEK, J. & ŠIMEK, K. (1992): Acidification of lakes in Tatra Mountains (Czechoslovakia) and its ecological consequences. In: MOSELLO, R., WATHNE, B. M. & GIUSSANI, G. (eds.): Limnology on groups of remote lakes: ongoing and planned activities. *Documenta Ist. ital. Idrobiol.* **32:** 69–81.

FOTT, J., PRAŽÁKOVÁ, M., STUCHLÍK, E. & STUCHLÍKOVÁ, Z. (1994): Acidification of lakes in Šumava (Bohemia) and in the High Tatra Mountains (Slovakia). *Hydrobiologia* **274:** 37–47.

FOTT, J., BLAŽO, M., STUCHLÍK, E. & STRUNECKÝ, O. (1999): Phytoplankton in three Tatra Mountain lakes of different acidification status. *J. Limnol.* **58:** 107–116.

FRIČ, A. & VÁVRA, V. (1898): Výzkum dvou jezer šumavských, Černého a Čertova. *Archív pro pro přírodovědný výzkum Čech* **10:** 1–66.

GUNN, J. M. & SANDØY, S. (2003): Introduction to the Ambio Special Issue on biological recovery from acidification: Northern lakes recovery study. *Ambio* **32(3):** 162–164.

HAVENS III, K. E. & DE COSTA, J (1984): The effects of acidification and phosphorus addition on phytoplankton biomass and productivity in a circum-neutral mesotrophic lake receiving acid precipitation. *Arch. Hydrobiol./Suppl.* **69(4):** 443–476.

HAVENS, K. & DE COSTA, J. (1985): An analysis of selective herbivory in an acid lake and its importance in controlling phytoplankton community structure. *J. Plankton Res.* **7(2):** 207–222.

HEDIN, L. O., LIKENS, G. E. & BORMAN, F. H. (1987): Decrease in precipitation acidity resulting from decreased SO_4^{2-} concentration. *Nature* **325:** 244–246.

HEJZLAR, J., KOPÁČEK, J., VRBA, J., ČÍŽKOVÁ, R., KOMÁRKOVÁ, J. & ŠIMEK, K. (1998): Limnological study of Plešné Lake in 1994–1995. *Silva Gabreta* **2:** 155–174.

HENRIKSEN, A. (1980): Acidification of freshwaters - a large scale titration. *Proc. Int. Conf. Ecol. Impact Acid. Precip., SNSF-project, Norway:* 68–74.

HINDÁK, F. & KOVÁČIK, L. (1993): Súpis siníc a rias Tatranského Národného parku. *Zborník Tanap* **33:** 235–279.

HINDÁK, F. (1994): Sinice a riasy. In: VOLOŠČUK, I. (ed.): *Tatranský národný park.* Gradus, Martin, 108–113.

HOŘICKÁ, Z., STUCHLÍK, E., HUDEC, I., ČERNÝ, M. & FOTT, J. (2006): Acidification and the structure of crustacean zooplankton in mountain lakes: The Tatra Mountains (Slovakia, Poland). *Biologia* **61**/Suppl. **18**: S121–S134.

HÖRNSTRÖM, E., EKSTRÖM, C. & DURAINI, O. (1984): Effects of pH and different levels of aluminium on lake plankton in the Swedisch west coast area. *Nat. Swed. Board of Fish., Inst. Of Freshwater Research Drottigholm, Lund, Report* **No 61:** 115–127.

HÖRNSTRÖM, E., HARBOM, A., EDBERG, F. & ANDRÉN, C. (1995): The influence of pH on aluminium toxicity in the phytoplankton species *Monoraphidium dybowskii* and *M. griffithii. Water Air Soil Pollut*. **85:** 817–822.

HÖRNSTRÖM, E. (1999): Long-term phytoplankton changes in acid and limed lakes in SW Sweden. *Hydrobiologia* **394:** 93–102.

HÖRNSTRÖM, E. (2002): Phytoplankton in 63 limed lakes in comparison with the distribution in 500 untreated lakes with varying pH. *Hydrobiologia* **470:** 115–126.

ISAKSSON, A. (1998) Phagotrophic phytoflagellates in lakes - a literature review. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* **51:** 63–90.

JANSSON, M. (1981): Induction of high phosphatase activity by aluminium in acidified lakes. *Arch. Hydrobiol.* **93:** 32–44.

JANSSON, M., PERSSON, G. & BROBERG, O. (1986): Phosphorus in acidified lakes: The example of Lake Gardsjön, Sweden. *Hydrobiologia* **139:** 81–96.

JEFFRIES, D. S., CLAIR, T. A., COUTURE, S., DILLON, P. J., DUPONT, J., KELLER, W., MCNICOL, D. K., TURNER, M. A., VET, R. & WEEBER R. (2003): Assessing the recovery of lakes in southeastern Canada from the effects of acidic depositon. *Ambio* **32(3):** 176–182.

JENKINS, A. (1999): End of the acid rain? *Nature* **401:** 537–538.

JOHNSON, D. W. & LINDBERG, S. E. (eds.) (1991): *Atmospheric deposition and forest nutrient cycling. A synthesis of the Integrated Forest Study*. Springer Verlag, 707 p.

JURIŠ, Š., ERTL, M., ERTLOVÁ, E. & VRANOVSKÝ, M. (1965): Niektoré poznatky z hydrobiologického výskumu Popradského plesa. *Zborník prác o TANAPe* **8:** 33–45.

JURIŠ, Š. & KOVÁČIK, L. (1987): Príspevok k poznaniu fytoplanktónu jazier vo Vysokých Tatrách. *Zbor. Slov. Nár. Múz., Prír. Vedy* **33:** 23–40.

KELLER, W., GUNN, J. M. & YAN, N. D. (1992): Evidence of biological recovery in acid-stressed lakes near Sudbury, Canada. *Environ. Pollut.* **78:** 79–85.

KOHOUT, L. & FOTT, J. (2006): Restoration of zooplankton in a small acidified mountain lake (Plešné Lake, Bohemian Forest) by reintroduction of key species. *Biologia* **61**/Suppl. **20:** S477–S483.

KOPÁČEK, J. & STUCHLÍK, E. (1994): Chemical characteristics of lakes in the High Tatra Mountains, Slovakia. *Hydrobiologia* **274:** 49–56.

KOPÁČEK, J., HEJZLAR, J., STUCHLÍK, E., FOTT, J. & VESELÝ, J. (1998): Reversibility of acidification of mountain lakes after reduction in nitrogen and sulphur emissions in Central Europe. *Limnol. Oceanogr.* **43(2):** 357–361.

KOPÁČEK, J., HEJZLAR, J., BOROVEC, J., PORCAL, P. & KOTOROVÁ, I. (2000a): Phosphorus inactivation by aluminium in the water column and sediments: Lowering of in-lake phosporus availability in an acidified watershed-lake ecosystem. *Limnol. Oceanogr.* **45(1):** 212–225.

KOPÁČEK, J., STUCHLÍK, E., STRAŠKRABOVÁ, V. & PŠENÁKOVÁ, P. (2000b): Factors governing nutrient status of mountain lakes in the Tatra Mountains. *Freshwater Biology* **43**: 369–383.

KOPÁČEK, J., ULRICH, K. U., HEJZLAR, J., BOROVEC, J. & STUCHLÍK, E. (2001): Natural inactivation of phospohus by aluminium in atmospherically acidified water bodies. *Water research* **35(16):** 3783–3790.

KOPÁČEK, J., STUCHLÍK, E., VESELÝ, J., SCHAUMBURG, J., ANDERSON, I. C., FOTT, J., HEJZLAR, J. & VRBA, J. (2002): Hysteresis in reversal of Central European Mountain Lakes from atmospheric acidification. *Water, Air, Soil, Pollut.: Focus* **2**: 91–114.

KOPÁČEK, J., HARDEKOPF, D., MAJER, V., PŠENÁKOVÁ, P., STUCHLÍK, E. & VESELÝ, J. (2004a). Response of alpine lakes and soils to changes in acid deposition: the MAGIC model applied to the Tatra Mountain region, Slovakia-Poland. *J. Limnol.* **63:** 143–156.

KOPÁČEK, J., BRZÁKOVÁ, M., HEJZLAR, J., NEDOMA, J., PORCAL, P. & VRBA, J. (2004b): Nutrient cycling in a strongly acidified mesotrophic lake. *Limnol. Oceanogr.* **49:** 1202–1213.

KOPÁČEK, J., STUCHLÍK, E. & HARDEKOPF, D. (2006): Chemical composition of the Tatra Mountain lakes: Recovery from acidification. *Biologia* **61**/Suppl. **18:** S21–S33.

LUKAVSKÝ, J. (1994): Algal flora of lakes in the High Tatra Mountains (Slovakia). *Hydrobiologia* **274:** 65–74.

LUKAVSKÝ, J. (2006): *Coelastrum pascheri* sp. n., a new green alga from lakes of the Bohemian Forest. *Biologia* **61**/Suppl. **20:** S485–S490.

MINKIEWICZ, S. (1914): *Przeglad fauny jezior tatrzanskich*. Spraw. Kom. Fizyogr. Akad. Umietnosci, Kraków **48:** 114–137.

NEDBALOVÁ, L. & VRTIŠKA, O. (2000): Distribution of phytoplankton of Bohemian Forest lakes. *Silva Gabreta* **4:** 213–222.

NEDBALOVÁ, L., VRBA, J., FOTT, J., KOHOUT, L., KOPÁČEK, J., MACEK, M. & SOLDÁN, T. (2006a): Biological recovery of the Bohemian Forest lakes from acidification. *Biologia* **61**/Suppl. **20:** S453–S465.

NEDBALOVÁ, L., STUCHLÍK, E. & STRUNECKÝ, O. (2006b): Phytoplankton of a high mountain lake (Ľadové pleso, the Tatra Mountains, Slovakia): seasonal development and first indications of a response to decreased acid deposition. *Biologia* **61**/Suppl. **18:** S91–S100.

NEDOMA, J. & NEDBALOVÁ, L. (2006): Chlorophyll content of Plešné Lake phytoplankton studied with image analysis. *Biologia* **61**/Suppl. **20:** S491–S498.

NILSSEN, J. P. & WÆRVÅGEN, S. B. (2002): Recent re-establishment of the key species *Daphnia longispina* and cladoceran community changes following chemical recovery in a strongly acid-stressed region in southern Norway. *Arch. Hydrobiol.* **153:** 557–580.

NILSSEN, J. P. & WÆRVÅGEN, S. B. (2003): Ecological distribution of pelagic copepods and species relationship to acidification, liming and natural recovery in a boreal area. *J. Limnol.* **62:** 97–114.

NYGAARD, K. & TOBIESEN, A. (1993): Bacteriovory in algae : A survival strategy during nutrient limitation. *Limnol. Oceanogr*. **38(2):** 273–279.

OLSSON, H. & PETTERSSON, K. (1993): Oligotrophication of acidified lakes - a review of hypothesis. *Ambio* **22:** 312–317.

PORTER, K. G. (1988): Phagotrophic phytoflagellates in microbial food webs. *Hydrobiologia* **159:** 89–97.

PECHLANER, R. (1971): Factors that control the production rate and biomass in high mountain lakes. *Mitt. Internat. Verein. Limnol.* **15:** 125–145.

PUGNETTI, A. & BETTINETTI, R. (1999): Biomass and species structure of the phytoplankton of an high mountain lake (Lake Paione Superiore, Central Alps, Italy). *J. Limnol.* **58:** 127–130.

PUHE, J. & ULRICH, B. (2001): *Global climate changes and human impacts on forest ecosystems*. Ecological Studies **143**, 592 p.

REYNOLDS, C. S. (1984): *The ecology of freshwater phytoplankton*. Cambridge University Press, 384 p.

ROSÉN, G. (1981): Tusen sjöar Växtplanktons mijlökrav. *Norstedts Tryckeri, Stockholm*, 120 p.

ROTT, E. (1988): Some aspects of the seasonal distribution of flagellates in mountain lakes. *Hydrobiologia* **161:** 159–170.

SACHEROVÁ, V., KRŠKOVÁ, R., STUCHLÍK, E., HOŘICKÁ, Z., HUDEC, I. & FOTT, J. (2006): Long-term change of the littoral Cladocera in the Tatra Mountain lakes through a major acidification event. *Biologia* **61**/Suppl. **18**: S109–S119.

SIMONA, M., BARBIERI, A., VERONESI, M., MALUSARDI, S. & STRAŠKRABOVÁ, V. (1999): Seasonal dynamics of plankton in a mountain lake in the southern Alps (Laghetto Inferiore, Switzerland). *J. Limnol.* **58(2):** 169–178.

SCHAUMBURG, J. (2000): Long-term trends in biology and chemistry of the acidified Bavarian Forest lakes. *Silva Gabreta* **4:** 29–40.

SCHINDLER, D. V. (1980): Experimental acidification of a whole lake: a test of the oligotrophication hypothesis. *Proc. Int. Conf. Ecol. Impact Acid. Precip., SNSF-project, Norway:* 370–374.

SCHINDLER, D. V. (1987): Detecting ecosystem responses to anthropogenic stress. *Can. J. Fish. Aquat. Sci.* **44:** 6–25.

SCHINDLER, D. V. (1988): Effects of acid rain on freshwater ecosystems. *Science* **239:** 149–157.

SKJELKVÅLE, B. L., EVANS, C., LARSEN, T., HINDA, A. & RADDUM, G. G. (2003): Recovery from acidification in European surface waters: A view to the future. *Ambio* **32(3):** 170–175.

STANGENBERG, M. (1938): Zur hydrochemie der Tatraseen. *Verh. Int. Verein. Limnol.* **8:** 211–220.

STODDARD, J. L., JEFFRIES, D. S., LÜKEWILLE, A., CLAIR, T. A., DILLON, P. J., DRISCOLL, M C., FORSIUS, T., JOHANNESSEN, M., KAHL, J. S., KELLOGG, J. H., KEMP, A., MANNIO, J., MONTEITH, D. T., MURDOCH, P. S., PATRICK, S., REBSDORF, A., SKJELKVALE, B. L., STAINTON, M. P., TRAAEN, T., VAN DAM, H., WEBSTER, K. E., WIETING, J. & WILANDER,

A. (1999): Regional trends in aquatic recovery from acidification in North America and Europe. *Nature* **401:** 575–578.

STRAŠKRABOVÁ, V., CALLIERI, C., CARRILLO, P., CRUZ-PIZARRO, L., FOTT, J., HARTMAN, P., MACEK, M., MEDINA-SÁNCHEZ, J. M., NEDOMA, J. & ŠIMEK, K. (1999): Investigations on pelagic food webs in mountain lakes - aims and methods. *J. Limnol.* **58(2):** 77–87.

STUCHLÍK, E., STUCHLÍKOVÁ, Z., FOTT, J., RŮŽIČKA, L. & VRBA, J. (1985): Vliv kyselých srážek na vody na území Tatranského národního parku. [Effect of acid precipitation on waters of the TANAP territory]. *Zborník TANAP* **26:** 173–211.

STUCHLÍK, E., KOPÁČEK, J., FOTT, J. & HOŘICKÁ, Z. (2006): Chemical composition of the Tatra Mountain lakes: Response to acidification. *Biologia* **61**/Suppl. **18:** S11–S20.

ŠTEFKOVÁ, E. (2006): Epilithic diatoms of mountain lakes of the Tatra Mountains (Slovakia). *Biologia* **61**/Suppl. **18:** S101–S108.

ŠTROJSOVÁ, A. & VRBA, J. (2006): Phytoplankton extracellular phosphatases: investigation using ELF (Enzyme Labelled Fluorescence) technique. *Polish J. Ecol.* **54:** 715–723.

TOLOTTI, M., MANCA, M., ANGELI, N., MORABITO, G., THALER, B., ROTT, E. & STUCHLÍK, E. (2003): Flagellate algae (Chrysophyceae, Dinophyceae, Cryptophyceae) in 48 mountain lakes of the Northern and Southern slope of the Eastern Alps: biodiversity, taxa distribution and their driving variables. *Hydrobiologia* **502:** 331–348.

VESELÝ, J. (1994): Investigation of the nature of the Šumava Lakes: a review. *Časopis Národního Muzea, Řada přírodovědná* **163(1-4):** 103–120.

VESELÝ, J., HRUŠKA, J. & NORTON, S. A. (1998): Trends in water chemistry of acidified Bohemian lakes from 1984 to 1995: II. Trace elements and aluminium. *Water Air Soil Pollut.* **108:** 425–443.

VRBA, J., KOPÁČEK, J., STRAŠKRABOVÁ, V., HEJZLAR, J. & ŠIMEK, K. (1996): Limnological research of acidified lakes in Czech part of the Šumava Mountains: trophic status and dominance of microbial food webs. *Silva Gabreta* **1:** 151–164.

VRBA, J., KOPÁČEK, J. & FOTT, J. (2000): Long-term limnological research on the Bohemian Forest lakes and their recent status. *Silva Gabreta*, **4:** 7–28.

VRBA, J., KOPÁČEK, J., FOTT, J., KOHOUT, L., NEDBALOVÁ, L., PRAŽÁKOVÁ, M., SOLDÁN, N. & SCHAUMBURG, J. (2003a): Long-term studies (1871–2000) on acidification and recovery of lakes in the Bohemian Forest (Central Europe). *Sci. Total Environ.* **310:** 73–85.

VRBA, J., NEDOMA, J., KOHOUT, L., KOPÁČEK J., NEDBALOVÁ, L. RÁČKOVÁ P. & ŠIMEK, K. (2003b): Massive occurrence of heterotrophic filaments in acidified lakes: seasonal dynamics and composition. *FEMS Microbiology Ecology* **46(3):** 281–294.

VRBA, J., KOPÁČEK, J., BITTL, T., NEDOMA, J., ŠTROJSOVÁ, A., NEDBALOVÁ, L., KOHOUT, L. & FOTT, J. (2006): A key role of aluminium in phosphorus availability, food web structure, and plankton dynamics in strongly acidified lakes. *Biologia* **61**/Suppl. **20:** S441–S451.

VYHNÁLEK, V., FOTT, J. & KOPÁČEK, J. (1994): Chlorophyll-phosphorus relationship in acidified lakes of the High Tatra Mountains (Slovakia). *Hydrobiologia* **274:** 49–56.

WÆRVÅGEN, S. B. & NILSSEN, J. P. (2003): Major changes in pelagic rotifers during natural and forced recovery from acidification. *Hydrobiologia* **499:** 63–82.

WEILNER, C. (1997): *Die Eiszeitseen des Bayrischen Waldes*. Regen, 284 p.

WRIGHT, R. F. & HENRIKSEN, A. (1978): Chemistry of small norwegian lakes, with a special reference to acid precipitation. *Ambio* **5:** 219–223.

WRIGHT, R. F., CONROY, W., DICKSON, T., HARRIMAN, R., HENRIKSEN, A. & SCHOFIELD, L. (1980): Acidified lake district of the world: a comparison of water chemistry of lakes in southern Norway, southern Sweden, southwestern Scotlan, the Adirondack Mountains of New York, and southeastern Ontario. *Proc. Int. Conf. Ecol. Impact Acid. Precip., SNSF-project, Norway:* 377–379.

WRIGHT, R. F., LARSSEN, T., CAMARERO, L. COSBY, B. J., FERRIER, R. C., HELLIWELL, R., FORSTUS, M., JENKINS, A., KOPÁČEK, J., MAJER, J., MOLDAN, F., POSCH, M., ROGORA, M. & SCHÖPP, W. (2005): Recovery of acidified European surface waters. *Environ. Sci. Technol.* **39:** 64A–72A.

YAN, N. D. (1979): Phytoplankton communities of an acidified heavy metal contaminated lake near Sudbury, Ontario: 1973–1978. *Water Air Soil Pollut.* **11:** 43–55.

YAN, N. D., WELSH, P. G., LIN, H., TAYLOR, D. J. & FILION, J. M. (1996): Demographic and genetic evidence of the long-term recovery of *Daphnia galeata mendotae* (Crustacea: Daphniidae) in Sudbury lakes following addition of base: the role of metal toxicity. *Can. J. Fish. Aquat. Sci.* **53:** 1328–1344.

ZNACHOR, P. & HRUBÝ, P. (2000): Cell specific primary production and phagotrophy of phytoplankton in acidified lakes of Bohemian Forest. *Silva Gabreta* **4:** 223–232.