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Long term study on the influence of eutrophication, restoration and biomanipulation on the structure and development of phytoplankton communities in Feldberger Haussee (Baltic Lake District, Germany)

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Abstract

Feldberger Haussee provides a classic example of eutrophication history of hardwater lakes in the Baltic Lake District (Germany) and of changes in their algal flora during the 20th century. The lake originally was regarded as slightly eutrophic. A process of drastic eutrophication from the 1950s until the end of the 1970s caused mass developments of blue-green and green algae. A restoration program was started in the 1980s to improve the water quality of the lake using both diversion of sewage outside the catchment area, and biomanipulation by altering the fish community. This restoration program led to positive changes in the lake ecosystem. Direct effects of biomanipulation resulted in an increase of herbivorous zooplankton, a decrease of phytoplankton biomass, and an increase of water transparency. The recovery of Feldberger Haussee also may have been indirectly enhanced by an increase in nutrient sedimentation as a consequence of intensified calcite precipitation, decrease in phosphorus remobilization due to a pH-decrease, increased N/P-ratio, and recolonization of the littoral zone by macrophytes. This paper concentrates on the long term development of the phytoplankton community as a response to changes in the food web structure as well as to alterations in the chemical environment of the algae. Both are reflected in four major stages passed by the algal assemblage between 1980 and 1994: (1) From 1980–summer 1985 dense green algal populations were found indicating similar conditions as in the 1970s during the period of maximum eutrophication. (2) A diverse phytoplankton community during summer 1985–1989 showed the first effects of a recovery. (3) From 1990–1992 the phytoplankton was characterized by ungrazeable filamentous blue-green algae first of all as a response to increased herbivory of zooplankton on edible species and to increasing N/P-ratios. (4) Finally, the algal species diversity increased in 1993 and 1994 whereas the phytoplankton biomass decreased showing the success of the combined restoration measures.

Introduction

Anthropogenic influences have been impairing the water quality of Northern German lakes during the 20th century. The most important effects are due to eutrophication processes. The uncontrolled inflow of nutrients into these lakes caused major changes in the structure and function of the planktonic primary producers (Koschel et al., 1985). The composition of phytoplankton communities and their changes in Feldberger Haussee have been published more or less regularly since Plümecke (1914). Therefore, this lake provides a classic example of the cultural eutrophication of hardwater lakes of the Baltic Lake District and the changes in their algal flora.

Originally, Feldberger Haussee was regarded as a moderately eutrophic lake. These conditions were indicated by dominance of diatoms (*Asterionella*) and chrysoflagellates (*Dinobryon*) in the summer of 1913 (Plümecke, 1914).

In the following decade Thienemann (1925) studied the relict shrimp *Mysis relicta* in this lake district, and was impressed by the untouched character of the lakes.

However, in the 1950s Uhlmann (1961) found Feldberger Haussee to be polluted because of waste water effluent from the town Feldberg. He observed blue-green algal blooms dominated by *Limnothrix redekei*.

Eutrophication continued until the end of the 1970s, when the lake was characterized by mass developments of monadal and coccal green algae (Hahmann et al., 1977; Schmidt, 1979). Koschel et al. (1981) surveyed limnological conditions during the period of maximum eutrophication. More than 60% of the algal taxa observed by these authors were coccal green algae that indicated undesirable water quality.

To improve water quality a restoration program was started in 1980. The first step was to divert sewage from the town of Feldberg outside of the catchment area of Feldberger Haussee. Despite a 90% reduction in loading, water quality did not improve until 1985. The reason was an enormous sediment nutrient pool, which was recycled every year due to anaerobic conditions in the hypolimnion. Therefore, a second step in the restoration program was initiated in 1985. A food web manipulation experiment involving selective removal of zooplanktivorous fish and restocking the lake with pikeperch was carried out (Kasprzak et al., 1988). Some of the results have been published by Kasprzak et al. (1992, 1993); Koschel et al. (1993) and Ronneberger et al. (1993).

Here we present the results obtained during the last 10 years concerning the influence of the restoration program on the structure and succession of phytoplankton communities in Feldberger Haussee. We define four successional stages of phytoplankton community change during that period. The investigations were designed for comparison with previous studies and for prospective studies of this model aquatic system. Keeping in mind the concept of the 'ecological memory' (Padisák, 1992) in addition to results concerning the dominant algal taxa we also document rare species occurrences. These algae represent a potential of the community to respond to future ecosystem changes. They contribute to biodiversity in this particular habitat. Correlative physico-chemical data, survey of selected crustaceans and of fish populations are also provided.

Study site and methods

Feldberger Haussee is a dimictic hardwater lake in the northeastern part of Germany (Mecklenburger Seenplatte). The main morphological characteristics are given in Table 1. Starting in 1985 samples were taken biweekly during May – September and monthly from October – April from various depths in epilimnion (0 m, 2.5 m, depending on the stratification pattern occasionally 5.0 m).

Table 1. Characteristics of Feldberger Haussee

Area	1.3 km^2
Volume	8.2 km^3
Max. depth	12.0 m
Mean depth	6.3 m
Retention time of water body	3–5 years
Catchment area	4.0 km

Ortho-phosphate (PO_4-P), total phosphorus (TP) and nitrate (NO_3-N) were measured with the Perstorp Analytical flow injection analysis system Tecator FIAstar 5010/5030. Atomic N/P-ratios were calculated using concentrations of inorganic and soluble reactive phosphorus. Field pH was recorded by means of a SensoLyt SETA electrode. The $CaCO_3$-concentration was measured using infrared gas analysis (modified according to Proft, 1984). The chlorophyll *a* content was detected spectrophotometrically using a LAMBDA 2 Perkin-Elmer and calculated according to Strickland & Parsons (1968).

The biomanipulation experiment involved intensive removal of planktivorous and benthivorous fish by means of beach seining. With the exception of 1991 we performed fish removal 14–20 times per year, and treated 50–75% of the lake area each year. The total catch was related to the area harvested (kg ha^{-1}) and is therefore a minimum value estimate of the standing stock. Samples of crustacean plankton were taken by vertical hauls from 6.5–0 m using nets (90–110μm). For details see Kasprzak et al. (1993).

Phytoplankton samples were fixed with Lugol's solution and counted in sedimentation chambers under an inverted microscope (Utermöhl, 1958). The biovolumes were calculated after Willén (1976) and the volumina were converted into biomass, assuming a specific gravity of 1.00 g cm^{-1}. Morphological studies were conducted on fresh samples with a compound microscope. The algae were concentrated onto membrane filters having a pore size of 1.0 μm and investigated under the light microscope. For scanning electron microscopy, air dried samples were mounted onto aluminium stubs, coated with platinium, and examined under a SEM JSM-35 (Jeol).

Results

Physico-chemical parameters

The Secchi depth has undergone dramatic changes during the past century: Thienemann (1925) measured a transparency of 5 m, but in the 1950s and 1960s Secchi depth dropped to values of about 2 m. Secchi readings less than 1 m were typical between 1973–1982. During the second half of the 1980s, after biomanipulation had been initiated, the values were 1.30–1.75 m (Figure 1a). At the beginning of the 1990s, the Secchi transparency decreased to 0.65–0.85 m, and this coincided with a chlorophyll *a* concentration maximum of 0.059 mg l^{-1} in 1992 (Figure 1b). The 1994 average of 1.80 m was the highest transparency since the 1960s.

Nutrient levels varied only little in the first years after the beginning of the restoration program. From 1980–1986 the spring maximum of TP was 1.2–1.4 mg l^{-1} while annual mean PO_4-P varied between 0.65–0.93 mg l^{-1}. From the mid-1980s the concentration of TP and PO_4-P decreased continuously (Figures 1c, 1d).

The NO_3-N concentration in Feldberger Haussee has been relatively low except 1991 when an annual mean of 1 mg l^{-1} was measured (Figure 1e). The annual atomic N/P-ratio was less than 1 until 1987, but increased continuously up to 16 in 1991 (Figure 1f). During the following years it decreased again to 4.3 in 1994.

The pH values have decreased markedly since the biomanipulation was started 10 years ago (Figure 1g). In contrast to the summer mean of 9.29 in 1985, we measured only 8.75 in summer of 1994.

The $CaCO_3$-concentration increased significantly during the experimental period, accompanied by a significant increase in autochthonous pelagic calcite precipitation. The $CaCO_3$-concentration amounted to 0.13 mg l^{-1} in 1987 and 1.04 mg l^{-1} in 1990. The summer mean concentration in the early 1990s was 0.33 mg l^{-1} in 1992 and 1.11 mg l^{-1} in 1993 (Figure 1h).

Fish, zooplankton

During the first few years after the beginning of biomanipulation (1985–1989) only a slight decrease in the annual standing fish stocks was observed. Between 1989 and 1990 we found a sudden and significant reduction with minimum values of about 36 kg ha^{-1}. In the subsequent years the fish biomass increased but was again as low as 40 kg ha^{-1} in 1994 (Figure 2a).

After the beginning of biomanipulation in 1985 the genus *Daphnia*, particularly *D. cucullata*, showed a remarkable biomass increase. Later we observed a pronounced decrease, especially in 1992/93 when the fish biomass increased again and the phytoplankton consisted almost entirely of filamentous blue-green algae. However, compared to the period before the biomanipulation the mean summer values had roughly doubled (Figure 2b).

Phytoplankton

Species occurring in Feldberger Haussee during 1985–1994 are listed in Table 2. The development of the most important algal groups that occurred during the period of investigation is summarized in Figures 2c–f, and the pattern of phytoplankton periodicity during the last 10 years is shown in Figure 3. Special emphasis upon the structure of blue-green algal populations is shown in Figure 4. Micrographs of algae which are characteristic of phytoplankton of Feldberger Haussee are demonstrated in Figures 5–23.

The phytoplankton community of Feldberger Haussee passed four major stages of development: stage 1 (1980–summer 1985) period of dense green algal populations, stage 2 (summer 1985–1989) period of highly diverse phytoplankton communities, stage 3 (1990–1992) period of dominance of ungrazeable filamentous blue-green algae, stage 4 (1993–1994) period of reestablishment of high species diversity.

Stage 1: In 1985, at the beginning of our regular qualitative and quantitative phytoplankton investigations, we found a pattern similar to that of previous years. The diverse chlorophycean community of spring and early summer was dominated by the monadal genera *Chlamydomonas* and *Pteromonas* and the coccoid genera *Coelastrum*, *Coenochloris*, *Dictyosphaerium*, *Oocystis*, *Quadricoccus* and *Scenedesmus* as well as by long fusiform species *Koliella* and *Elakatothrix*.

Stage 2: The green algal assemblage became subdominant during the summer of 1985 when coccoid and filamentous blue-green algae prevailed. Interesting cyanophycean assemblages were observed during autumn of 1985, 1986 and 1987. The very small-celled colonial chroococcoid blue-green alga *Cyanogranis ferruginea* (Figure 8) occurred in high abundances (20–30 million colonies per litre). This species is characterized by iron-encrosted colonies and can easily confused with detritus particles. Furthermore, slimy, net-like colonies of *Cyanodictyon planctonicum* (Figure 7) appeared in the autumn successions. From

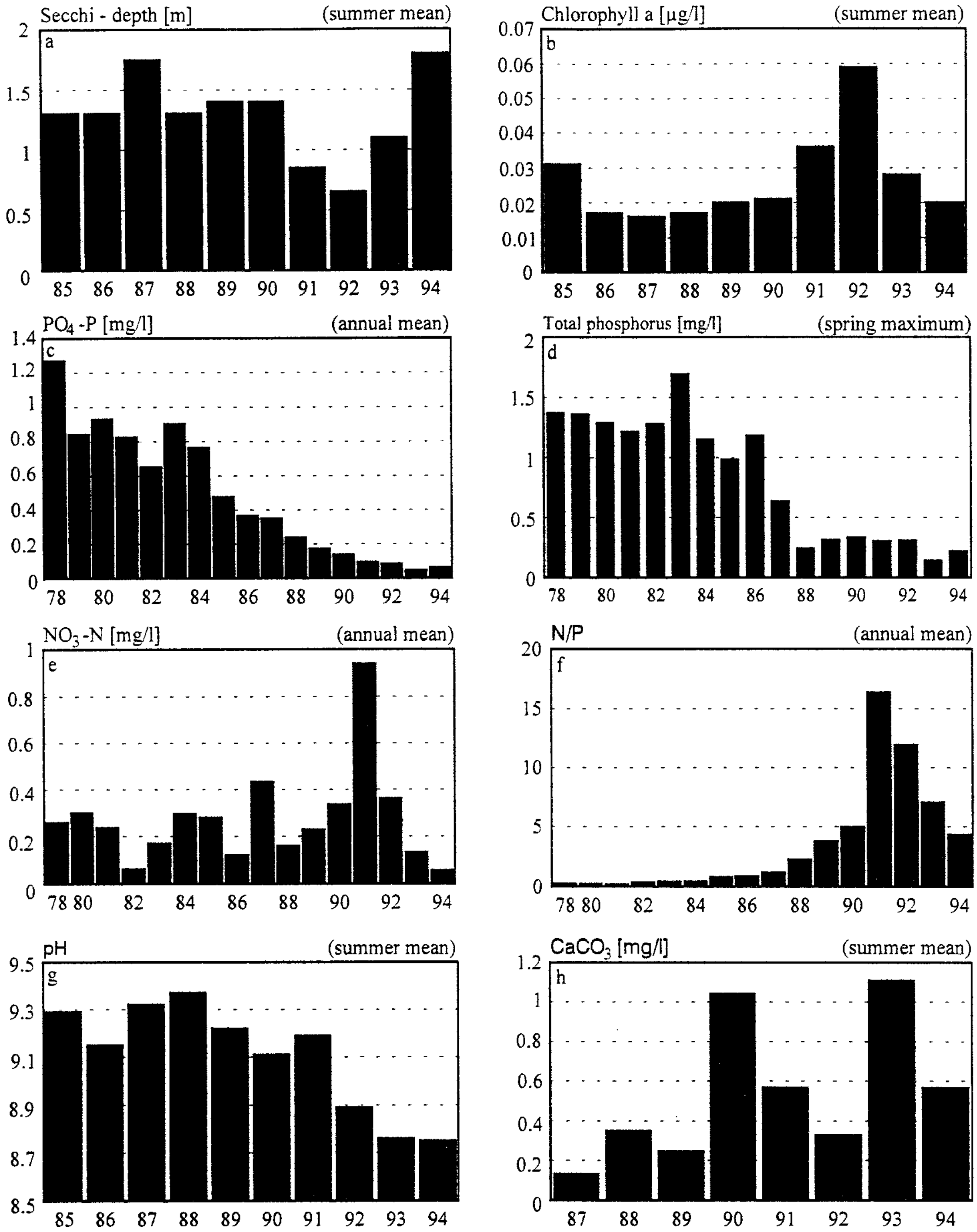

Figure 1. Physico-chemical parameters in Feldberger Haussee.

1987–1989 changes occurred within the phytoplankton dominance structure. Although the chlorophyte flora remained diverse the contribution of green algae to spring biomass decreased. Cryptophytes, especially *Cryptomonas* sp. and *Rhodomonas lens* contributed significantly to total biomass in spring 1988, while

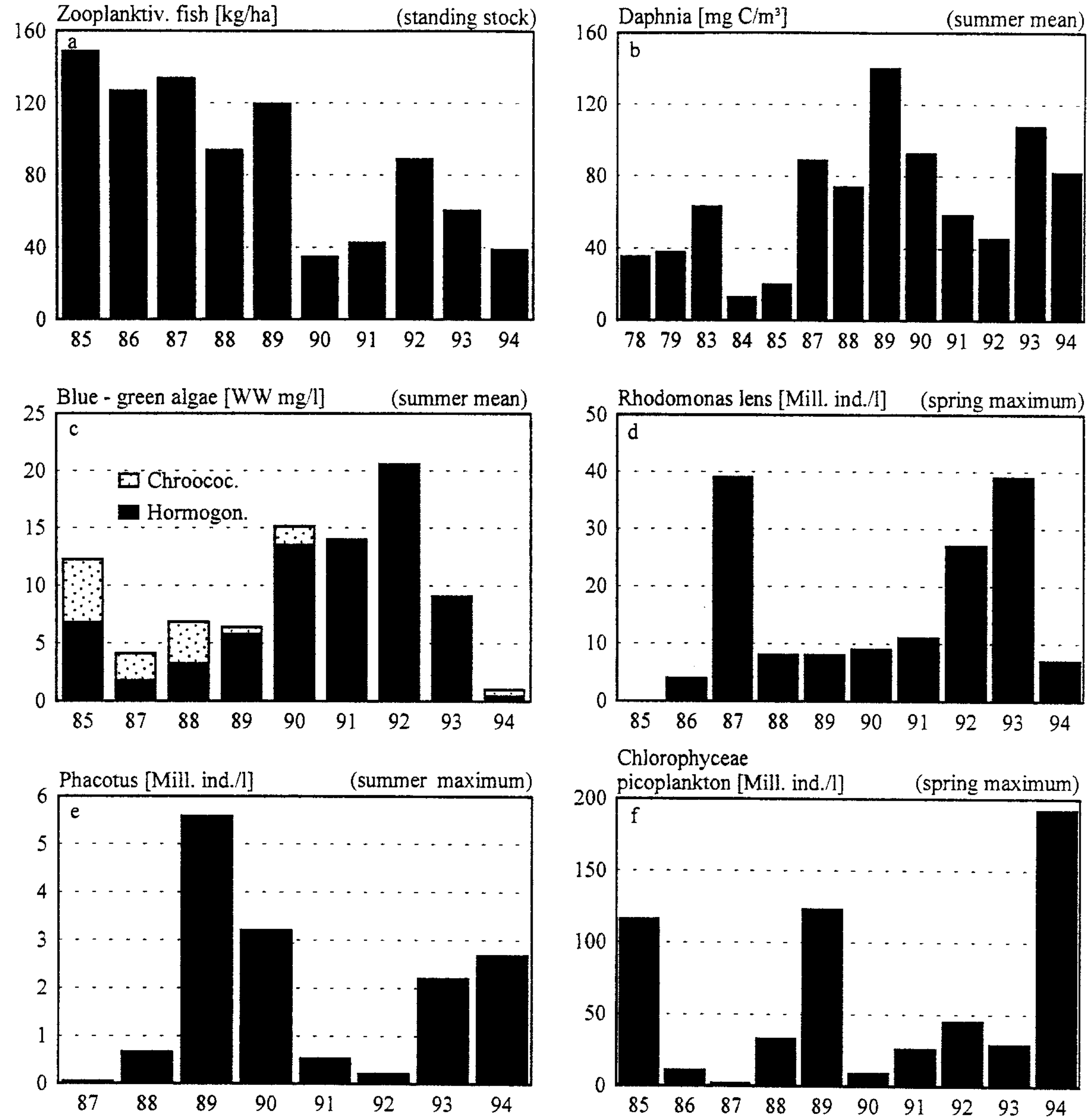

Figure 2. Limnological parameters in Feldberger Haussee.

in 1989 centric diatoms (*Stephanodiscus minutulus* and *S. hantzschii)* reached considerable biomass. The late summer assemblage was characterized by different groups. In 1987 and 1988 biomass of coccal and filamentous blue-green algae, dinoflagellates, diatoms and green algae were almost equally important. In terms of abundance, the most notable taxa were: *Cyclotella* spp., *Fragilaria reicheltii*, *Ceratium hirundinella*, and *Gymnodinium* spp. At the same time the abundance of the calcite-loricated phytoflagellate *Phacotus* increased. Before 1980 the genus was not mentioned in plankton lists, and even in the early 1980s we observed this alga only sporadically. However, from 1986 to 1989 the maximum *Phacotus* cell numbers increased tenfold (Krienitz et al., 1993). The highest density of approximately 5.5 million individuals per litre was observed in August 1989 when *Phacotus* represented 15% of the total phytoplankton biomass (Figure 2e). During the following years the abundances oscillated between 10^5 and $2–10^6$ cells per litre. The

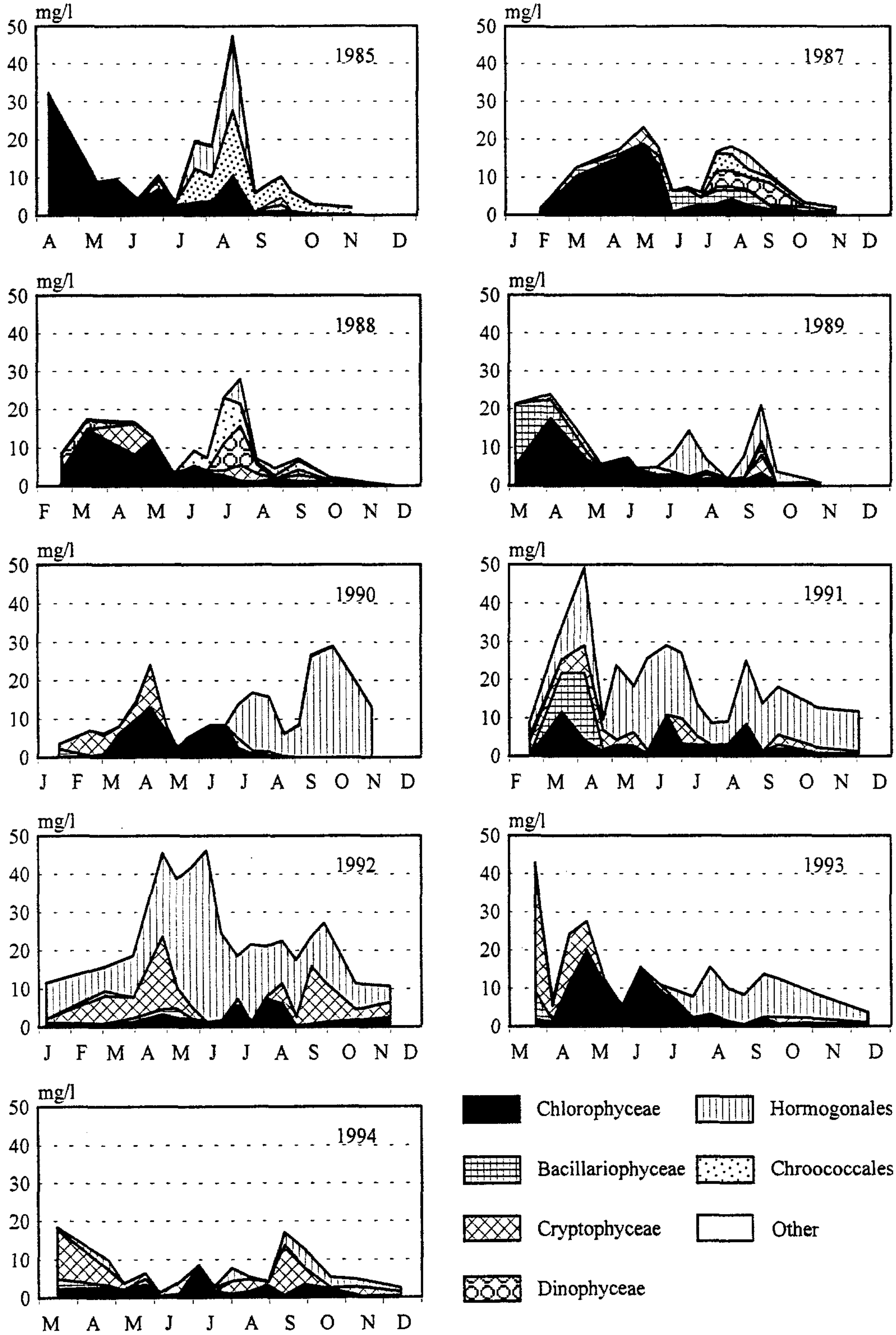

Figure 3. Phytoplankton successions in Feldberger Haussee.

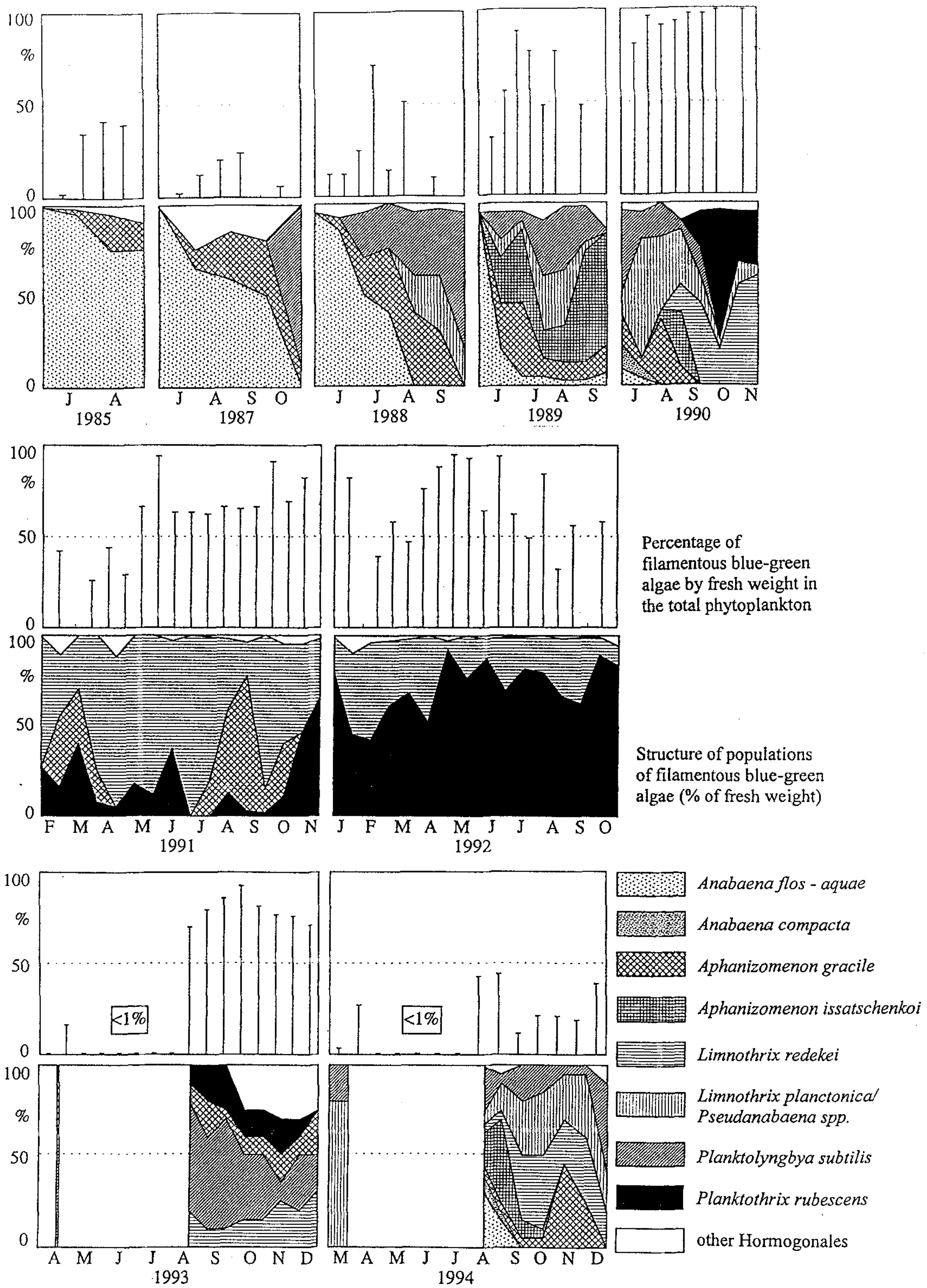

Figure 4. Filamentous blue-green algae in the phytoplankton of Feldberger Haussee: Percentage in the total phytoplankton biomass and population structure.

Phacotus-population was dominated by *P. lenticularis* (Figures 19–22). However, another taxon, *P. sphaericus* (Giering et al., 1990b), was also regularly observed (Figure 18). It differs from *Phacotus lenticularis* by its spherical lorica and the special shape of the contact zone between lorica-halves.

Stage 3: During the following years the biomass of filamentous blue-green algae increased continuously (Figure 2c). Before the summer of 1990 they did not increase to more than 20–40% of the phytoplankton biomass, but between 1990 and 1992 they often exceeded 90%, and they began to dominate the phytoplankton for longer periods of time. From 1991–1992 filamentous blue-green algae continuously dominated. The highest summer mean value of total cyanophyte biomass was found in 1992 of about 21 mg l^{-1}. Finally a reduction in cyanophytes was observed in 1993, and in 1994 they only occurred as a subdominant group (Figure 3). In each year of the investigation a different assemblage of Hormogonales was observed (Figure 4). During the first years heterocyst-forming taxa dominated. In summer 1985 *Anabaena flos-aquae* was the most important species, but from 1986–1988 it was gradually replaced by *Aphanizomenon issatschenkoi* (Figure 9), *A. gracile* (Figure 6), and *Planktolyngbia subtilis. Aphanizomenon gracile* which is characterized by single trichomes (in contrast to the bundle-building species *Aphanizomenon flos-aquae*) was the subdominant taxon during several blue-green assemblages from 1985 to 1991. A further remarkable taxon was *Anabaena compacta* (Figure 5), a subdominant species in 1990 and 1994. During 1991/92 the *Limnothrix redekei* and *Planktothrix rubescens* (Figure 10) were most important.

Stage 4: During the period of decline of Hormogonales (1993/94) we observed a heterogenous mixture of different heterocyst- and nonheterocyst-producing cyanophyte taxa. During these years, especially in spring, very low abundances of the blue-green algae were recorded (less than 1% of the total phytoplankton biomass). The phytoplankton maxima in spring of 1993 and 1994 were dominated by cryptomonads, mainly *Cryptomonas ovata* and the very small *Rhodomonas lens* (Figure 3). The latter was important because of its high cell numbers in 1987 and 1993 (Figure 2d). In early summer of 1994 a distinct clear water stage was detected. Nevertheless, a high number of picoplanktonic green algae, especially *Choricystis minor*, were observed (Figure 2f). Two important features of Feldberger Haussee were evident in 1994. For the first time since the beginning of the restoration program the total phytoplankton biomass had decreased significantly. Moreover, whereas in the eighties the submersed macrophyte communities almost completely disappeared as a consequence of light limitation, they recolonized all the appropriate area of the littoral zone in 1994 (Krausch, pers. comm.).

Within the period from 1985–1989 a large number of different algal taxa (159 species) was observed in Feldberger Haussee, but in 1990/1992 blue-green algae dominance coincided with an impoverishment of biodiversity (59 species). Although the number of species increased again to 106 species only after the high point of blue-green algae dominance was over (1993/94), the high number of taxa typical of the eighties had not yet been reached. However, some algal species were able to develop extremely high abundances for short periods. For example, *Oocystis parva* (Figure 14) attained cell densities of 40 million individuals per litre during June/July 1993. Taxa with offer proofs a grazing resistent morphology were more frequently observed, such as needleformed species (*Ankyra judayi*, Figure 11), bigger sized colonies (*Scenedesmus raciborskii*, Figure 12, *Elakatothrix subacuta*, Figure 13, *Botryococcus terribilis*, Figure 18), species with gelatinous sheaths (*Oocystis lacustris*, Figure 15, *Coenochloris polycocca*, Figure 16), and filamentous forms (*Planktonema lauterbornii*, Figure 17). Altogether 175 algal taxa (85 of them green algae) were found in Feldberger Haussee. Table 2 contains 64 algal taxa which were also mentioned by earlier investigators.

Discussion

Feldberger Haussee, like many other northern German lakes, has been subjected to dramatic changes in water quality during the 20th century. The period of relative virginity lasted until the 1950s. During the following three decades cultural eutrophication resulted in undesirable water quality. Since the beginning of the 1980s, there have been efforts to improve water quality by means of load reduction and biomanipulation. After the beginning of the restoration program in 1980 Feldberger Haussee passed through four major stages. These were: Stage 1 (1980–summer 1985) was characterized by no remarkable response to load reduction. The nutrient concentration remained high due to internal recycling, and dense green algal populations indicate that conditions were similar to those of the 1970s.

Table 2. List of phytoplanktonic algae of Feldberger Haussee.
(Frequency: + = present; ++ = abundant; +++ = dominant)
1985–89: period after beginning of biomanipulation characterized by heterogeneous species composition;
1990–92: period of established effects of biomanipulation characterized by dominance of filamentous blue-green algae;
1993–94: period of first success of biomanipulation characterized by decrease of blue-green algae dominance, summer clear waters and restoration of higher species diversity.
[1)] Species found by Hahmann et al. (1977), Schmidt (1979) and Koschel et al. (1981) during the 1970s.

Species	1985–89	1990–92	1993–94
Cyanophyceae			
Anabaena compacta (NYG.) HICK.		++	++
Anabaena lemmermannii P. RICHT.			+
Anabaena solitaria KLEB. f. *planctonica* KOM.	++		
Anabaena flos-aquae (LYNG.) BRÈB. [1)]	+++	++	++
Anabaenopsis elenkinii MILL.		+	+
Aphanocapsa conferta (W. et G.S. W.) KOM.-LEGN. et CRONB.	++		+
Aphanocapsa delicatissima W. et G.S. WEST	++		
Aphanothece clathrata W. et G.S. WEST [1)]	++		+
Aphanizomenon flos-aquae (L.) RALFS [1)]	++		
Aphanizomenon gracile LEMM.	+++	++	++
Aphanizomenon issatschenkoi (USSAC.) PROS.-LAVR.		++	+
Chroococcus limneticus LEMM. [1)]	+		
Cyanocatena planctonica HIND.	+		
Cyanodictyon imperfectum CRONB. et WEIB.	+++		
Cyanodictyon planctonicum Meyer	+++		
Cyanodictyon reticulatum (LEMM.) GEITL. in PASCH.	++		
Cyanogranis ferruginea (WAWR.) HIND.	+++		
Limnothrix planktonica (WOLOSZ.) MEFF.	+	++	+
Limnothrix redekei (v. GOOR) MEFF.		+++	++
Merismopedia tenuissima LEMM.	+		
Microcystis aeruginosa (KÜTZ.) KÜTZ.	+		
Microcystis flos-aquae (WITTR.) KIRCHN. [1)]	+		
Microcystis wesenbergii (KOM.) KOM. in KONDR.	+		
Planktolyngbia subtilis (W. WEST) ANAGN. et KOM.	++	++	+++
Planktothrix agardhii (GOM.) ANAGN. et KOM.	+		
Planktothrix rubescens (DC. ex GOM.) ANAGN. et KOM.		+++	++
Pseudanabaena catenata LAUTERB.	++	+	+
Pseudanabaena limnetica KOM.	++	+	+
Snowella lacustris (CHOD.) KOM. et HIND. [1)]	++		
Chrysophyceae			
Chrysococcus rufescens KLEBS	+++		+
Dinobryon divergens IMHOF [1)]	+		
Dinobryon spp. [1)]	+		
Mallomonas akrokomos RUTTN.	+		+
Mallomonas bacterium CONR. [1)]			
Mallomonas spp. [1)]	+		
Synura petersenii KORSH.	+		
Synura spec. [1)]	+		

Table 2. Continued

Species	1985–89	1990–92	1993–94
Xanthophyceae			
Centritractus belonophorus LEMM.	+		+
Goniochloris mutica (A. BRAUN) FOTT [1)]	+		+
Pseudogoniochloris tripus (PASCH.) KRIE. et al. [1)]	+		+
Tetraedriella verrucosa (G.M. SMITH) KRIE. et HEYN.	+	+	+
Trachydiscus sexangulatus ETTL	+		+
Bacillariophyceae			
Centrales			
Aulacoseira granulata (EHRENB.) SIMONS.	+++		+
Cyclotella radiosa (GRUN.) LEMM.	+++	++	++
Cyclotella stelligera CLEV. et GRUN.	+		
Cyclotella spec. [1)]		+++	
Cyclostephanos dubius (FRICKE) ROUND	+		
Cyclostephanos invisitatus (HOHN et HAK.) THER. et al.	+++		
Stephanodiscus "astraea" (E.) GRUN. [1)]			
Stephanodiscus alpinus HUST.	+	+	
Stephanodiscus hantzschii GRUN.[1)]	+++		
Stephanodiscus minutulus (KÜTZ.) CLEV. et MÖLL.	++	++	+++
Stephanodiscus neoastraea HAK. et HICK.	+	+	++
Pennales			
Asterionella formosa HASS.	+		+
Diatoma elongatum (LYNG.) AG. [1)]	+	++	+
Fragilaria crotonensis KITT.	+	++	++
Fragilaria reicheltii (VOIGT) LANGE-BERTAL.	++		
Fragilaria ulna (NITZSCH) LANGE-BERTAL. [1)]	+	++	++
Nitzschia spec. [1)]	++		
Tabellaria fenestrata (LYNG.) KÜTZ.	+		+
Cryptophyceae			
Chroomonas caudata GEITL. [1)]	+		
Cryptomonas curvata EHRENB.	+		
Cryptomonas ovata	+	+++	+++
Cryptomonas spec. [1)]	++		
Rhodomonas minuta SKUJA var. *nannoplanctica* SKUJA	+	+	++
Rhodomonas lens PASCH. et RUTTN.	+++	++	+++
Dinophyceae			
Ceratium hirundinella (O.F.M.) Dujardin [1)]	+++		
Gymnodinium paradoxum SCHILLING [1)]	++		
Gymnodinium spec.	+		+
Peridinium umbonatum STEIN [1)]	++		+
Peridinium spec. [1)]	++		+
Euglenophyceae			
Euglena spec. [1)]	++		

Table 2. Continued

Species	1985–89	1990–92	1993–94
Trachelomonas hispida (PERTY) STEIN	++	+	++
Trachelomonas volvocina EHRENB.	++	+	++
Prasinophyceae			
Tetraselmis cordiformis (CART.) STEIN	++	+	+
Chlorophyceae			
Chlamydomonadales			
Chlamydomonas reinhardtii DANG.	+++		++
Chlamydomonas debaryana GOROSCH.	+	+	++
Chlamydomonas spp.	+++	++	+++
Chlorogonium elongatum (DANG.) DANG. [1)]	++		
Phacotus lenticularis (EHRENB.) STEIN	+	+++	++
Phacotus sphaericus (WISL.) GIERING	+	+	+
Pteromonas aculeolata LEMM.	+	+	+
Pteromonas angulosa (CART.) LEMM. [1)]	++	+	+
Volvocales			
Eudorina elegans EHRENB.	+		
Pandorina morum (O.F.M.) BORY [1)]	+		
Tetrasporales			
Pseudosphaerocystis lacustris (LEMM.) NOVAK. [1)]			
Chlorococcales			
Actinastrum hantzschii LAGERH.	++		+
Ankistrodesmus falcatus (CORDA) RALFS	++		
Ankyra judayi (G.M. SMITH) FOTT	++		++
Ankyra ocellata (KORSH.) FOTT	+		++
Botryococcus braunii KÜTZ. [1)]	++	+	++
Botryococcus terribilis KOM. et MARV.	++	+	++
Chlorella vulgaris BEIJ.	+		+
Chlorotetraedron incus (TEIL.) KOM. et KOV.	+		+
Choricystis minor (SKUJA) FOTT	++		+++
Coelastum astroideum DE-NOT.	+	+	+
Coelastum microporum NÄG. in A. BRAUN [1)]	++	+	+
Coelastrum proboscideum BOHL. in WITTR. et NORDST. [1)]	+		
Coelastum reticulatum (DANG.) SENN	+		+
Coenochloris polycocca (KORSH.) HIND.	+		+++
Crucigenia quadrata MORR. [1)]	+		
Crucigeniella apiculata (LEMM.) KOM.	+		+
Crucigeniella rectangularis (NÄG.) KOM. [1)]		++	
Dactylosphaerium jurisii HIND.	++		+++
Dictyosphaerium ehrenbergianum NÄG. [1)]	+	+	+
Dictyosphaerium pulchellum WOOD [1)]	+		
Dictyosphaerium tetrachotomum PRINTZ	++		+
Kirchneriella aperta TEIL.	+		+
Kirchneriella lunaris (KIRCHN.) MOEB. [1)]	+		
Kirchneriella obesa (W. WEST) SCHMIDLE[1)]	+		+

Table 2. Continued

Species	1985–89	1990–92	1993–94
Lagerheimia ciliata (LAGERH.) CHOD.	++		+
Lagerheimia citriformis (SNOW.) COLL. [1)]			
Lagerheimia genevensis (CHOD.) CHOD. [1)]	+		
Lagerheimia longiseta (LEMM.) WILLE [1)]	++		
Lagerheimia marssonii LEMM.	+	+	+
Lagerheimia subsalsa LEMM. [1)]	+		+
Micractinium appendiculatum KORSH.	+		+
Micractinium pusillum FRES. [1)]	+		++
Monoraphidium contortum (THUR.) KOM.-LEGN.[1)]	++	+	++
Monoraphidium convolutum (CORDA) KOM.-LEGN.	++	+	+
Monoraphidium griffithii (BERK.) KOM.-LEGN.	+		+
Monoraphidium pusillum (PRINTZ) KOM.-LEGN.	++		
Nephrochlamys subsolitaria (G.S. WEST) KORSH.[1)]	+		
Nephrocytium agardhianum NÄG.[1)]	+		+
Oocystis lacustris CHOD.	++	+	+
Oocystis parva W. et G.S. WEST			+++
Oocystis solitaria WITTR. [1)]			
Oocystis spp. [1)]	++		
Pediastrum angulosum EHRENB. ex MENEGH.	+	+	+
Pediastrum duplex MEYEN [1)]	+	+	+
Pediastrum boryanum (TURP.) MENEGH. [1)]	+	+	+
Pediastrum tetras (EHRENBG.) RALFS [1)]	+	+	+
Pseudoschroederia antillarum (KOM.) HEG. et SCHNEPF	+		++
Quadricoccus ellipticus HORTOB.	++		+
Raphidocelis subcapitata (KORSH.) NYG. et al.	+	+	+
Scenedesmus acuminatus (LAGERH.) CHOD.	++	+	+
Scenedesmus acutus MEYEN [1)]	++	+	+
Scenedesmus armatus CHOD.	++	+	+
Scenedesmus arthrodesmiformis SCHRÖD.	++	+	++
Scenedesmus communis HEGEWALD	+	+	+
Scenedesmus costato-granulatus SKUJA	+		+
Scenedesmus denticulatus LAGERH. [1)]	+		
Scenedesmus falcatus CHOD.	++		+
Scenedesmus opoliensis P. RICHT. [1)]	+		
Scenedesmus pannonicus HORTOB.	+		
Scenedesmus raciborskii WOLOSZ.	++		+++
Scenedesmus verrucosus ROLL	++		
Scenedesmus subspicatus CHOD.	+		
Schroederia setigera (SCHRÖD.) LEMM. [1)]	++		++
Selenastrum gracile REINSCH	++		
Tetrachlorella alternans (G.M. SMITH) KORSH.	+		+
Tetraedron caudatum (CORDA) HANSG. [1)]	+	+	+
Tetraedron minimum (A. BRAUN) HANSG.[1)]	+	++	
Tetraedron regulare KÜTZ. [1)]	+		
Tetrastrum komarekii HIND.	++		+

Table 2. Continued

Species	1985–89	1990–92	1993–94
Tetrastrum staurogeniaeforme (SCHRÖD.) LEMM. 1)	+	+	+
Treubaria schmidlei (SCHRÖD.) FOTT et KOV.	+		+
picoplanktonic algae (0.2 - 2.0 μm)	+++	++	+++
Microsporales			
Planctonema lauterbornii SCHMIDLE	+		++
Charophyceae			
Klebsormidiales			
Elakatothrix acuta PASCH. 1)			
Elakatothrix gelatinosa WILLE 1)			
Elakatothrix genevensis (REVERD.) HIND.	+	+	++
Elakatothrix lacustris KORSH. 1)			
Elakatothrix subacuta KORSH.	++	+	++
Koliella longiseta (VISCH.) HIND.	++	+	++
Koliella spiculiformis (VISCH.) HIND.	++	+	++
Conjugatophyceae			
Closterium acutum RALFS var. *variabile* (LEMM.) W. KRIEG	+	+	+
Closterium leibleinii KÜTZ. ex RALFS 1)	+		
Closterium spp.	++		
Cosmarium humile (GAY) NORDST. in de TONI 1)	+		
Cosmarium punctulatum BRÈB. 1)	+		
Cosmarium spp.	+	+	+
Staurastrum gracile RALFS1)	+		
Staurastrum spec.	+		+

Stage 2 (summer 1985–1989) reveals the first influence of biomanipulation. Crustacean grazers (*Daphnia*) increased in biomass. Nutrient concentrations began to decrease and the intensification of autochthonous calcite precipitation became obvious. There was a diverse assemblage of phytoplankton.

During stage 3 (1990–1992), long term effects of biomanipulation became stable. Phytoplankton communities had changed in response to zooplankton grazing pressure and increasing N/P-ratio. Nonedible or indigestible filamentous cyanobacteria dominated.

Stage 4 (1993–1994) was characterized by biotic evidence of the success of combined restoration measures. Remarkable decreases in nutrients and pH, together with the occurrence of clear water stages were observed. The littoral zone of the lake was reoccupied by macrophytes and the algal community showed increasing species diversity.

Planktonic algae are influenced by nutrient ressources (bottom-up) as well as consumer (top-down) influences (McQueen, 1986). Although a large number of studies have focused upon monocausal relationships between growth and development of algae and the factors, that influence them, it has been difficult to apply these results to real ecosystems. To understand the composition and succession of phytoplankton we need to know both, the autecological characteristics of certain species as well as the synecological features of particular taxonomical and ecological groups.

Mass developments of blue-green and green algae are a common phenomenon of eutrophication (Smith, 1990). Our investigations revealed that mass developments of blue-green algae exhibited changes in species composition from mixed chroococcalean/hormogonalean assemblages to exclusively Hormogonales with and without heterocyst-forming taxa respectively. Whereas the reason for the drastic increase of blue-green algal biomass after the beginning of biomanipulation seems to be rather clear, changes within the community structure are more difficult to explain.

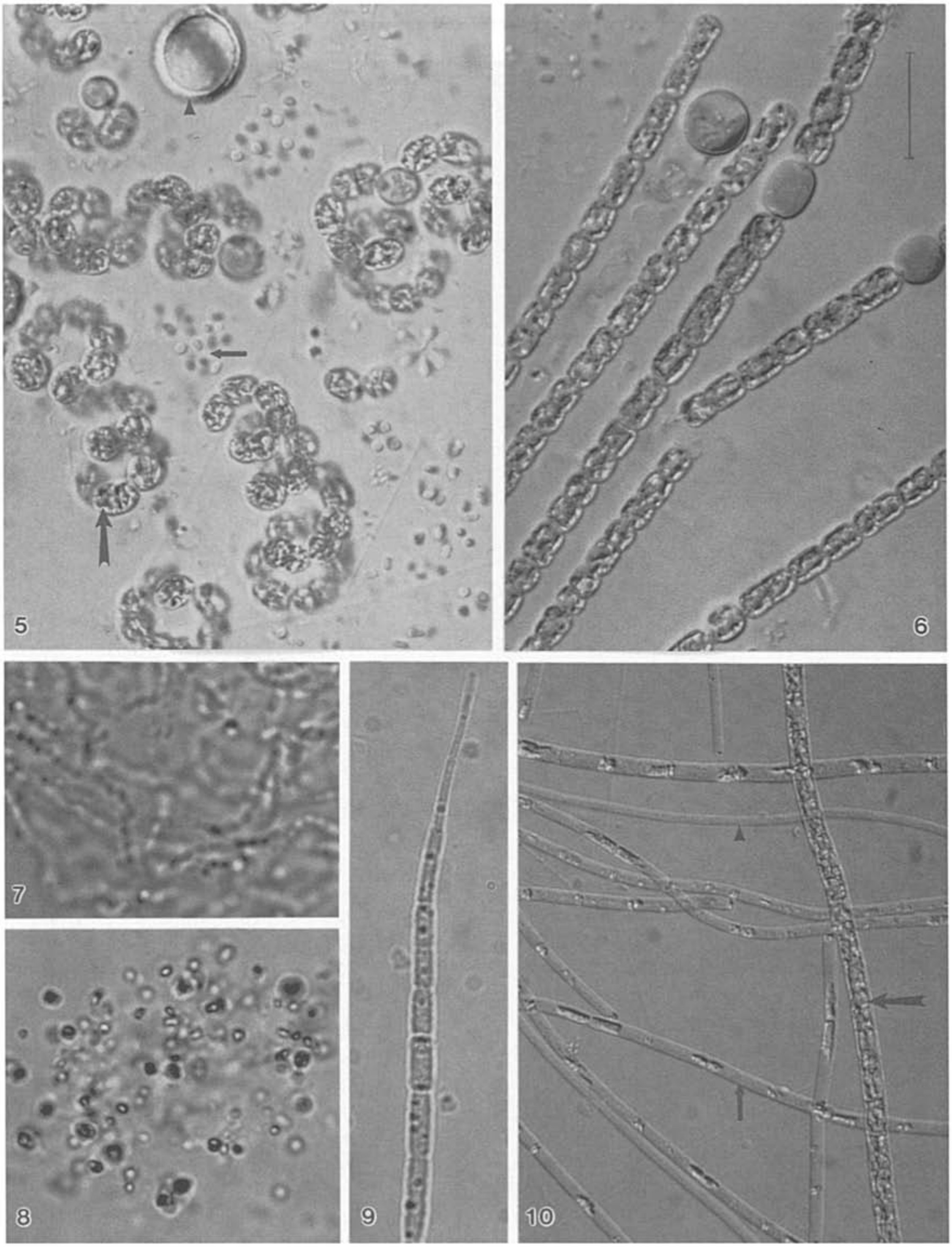

Plate I. Dominant blue-green algae in Feldberger Haussee. Figure 5. *Anabaena compacta* (large arrow), *Aphanothece clathrata* (small arrow), an empty calcite shell of the green alga *Phacotus lenticularis* (arrowhead). Figure 6. *Aphanizomenon gracile*. Figure 7. *Cyanodictyon planctonicum*. Figure 8. *Cyanogranis ferruginea*. Figure 9. *Aphanizomenon issatschenkoi*. Figure 10. *Limnothrix redekei* (small arrow), *Planktothrix rubescens* (large arrow), *Pseudanabaena limneticum* (arrowhead). Scale = 10 μm.

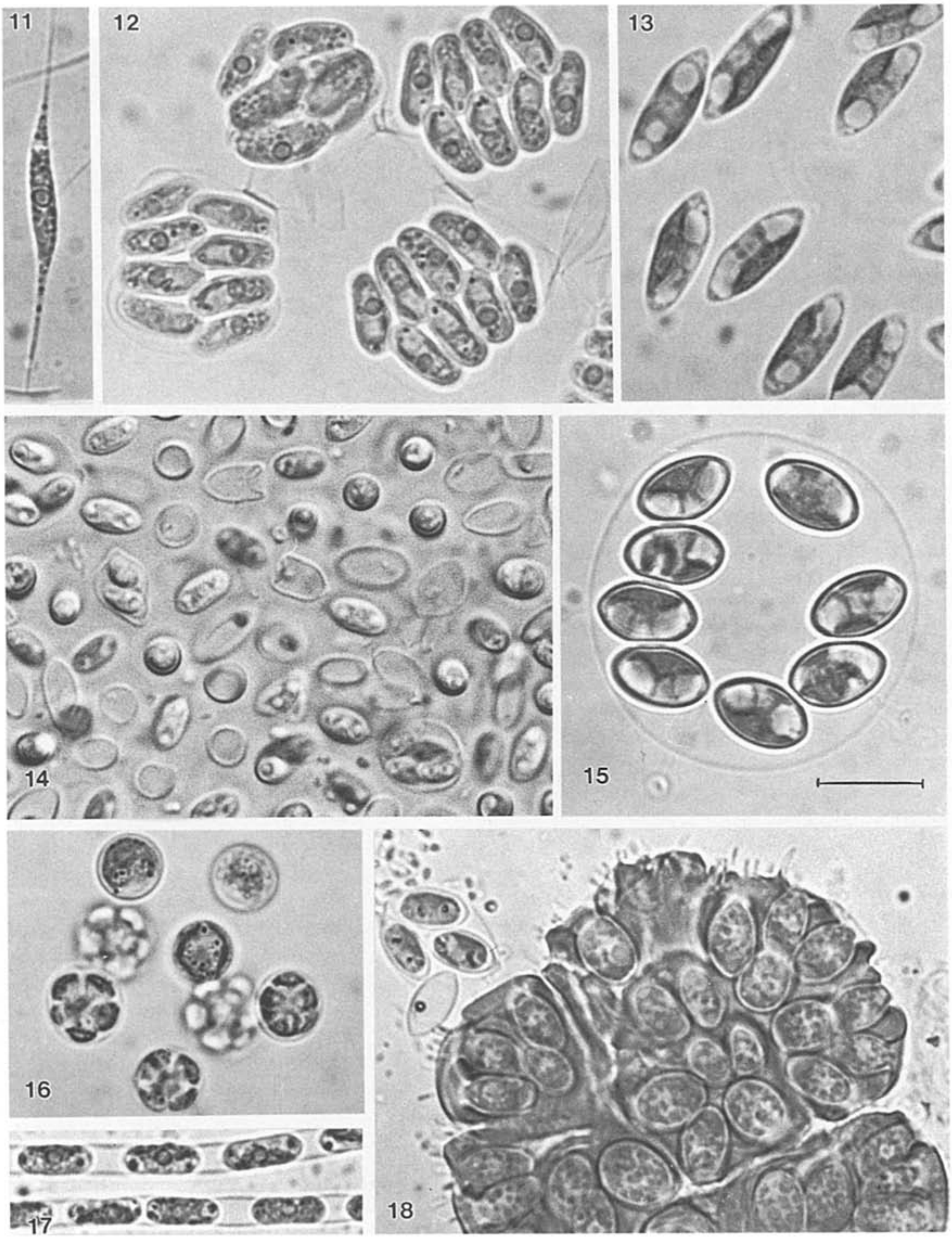

Plate II. Dominant green algae in Feldberger Haussee. Figure 11. *Ankyra judayi.* Figure 12. *Scenedesmus raciborskii.* Figure 13. *Elakatothrix subacuta.* Figure 14. *Oocystis parva.* Figure 15. *Oocystis lacustris.* Figure 16. *Coenochloris polycocca.* Figure 17. *Planctonema lauterbornii.* Figure 18. *Botryococcus terribilis.* Scale = 10 μm.

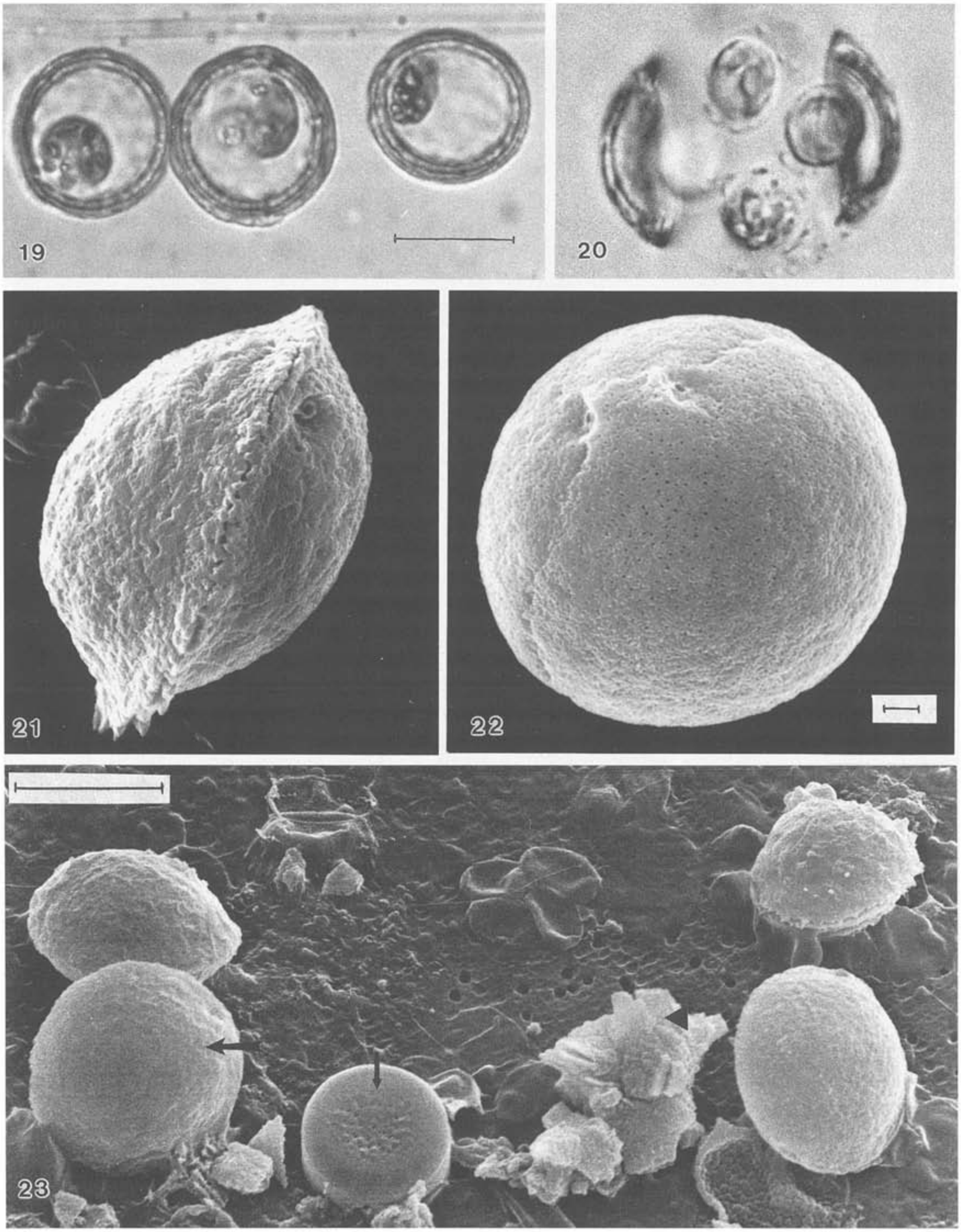

Plate III. Phacotus-species in Feldberger Haussee. Figure 19. Free living young cells of *Phacotus lenticularis* (LM). Figure 20. Mother cell with four zoospores of *Phacotus lenticularis* (LM). Figure 21. Calcite-lorica of *Phacotus lenticularis* (SEM). Figure 22. Calcite-lorica of *Phacotus sphaericus* (SEM). Figure 23 *Phacotus lenticularis* (large arrow), *Cyclotella radiosa* (small arrow), and calcite crystals (arrowhead) in summer plankton of Feldberger Haussee (July 1993). Scale = 10 μm (Figure 19, 20, 23), 1 μm (Figures 21, 22).

Because populations of an effective grazer, namely *Daphnia*, increased significantly since 1987, grazing pressure on small blue-green and edible algae resulted in an increase of phytoplankton species that were better adapted to avoid zooplankton grazing (e.g. bigger cells, coenobial or filamentous taxa). Although there are contradictory observations concerning the suitability of blue-green algae as food for planktonic animals (summarized by Bernardi & Giussani, 1990), an increase in colonial and filamentous blue-green algae under high zooplankton grazing has often been demonstrated (Burns, 1987; Haney, 1987; Lampert, 1987). Therefore, the mass development of filamentous blue-green algae in Feldberger Haussee can be attributed to indirect effects of zooplankton grazing. More details concerning the possible interactions between zooplankton and filamentous blue-green algae in Feldberger Haussee are provided by Kasprzak et al. (1993).

The mixed assemblage of blue-green algae occurring in 1985 (*Cyanogranis*, *Cyanodictyon*, *Microcystis*, *Aphanizomenon*, *Anabaena*) is typical for highly eutrophic lakes. The first two taxa are species of small celled colonial cyanophytes. They are common organisms in waters of various trophic status (Komárková-Legnerová & Cronberg, 1994). Due to their small size colonies of *Cyanogranis* and *Cyanodictyon* should be grazeable. Although Lampert (1987) suggested that small blue-green algae were poor in nutritive quality, enclosure experiments have demonstrated that large daphnids ingest small colonies of *Microcystis* (Ferguson et al., 1982). Since the major consumer in Feldberger Haussee is a large daphnid we assumed that populations of the small colonial taxa could be reduced by zooplankton grazing.

Larger colonial coccoid blue-green algae, such as *Microcystis wesenbergii,* were observed only in low densities in Feldberger Haussee until 1987. The absence of *Microcystis* blooms and the increase of *Anabaena*/*Aphanizomenon* in Feldberger Haussee seems to be a result of different physical and nutritional preferences. According to Reynolds (1984a, b) *Anabaena*/*Aphanizomenon* tend to predominate under conditions of high water column stability and intermediate levels of nutrient availability, whereas *Microcystis* typically prevail under conditions of lower stability and high nutrient supply. A comparison of our observations with other biomanipulated experimental waters, such as the hypertrophic Bautzen reservoir (Germany), supports this assumption. Whereas Feldberger Haussee is stably stratified from May to September, Bautzen reservoir lacks horizontal wind protection and therefore stratifies for only a few weeks during summer. The Bautzen reservoir nutrient load is much higher and its phytoplankton community is strongly dominated by *Microcystis* (Benndorf et al., 1988).

In Feldberger Haussee a shift from heterocyst-forming taxa to *Limnothrix redekei* and *Planktothrix rubescens* (which both lack heterocysts) coincided with a threefold increase of nitrate-concentration and an even higher increase in N/P-ratio. Presumably, under elevated nitrogen supply, heterocyst formation was no longer induced (Kohl et al., 1982; Kasprzak et al., 1993). Burns (1987) reported suppression of N-fixing blue-green algae by ammonia-excretion of zooplankton.

Aphanizomenon gracile was a subdominant but persistent blue-green algal taxon in Feldberger Haussee. This common species has been well characterized, morphologically and ecologically by Schwabe & Stange-Bursche (1964) and Kohl et al. (1985). The latter authors observed a higher abundance of this cyanophyte following significant reduction of zooplanktivorous fish stock. *Aphanizomenon issatschenkoi* has been only rarely observed in Northern Europe (Hickel, 1988), but rather is more common in Southern Europe (Komárek, pers. comm.; Padisák, 1992). We observed this taxon in Feldberger Haussee in 1989/90 and 1994 as a subdominant member of a very heterogeneous hormogonalean community. *Anabaenopsis elenkinii* is also an 'exotic' member of the blue-green algal populations of Feldberger Haussee. According to Komárek (1958) and Jeeji-Bai et al. (1977) this genus is typically more abundant in tropical, subtropical and South European waters. However, Olrik et al. (1984) observed this taxon in a Danish lake. These observations support a concept of increasing invasion of northern lakes by subtropical or Southern European blue green algal species. One of the best documented examples is the migration of *Cylindrospermopsis raciborskii* (Wolosz.) Seen. et S. Raju from Southern to Northern Europe (Horecká & Komárek, 1979; Padisák, 1990–91; Padisák, unpubl.). We have found this species in the Northern German lake Lieps near town of Neubrandenburg (Krienitz & Hegewald, unpubl.).

Our attempts to explain the blue-green algal succession in Feldberger Haussee cannot yet be comprehensive. Shapiro (1990) reviewed the hypotheses that have been proposed to explain the 'myriad adaptations to survive, compete and achieve dominance in, especially freshwater, environments' (loc. cit. p. 38). Ecological investigations on blue-green algae are complicated because of the high degree of physiological flexibility of these organisms. The possibility that one is dealing with different 'strains' of one and the same species should be taken into account when dominance patterns are difficult to explain (Bernardi & Guissani, 1990). Finally, the high ecological flexibility of blue-green algae is reflected by their overwhelming morphological variability which is difficult to handle taxonomically because of the lack of a modern determination key. The last comprehensive work for our region was published by Geitler in 1932.

In Feldberger Haussee green algae have been the group with highest species diversity during the last three decades. Comparison of previous and present studies reveal some difficulties originating from changes in taxonomic concepts in the meantime. Therefore, a critical reinvestigation of the plankton lists from the 1970s was necessary to interprete some unclear taxa, namely of common green algae, which occurred in Feldberger Haussee. Here we point out some examples of green algal taxa which are ecologically important but often misidentified.

Sphaerocystis schroeteri is stated on most of the plankton lists. The species propagates by zoospores and occurs in very clear waters. Komárek & Fott (1983) pointed out that authentic occurrences of *S. schroeteri* have only been known from Switzerland and Sweden, and that this taxon is often confused with *Eutetramorus fottii* (Hind.) Kom. Hindák (1984), who reviewed the history and synonymy of this group, concluded that *Eutetramorus fottii* is a synonym of *Coenochloris polycocca*. Therefore, we suspect that most of records of '*S. schroeteri*' actually represent occurrence of *Coenochloris polycocca*. Koschel et al. (1981) included '*S. schroeteri*' in the plankton list of Feldberger Haussee. However, later studies explained this as a confusion with *Coenochloris polycocca*. The determination of spherical taxa characterized by gelatinous envelopes required critical observations, because the number of taxa that look very similar is rather high (Komárek & Fott, 1983; Hindák, 1988).

A recently published study on *Botryococcus* (Komárek & Marvan, 1992) distinguished 12 taxa, characterized by morphological features. Consequently, listings of the often cited species *Botryococcus braunii* should be reevaluated. In Feldberger Haussee we found two species of *Botryococcus*: *B. braunii* and *B. terribilis*. The latter clearly differs from the former by the complete immersion of cells within the mucilaginous sheath.

Similarly the name *Dictyosphaerium pulchellum* has often been used for a number of different species of the genus. In Feldberger Haussee we found three species. The widespread occurrence of *Dictyosphaerium tetrachotomum* (unpubl. observations) confirms the assumption of Komárek & Perman (1978) that this is the most common species of *Dictyosphaerium* in eutrophic waters.

Species of the genus *Oocystis* are also rather difficult to identify. A revision is urgently needed. Such a work should evaluate the taxonomic utility of the pyrenoid. Hindák (1988) suggested that numerous common taxa having a pyrenoid should be moved into the genus *Oocystella* Lemm. These would include forms observed in Feldberger Haussee: *Oocystis parva* and *O. lacustris*.

Highly productive picoplanktonic chlorophytes having cell densities of $100–190 \times 10^6$ l^{-1} played an important role during early summer in Feldberger Haussee, but are difficult to identify correctly. For such organisms, unfortunately, provisional names as '*Chlorella*-like' and '*Nannochloris*-like' algae are repeatedly used in the literature. As demonstrated by *Choricystis minor* the systematics can be clarified only by means of combination of traditional and modern approaches (ecology, light and electron microscopy, molecular biology) for investigation of algal material both from the field and from culture (Krienitz et al., 1996).

The green filamentous algae *Koliella* and *Elakatothrix* represent another problematic group. Several *Koliella*-taxa are very common in waters during the colder seasons (as occurs in Feldberger Haussee). However they are often confused with coccal ankistrodesmacean algae that propagate by autosporulation. *Koliella* is clearly distinct because it reproduces by simple binary fission of the cells (Hindák, 1979). Different *Elakatothrix*-taxa, e.g. *E. genevensis* and *E. subacuta* occur mainly in summer and are often misidentified as *E. gelatinosa* (Hindák, 1962).

Most of the green algal taxa observed in Feldberger Haussee are characterized as fast growing r-strategists (Sommer, 1981; Reynolds, 1984 a, b), like *Chlamydomonas*, single celled and some coenobial Chlorococcales and chlorophycean picoplanktonts. Recent studies discussed their rather uniform ecological characteristics and high species number by their weed-like occurrence (Padisák & Tóth, 1991). However, we found grazing-resistant K-strategists too (Volvocales; some colonial and mucilage-producing Chlorococcales, e.g. *Botryococcus* and *Coenochloris*; filamentous green phytoplanktonts, big desmids). Obviously, the restoration program and biomanipulation in Feldberger Haussee led to the development of both K- and r-adapted species.

Porter (1973) classified the algae by their response to grazing 'into three major groups that cut across taxonomic lines' (loc. cit. p. 180) as: (1) large or filamentous algae which are unaffected by grazing, (2) small edible, digestible species suppressed by grazers, (3) edible algae with thick envelopes which pass through the digestive tract of grazers, but remain viable and grow after excretion (stimulatory effect of passage).

The second group should be supplemented by those taxa which show positive response to grazing pressure by having high growth rates to withstand even intensive grazing (Benndorf et al., 1984; Elser & Carpenter, 1988; James & Forsyth, 1990). Examples of this group of green algae in Feldberger Haussee are *Chlamydomonas debaryana*, occurring together with filamentous blue-green algae in 1992–94 in spring after development of the *Daphnia* population, *Oocystis parva* in the summer plankton, several chlorophycean picoplanktonts and *Ankyra* as common species of spring clear water stages. Although the latter taxon is needleshaped and possesses an anchor on the basal end of the cell, appears to be edible and digestible because Ferguson et al. (1982) found remnants of cells as well as distinctive forked tailpieces in guts of *Daphnia*. We assume that other needleshaped taxa such as *Ankistrodesmus*, *Monoraphidium*, *Koliella*, may be also edible, until they reach a size limit. Therefore, McQueen & Post (1988) termed needleshaped *Schroederia* cells of about 60 μm length were a poor food source for *Daphnia* because of handling problems during feeding.

Although green picoplankton should be highly grazeable, we found this size fraction to occur in relatively high abundances even during periods of high grazing pressure. One explanation might be the remarkable growth rate of these small algae under conditions of nutrient recycling associated with zooplankton grazing. One example is *Choricystis* (1–3 μm) which occurs during high abundances of *D. cucullata*. Lampert's (1987) experiments with the cyanobacterium *Synechococcus* suggest that *Daphnia* is not able to filter particles smaller than 1 μm whereas algae of 1–3 μm are well within the size range (Geller & Müller, 1981).

Examples of green algae that are stimulated by passage through the digestive tract of zooplankton in Feldberger Hausssee might be *Coenochloris*, *Oocystis lacustris*, *Scenedesmus*-species with mucilaginous envelopes, e.g. *S. raciborskii* and smaller colonies of *Elakatothrix*. Larger colonies of *Pandorina*, *Eudorina* and *Botryococcus* are probably not edible. The same is true for large colonies of *Elakatothrix* and the filamentous alga *Planktonema*. Ferguson et al. (1982) indicated that 50 μm is probably the size-limit of *Eudorina*-colonies that can be used as food particles. McQueen & Post (1988) classified *Sphaerobotrys* (similar to *Botryococcus*) as poor food source.

The green phytoflagellate *Phacotus* is an indicator of high lime content in the lake. This chlamydophycean algae often accompanies autochthonous calcite precipitation. *Phacotus* incorporates $CaCO_3$ in its two-shelled lorica (Pocratsky, 1982; Steinberg & Klee, 1983; Giering et al., 1990a); this process is known as 'organismic calcite precipitation' (Krienitz et al., 1993). The relationship between autochthonous and organismic calcite precipitation is still rather unclear. However, the massive occurrence of *Phacotus* may indicate a certain stage in the nutritional status of a lake between highly and less eutrophic conditions (Koschel, 1990; Koschel et al., 1990).

Dinoflagellates (*Peridinium, Ceratium*) occured during the second half of the 1980s but have completely disappeared since 1990. This corresponds with the results of other biomanipulation experiments (Benndorf et al., 1984; Elser & Carpenter, 1988). However, it is unclear whether or not zooplankton may be directly or indirectly involved in this process, as large-sized spezies of *Peridinium* and *Ceratium* are effectively protected against grazing.

Chrysophytes were important in the phytoplankton of Feldberger Haussee at the beginning of this century (Plümecke, 1914), but this group did not occur very frequently during our investigation period because they are more adapted to higher light and lower nutritional conditions (Sandgren, 1991). *Mallomonas akrokomos* and *Chrysococcus rufescens* were sporadically present in early spring. Grazing experiments with *M. akrokomos* have indicated that this chrysoflagellate is not accepted by zooplankton (Lehman & Sandgren, 1985).

Cryptomonads have been characterized as couplers in planktonic community dynamics (Stewart & Wetzel, 1986), a flexible ecological group with high motility (Sommer, 1985), and organisms which are able to grow quickly from small residual inocula (Reynolds, 1986). Braunwarth & Sommer (1985) found very short doubling times of t_D 1.7 h and 1.87 for *Rhodomonas minuta* and *Cryptomonas ovata*. According to Elser & Carpenter (1988) the nutrient excretion of zooplankton may have a stimulating effect on cryptomonads. These characteristics indicate that cryptomonads are a favoured group in periods of strong grazing pressure (Fott, 1975; Benndorf et al., 1984; Reinertsen & Olsen, 1984). Therefore, the increasing abundances of Cryptophyceae that we observed in Feldberger Haussee after biomanipulation correspond with the findings of previous authors.

Diatoms developed high abundances in the summer of 1987, as well as in spring of 1989 and 1991. Nevertheless, this algal group exhibited a tendency to decrease in abundance during the last years of the investigation period. This is most likely a result of the low Si/P-ratio. The annual mean of Si/P-ratio in Feldberger Haussee amounted to 4–6:1 from 1992–1994 (Koschel, unpubl.). According to Tilman et al (1986) and Sommer (1988) low Si/P-ratios inhibit diatom development. Moreover, zooplankton grazing can recycle phosphorus but not silicon resulting in a dominance switch from diatoms to cyanophytes (Burns, 1987).

The ecosystem of Feldberger Haussee did not respond immediately to load reduction and biomanipulation with a decrease of phytoplankton biomass. At the beginning only a shift within the community structure was observed, but in the long-term a decrease of biomass became evident. While the lake continues to change, we believe that biomanipulation did accelerate the recovery of a damaged ecosystem after the sources of pollution had been removed. Köhler et al. (1989), working on similar problems, concluded that physico-chemical and bottom up effects generate internal ecological mechanisms that cause response time-lag. In general, our observations are in accordance with results found in other experimental waters used for biomanipulation experiments such as the control of the fish community, the stabilization of a *Daphnia* population, the sufficient reduction of nutrients, the decrease of phytoplankton biomass, and consequently the increase of water transparency (Hrbácek et al., 1961; Shapiro et al., 1975; Leah et al., 1980; Benndorf et al., 1984; Reinertsen & Olsen, 1984; Mc Queen et al., 1986; Carpenter et al., 1987; Van Donk et al., 1989; Faafeng et al., 1990).

In the long term run, direct effects of the trophic cascade are supposed to be most effective and stable if they are accompanied by indirect effects such as increased nutrient sedimentation by calcite precipitation, decrease of phosphorus remobilization as a consequence of pH-decrease, increased N/P-ratio, and recolonization of the littoral zone by macrophytes (summarized by Kasprzak et al., 1993). Nervertheless, the nutrient concentration in Feldberger Haussee is still comparatively high indicating that mass developments of algae are again likely to happen. According to Sas (1989) the following concentrations of nutrients are sufficient to induce phytoplankton mass developments: soluble reactive phosphorus 10 $\mu g\ l^{-1}$, inorganic nitrogen 100 $\mu g\ l^{-1}$; silica 500 $\mu g\ l^{-1}$. Therefore, the long term experiment in Feldberger Haussee challanges further scientific activity.

Acknowledgments

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