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Basic Limnological Characteristics of the Shallow Eutrophic Lake Grimnitzsee (Brandenburg, Germany)

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With 10 Figures and 2 Tables

Key words: Shallow lake, mixing, plankton dynamics, trophic state, eutrophication

Abstract

The medium shallow lake Grimnitzsee (maximum depth: 9.9 m; mean depth: 4.6 m; area: $7.7 \cdot 10^6$ m^2) which is situated in the biosphere reserve "Schorfheide-Chorin" in northern Brandenburg (Germany) was studied in 1994 and 1995. A bathymetric map of Grimnitzsee is given for the first time. The lake is usually polymictic although in 1994 and 1995 relatively long summer stratification was observed due to very high global radiation input. Nutrient concentration, light climate, oxygen status, phytoplankton biomass and the species composition of littoral diatoms characterize the lake as eutrophic. Special features deducible from the lake's polymictic character were the multiple development of aerobic or anaerobic strata above the sediment, the fast recovery of silicon concentration in the water column after diatom sedimentation, the importance of resuspension for the success of planktonic diatom populations, and an only moderate correlation between chlorophyll *a* concentration and light attenuation as well as seston dry weight probably due to the influence of suspended particles.

1. Introduction

Many shallow lakes in several regions have been subject to eutrophication in this century (SCHEFFER 1998). This process is coupled with dramatic changes in the shallow lake ecology, i.e. the shift from a clear state dominated by submerged macrophytes to a state that is turbid due to the dominance of phytoplankton and due to sediment resuspension (SCHEFFER 1998). The same holds true for Berlin and Brandenburg since most lakes are eutrophic or polytrophic (WÖBBECKE 1996; NIXDORF & DENEKE 1997), and the disappearance of macrophytes from shallow lakes in this region has been reported (KALBE 1971, 1984; DRIESCHER et al. 1993).

The present contribution represents the first detailed investigation of the medium shallow lake Grimnitzsee since the work of PANKNIN (1941). In line with the studies of MIETZ & KASPRZAK (1992), ARP & RIEMER (1996), NIXDORF et al. (1995), NIXDORF & KLEEBERG (1996), CASPER & KOSCHEL (1995) the aim is to increase knowledge of Brandenburg lakes. On the basis of nutrient concentrations, light climate, oxygen status, phytoplankton biomass and the species composition of littoral diatoms, we discuss the trophic state of Grimnitzsee. Moreover, the plankton succession is analysed before the background of polymixis. The basin morphology of more than 50% of the large lakes in Brandenburg (area: 450–1200 ha) is unknown (MIETZ 1996a). The present survey gives detailed information on the morphometry of Grimnitzsee for the first time. Our study covers the beginning of the period in which the human impact on Grimnitzsee has been considerably reduced. Future reference to this study will help in assessment of the effectiveness of restoration measures.

2. The studied lake

Lake Grimnitzsee is situated in northern Brandenburg (north-eastern Germany) in the centre of the UNESCO biosphere reserve "Schorfheide-Chorin" (52°58′ N, 13°50′ E; 65 m above sea level). It is of glacial origin (MARCINEK et al. 1996). In terms of area, it is one of the 10 largest natural lakes in Brandenburg (KALBE 1993; MIETZ 1996a). The catchment area is inhabited by about 3500 people in two settlements (Joachimsthal, Althüttendorf). VIETINGHOFF (1995) showed that the catchment area is characterized by forests (47%), grassland (26%), wetland (9%), arable land (7%) and housing areas (7%).

3. Methods

3.1 Hydrographic survey

Topographical parameters were measured and calculated using infrared aerial photographs (scale: 1:10000; taken in July 1991 and May 1992 by Luftbild Brandenburg). To gain a bathymetric map of Grimnitzsee, the lake bottom was surveyed with the help of a Lowrance X-16 recording depth echosounder (8° cone angle transducer) on 29 continuous tracks (total length: 48420 m; Fig. 1) according to HÅKANSON (1981) on April 5th and 11th 1995. Water depths (1 m distance) were marked on the track line of the echogram and transferred to a lake map derived from the aerial photographs (using the technique of HÅKANSON 1981). This resulted in 309 measurement points. Bathymetric contour lines were drawn by connecting all points of each depth. The calculation of the information value of the bathymetric map and of the morphometric parameters was according to HÅKANSON (1981).

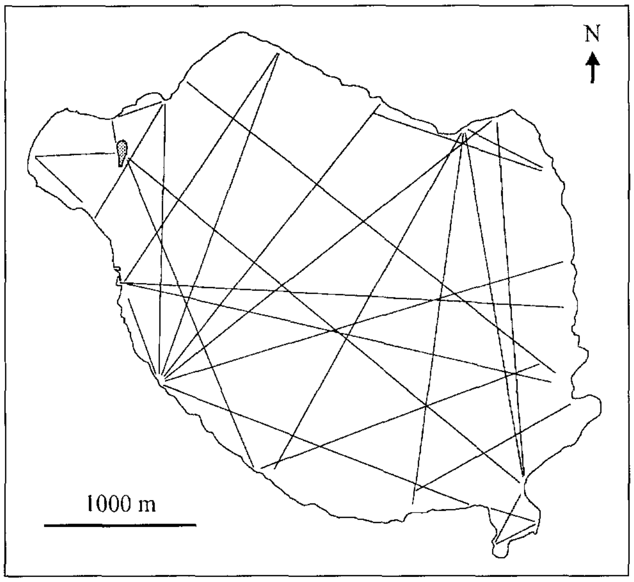

Fig. 1. Location of the tracks on which echosounding of the bottom of Grimnitzsee was performed.

3.2 Limnological survey

Grimnitzsee was studied fortnightly (and monthly in winter) at 42 days between March 1994 and December 1995. Sampling and *in situ* measurements were performed west of the centre of the lake (water depth about 7 m; Fig. 9c) in the morning. On May 26th 1995, water samples were taken at 10 different locations along two horizontal tracks across the lake (Fig. 9c) between 8:30 a.m. and 1:30 p.m.

Water temperature, oxygen saturation, pH and specific conductance were registered *in situ* with an H20 Multiparameter Water Quality Data Transmitter (Hydrolab Corporation). The mixing depth (z_{mix}) was determined as the depth where $\Delta T > 0.5$ °C 0.5 m^{-1}. In the case of a mixed water column, z_{mix} was assumed to be 7 m. For measuring underwater photosynthetically active radiation (PAR), two scalar LI 193 SB Spherical Quantum Sensors (LiCor) were used. Euphotic depth was calculated from the mean of the vertical attenuation coefficients which were measured every 50 cm below 1 m water depth. Secchi depth was determined with a white disc of 22 cm diameter. The spectral composition of the downwelling light was characterized with a LI-1800 UW Underwater Spectroradiometer (with a cosine receptor; LiCor).

Water samples covered the entire water column profile and were taken with a vertical sampler (height: 1 m, volume: 4 l). When the water column was mixed, samples from all depths were integrated. In the case of stratification, integrated samples from the epilimnion and from the meta-/hypolimnion were taken. The smell of hydrogen sulphide in the water samples was used as qualitative evidence for its occurrence.

Nutrients and other chemical water constituents were determined according to the following DIN methods (DEV 1982–1995). Dissolved substances were analysed in subsamples filtered through 0.6 μm membrane filters.

Soluble reactive phosphorus (SRP) and total phosphorus (TP, disintegration with H_2O_2 and H_2SO_4 at 150 °C for 10 h): spectrophotometric determination (Varian Cary 1E) following a modification of DIN 38405-D11.

Dissolved silicon (DSi) and total silicon (TSi, disintegration with NaOH at 120 °C for 90 min): spectrophotometric determination (Shimadzu UV 2101 PC) following DIN 38405-D21. Ammonium-N: spectrophotometric determination (Shimadzu UV 2101 PC) following DIN 38 406-E5.

Nitrate-N, chloride, sulphate: ion chromatography (Sykam) following DIN 38 405-D19.

Dissolved inorganic carbon (DIC) and dissolved organic carbon (DOC): Shimadzu Analyser TOC-5000 following DIN 38409-H3-1.

Total nitrogen (TN) and dissolved nitrogen (DN, only measured in 1995): chemiluminescence method (TN-Analyzer Abimed TN-05) following DIN 38 409-H27.

Calcium: atomic absorption spectrometry (Perkin Elmer) following DIN 38406-E3-1.

Subsamples were filtered through Whatman GF/F glass fibre filters (precombusted at 400 °C for 4 h) for determination of seston dry weight (drying of filters at 105 °C for 24 h, mass measurement with balance BP 210 D, Sartorius) and content of particulate carbon and nitrogen (PC and PN) (C/N-analyser NA 1500 series 2, Carlo Erba Instruments/Fisons Instruments).

Subsamples for the analysis of chlorophyll *a* (chl *a*) and phaeopigments were filtered through Whatman GF/C glassfibre filters and stored at –20 °C for maximal 6 weeks. The subsequent hot ethanol extraction of the filters, the spectrophotometric determination of the absorption of pure and acidified extracts and the calculation of chlorophyll *a* and phaeopigment concentration were performed according to DIN 38412-L16 in DEV (1983).

In order to quantify the C and N content of phytoplankton the method of BEHRENDT & KROCKER (1990) was used to separate abiotic seston, zooplankton and phytoplankton from samples taken with a 10 μm net from the upper 3 m of the lake. With this method, abiotic seston is separated from the water sample using its fast sedimentation and zooplankton is removed by taking advantage of its phototactic migration. The phytoplankton fraction was concentrated by filtration, dried (105 °C for 24 h) and analysed (C/N-analyser NA 1500 series 2, Carlo Erba Instruments/Fisons Instruments).

Phytoplankton species were identified by light microscopic observation (Zeiss Axioskop, Leitz Dialux 20) of living and

Lugol fixed samples. Phytoplankton biomass was determined in Lugol fixed subsamples by determination of cell concentration according to UTERMÖHL (1958) and estimation of cell volumes according to ROTT (1981) using inverted microscopes (Leitz Fluovert FS, Nikon Diaphot 300). The enumeration of autotrophic picoplankton (APP) was based on counting of autofluorescing cells (MACISAAC & STOCKNER 1993). Subsamples (only in 1995) were prefixed with 0.2% formaldehyde and concentrated onto black polycarbonate membranes (pore size 0.45 µm, Nuclepore) within a few hours. The filters were embedded in immersion oil and analysed with a Zeiss Axioskop epifluorescence microscope (green excitation: filter set 48 77 15; blue excitation: filter set 48 77 09).

Samples for the characterization of zooplankton were taken with a transparent vertical sampler (height: 0.5 m, volume: 8 l) in vertical distances of 1 m over the entire water column profile. The samples were immediately concentrated by filtration through a 30 µm mesh sieve, narcotised with CO_2 and preserved with 4% formaldehyde. The abundance of the different species (>30 µm) of cladocerans, copepods, rotifers and of protozoans preserved by formaldehyde was counted under a Jenaval microscope.

To sample littoral diatoms, old stalks of reed [*Phragmites australis* (CAV.) TRINIUS ex STEUDEL] were broken and conveyed to polyethylene bags together with the adherent periphyton on April 17th 1995. Additionally, about 10 ml of subliquid sludge from the bottom of the reed belt provided the subrecent flora of the last weeks before sampling. The diatom frustules were prepared according to KRAMMER & LANGE-BERTALOT (1986), using hydrogen peroxide as oxidant and Naphrax (refractive index 1.74, Northern Biological Supplies) as mountant. Microscopic identification (Olympus BX and Nikon FXA microscopes with 60× and 100× objectives, numerical aperture 1.4, Nomarski interference optics) followed KRAMMER & LANGE-BERTALOT (1986, 1988, 1991a, 1991b), KRAMMER (1992), LANGE-BERTALOT (1993), SCHEFFLER (1994) and LANGE-BERTALOT & METZELTIN (1996). In the periphyton and epipelon sample 649 and 668 valves were determined and enumerated. The results of both samples were averaged to compensate for substrate differences. The relative abundance of the different diatom species was used to infer the TP conditions of Grimnitzsee according to the regional transfer function developed by SCHÖNFELDER (1997). The transfer function used in the present study was based on 415 diatom taxa identified in 46 littoral diatom samples taken from 11 alkaline lakes and 4 rivers in Brandenburg in 1992-1995 (SCHÖNFELDER 1997) and in 12 additional samples taken from 12 lakes in 1996. The data set of this transfer function was used according to SCHÖNFELDER (1997) to create preference series for all taxa within the TP range of the waters studied (2–285 µg l^{-1}, yearly means from 1992 to 1996 derived from epilimnion samples taken every fortnight) based on the method proposed by ZELINKA & MARVAN (1961). The studied TP range was divided into 10 sections (see Fig. 10) which were equidistant when transformed to logarithmic values. In addition, the diatom taxa were grouped into four classes of stenoecy according to their different TP tolerance. The most tolerant species [e.g. *Fragilaria ulna* (NITZSCH) LANGE-BERTALOT] were assigned to stenoecy factor (SF) 0 whereas highly specialized species (e.g. *Cymbella delicatula* KÜTZING) were assigned to stenoecy factor 3 (SCHÖNFELDER 1997). To show the TP preference of the littoral diatom assemblage of Grimnitzsee, the preference spectra of all taxa in the samples' mean were weighted by the relative abundance of the taxa and added in groups according to the different TP stenoecy factor of the taxa.

4. Results

4.1 Topographic and morphometric characteristics

Grimnitzsee is a shallow lake with two sheltered creeks and one little island. At the northern and southern lakeside the lake bottom drops to depths of more than 5 m rather steeply whereas in the eastern part there is a very shallow area (Fig. 2, Fig. 3, Table 1).

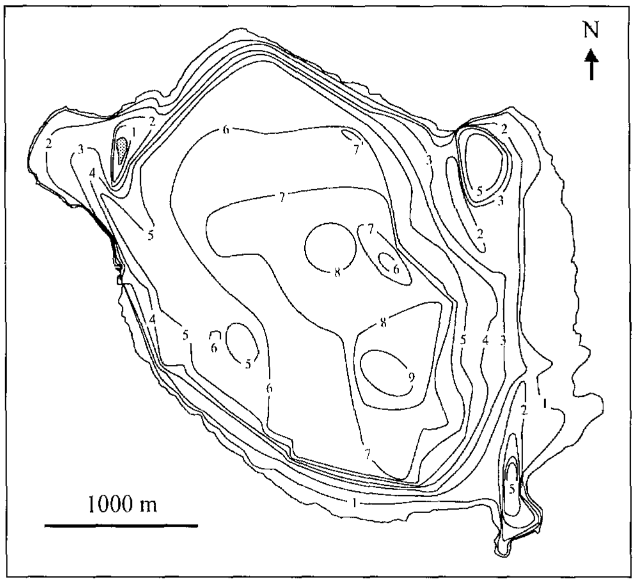

Fig. 2. Bathymetric map of Grimnitzsee with 1 m contour-line interval. According to HÅKANSON (1981) the information value of this map was calculated to be I = 0.91 (I = 1 if the bathymetric map is complete and completely correct). The correctly identified area (*sensu* HÅKANSON 1981) in this bathymetric map is I′ = 0.93. This means that on an average 7% of the lake area are not related to the real depth. As the echosounding tracks were not evenly distributed (Fig. 1) the area error is not the same in all parts of the map.

Table 1. Topographic and morphometric characteristics of Grimnitzsee sensu VENTZ (1974) (z_{epi}), NIXDORF & DENEKE (1997) (z_{90}) and HÅKANSON (1981) (other parameters).

Maximum length (L_{max})	4170 m
Maximum width (B_{max})	2870 m
Theoretical epilimnion depth (z_{epi})	8.3 m
Shoreline length (L_0)	12900 m
Shore development (F)	1.31
Lake area (a)	$7.73 \cdot 10^6$ m^2
Maximum depth (z_{max})	9.9 m
90% depth (z_{90})	5.9 m
Mean depth (z_{mean})	4.6 m
Volume (V)	$35.3 \cdot 10^6$ m^3

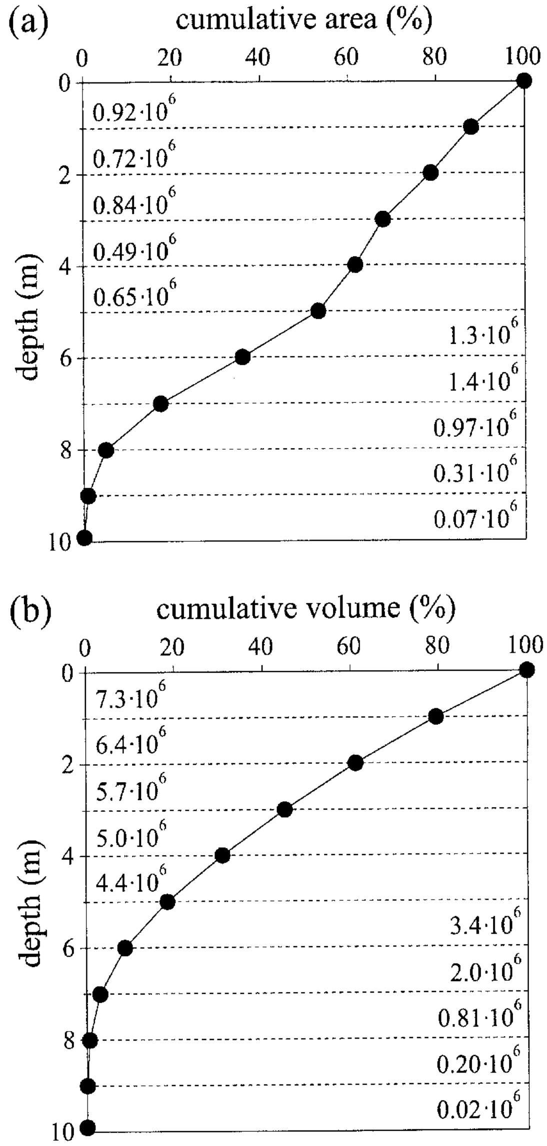

Fig. 3. Percentage hypsographic curve (**a**) and percentage volume curve (**b**) for Grimnitzsee. The inserted values give the area in m^2 (a) and the volume in m^3 (b) of the different 1 m water layers.

4.2 Hydrophysical and hydrochemical conditions

The lake was ice-covered for three weeks in February/March 1994, for one week in January 1995 and for the last three weeks of December 1995.

In 1995, the water level showed fluctuations with a maximal amplitude of 20 cm.

From May to August the lake was thermally stratified on all sampling days (Fig. 4a). The largest temperature difference between 0 m and 6.5 m depth was, however, quite low (6.8 °C in July 1994; 5.5 °C in May 1995) so that thermal stratification only was of short duration. Even short periods of slight thermal stratification led to an obvious decrease of oxygen concentration in deeper water layers (e.g. in October 1995; Fig. 4b). Especially in the summer of 1994, this resulted in anoxic conditions below 5 m depth (Fig. 4b). The smell of sulphide was obvious in the anoxic water layers.

Specific conductivity was in the range between 490 and 590 $\mu S\ cm^{-1}$. Chloride and sulphate concentrations amounted to values between 31 and 52 $mg\ l^{-1}$ and 71 and 98 $mg\ l^{-1}$, respectively.

The value of pH was between 7.0 (above the sediment during summer stratification) and 8.8 (in the epilimnion in summer). The pH in the mixed water column (Fig. 4a) was never below 7.9. Calcium concentration amounted to values between 65 and 119 $mg\ l^{-1}$ in samples taken in a preliminary study from March to December 1993.

Secchi depth was always higher than 1.0 m except in August 1994 (Fig. 5a). The annual mean of the Secchi depth amounted to 2.0 m in both years. The annual mean of the coefficient of vertical attenuation of PAR was 1.01 m^{-1} in 1994 and 0.80 m^{-1} in 1995. The euphotic depth reached minima in February/March and in summer (Fig. 5a). The euphotic depth was distinctly higher than the mixed depth in June and July (Fig. 5b). The linear regression between the chlorophyll *a* concentration (see below) and the scalar PAR revealed a background attenuation of 0.57 m^{-1} and a chlorophyll specific attenuation coefficient of 0.022 (mg chl $a)^{-1}$ m^{-2} ($r = 0.72$, $P = < 0.0001$).

The spectral distribution of the downward radiation distinctly changed with water depth, in deeper water layers only green/yellow light (550–600 nm) was observed (Fig. 6a). This was due to the fact that the vertical attenuation coefficient (k_d) regularly had its minimum between 565 and 585 nm (Fig. 6b and c). K_d steeply decreased from 400 to about 530 nm and slightly increased above 590 nm (Fig. 6b and c). The height of the small maximum of k_d in the range of 670 to 680 nm (Fig. 6b and c) was positively correlated with chlorophyll *a* concentration ($r = 0.80$, $P < 0.0001$; Fig. 6d). The correlation of the mean k_d between 400 and 700 nm and the chl *a* concentration revealed a lower correlation coefficient ($r = 0.72$, $P < 0.001$) suggesting a slight selectivity in wavelength-specific attenuation by the phytoplankton due to chlorophyll *a*.

The chlorophyll *a* concentration was positively correlated with seston dry weight ($r = 0.75$, $P < 0.001$), particulate carbon ($r = 0.75$, $P < 0.001$) and particulate nitrogen ($r = 0.68$, $P < 0.001$). In August/September 1994 and February 1995 relatively high chl *a* concentrations resulted in high values of dry weight and PC and PN concentration (Fig. 7d, i, l). The concentration of TN and particularly of DIC and DOC showed only low variability with time (Fig. 7a, j, k). 77% of TN were due to dissolved organic nitrogen on average in 1995. The concentration of TP showed large fluctuations (Fig. 7b) which were not correlated with chl *a* or SRP concentration. TSi and DSi concentrations were positively correlated ($r = 0.88$, $P = < 0.001$). Silicon concentration uni-

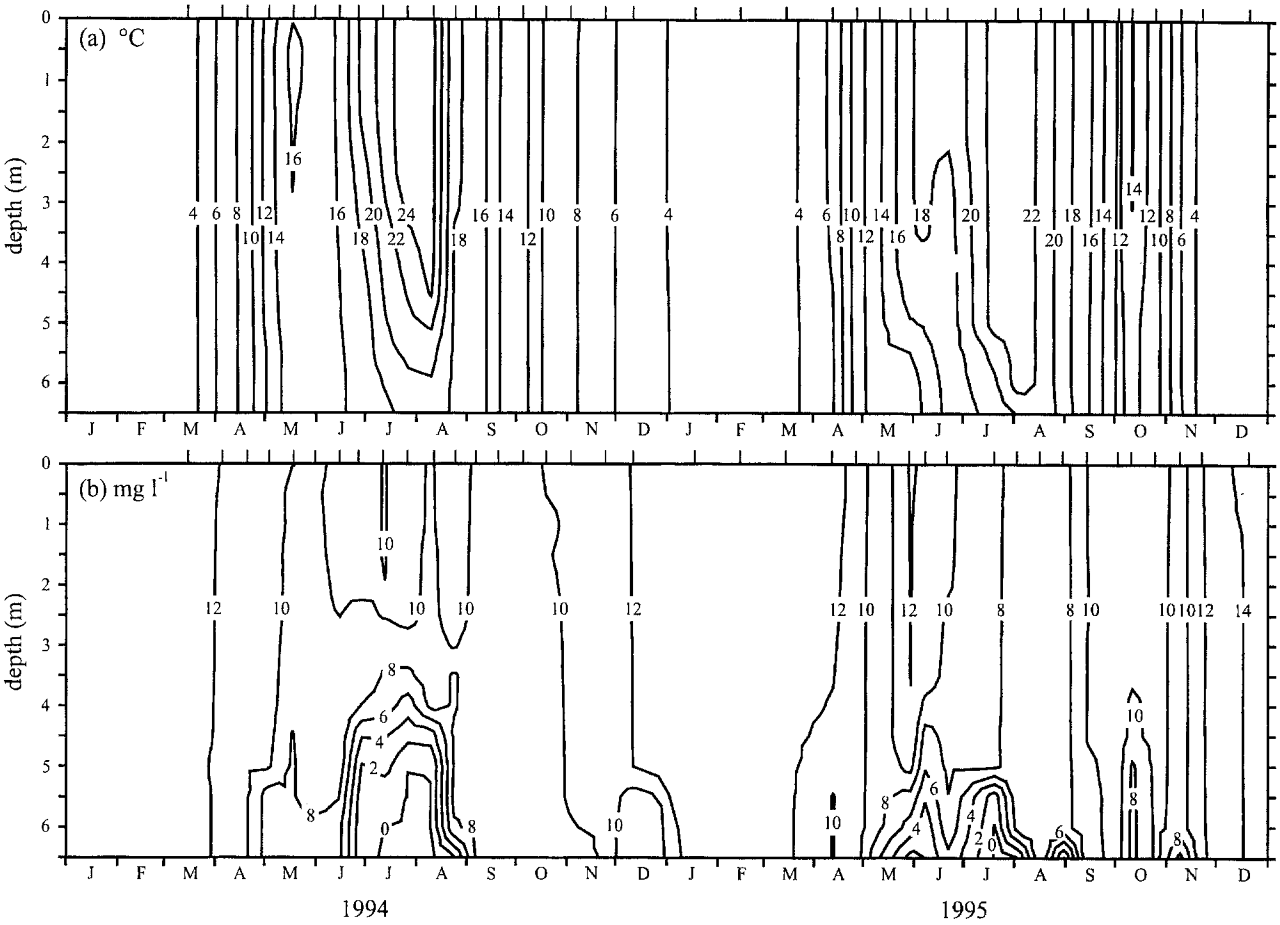

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Fig. 4. Depth-time diagram of isopleths of water temperature in °C (**a**) and dissolved oxygen concentration in mg l^{-1} (**b**) of Grimnitzsee in 1994 and 1995. Dates of measurements are marked on the upper time axes. The diagrams represent the upper 6.5 m of the lake which correspond to 94% of lake volume (Fig. 3b).

formly increased from May to July in both years (Fig. 7c, g). The wax and wane of large diatom populations in winter and autumn 1995 (Fig. 8) led to a dramatic decrease of DSi concentration and a subsequent reduction of TSi concentration (Fig. 7c, g). In general, the Si concentration in Grimnitzsee was low compared to other lakes (WETZEL 1983: 337). Except from November 1994 to January 1995 the concentration of SRP was usually lower than 10 µg l^{-1} (Fig. 7f). In summer, integral SRP values higher than 10 µg l^{-1} (Fig. 7f) were mostly due to high (up to 54 µg l^{-1}) SRP concentrations in the meta/hypolimnion. Nitrate was not detected in summer

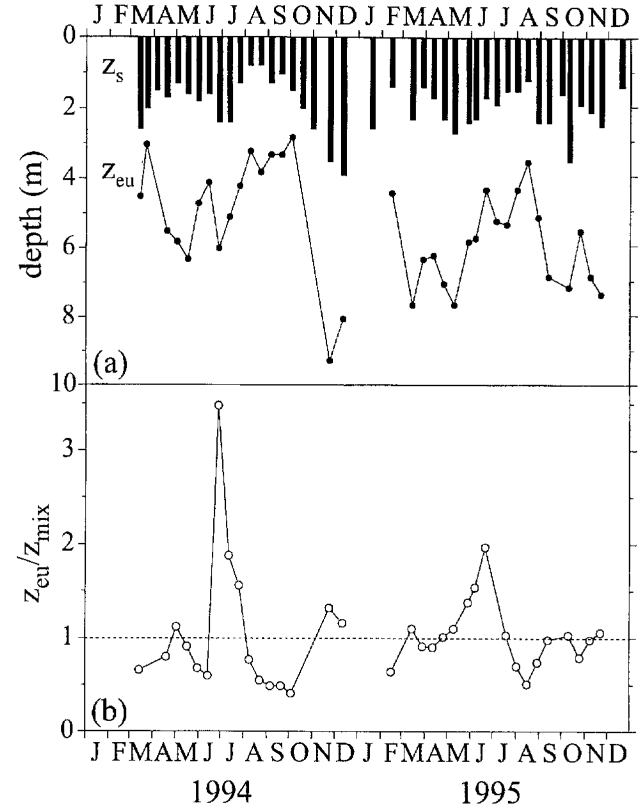

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Fig. 5. Annual course of Secchi depth (z_s), euphotic depth (z_{eu}) (**a**) and annual course of the ratio of euphotic depth to mixing depth (z_{eu}/z_{mix}) (**b**) in 1994 and 1995.

(Fig. 7e). Analogous to SRP, the NH_4^+ concentration was high in the winter of 1994/1995 (Fig. 7e). In summer, NH_4^+ was not detected in the epilimnion, higher integral values during that season (Fig. 7e) were caused by hypolimnetic accumulation (up to 0.44 mg NH_4^+-N l^{-1}). The C/N ratio of the phytoplankton was higher than 8.3 [indicating N deficiency of phytoplankton growth according to HECKY et al. (1993)] for two long periods in 1994 whereas in 1995 C/N ratios >8.3 where only observed in May (Fig. 7 m).

The annual means of TP, TN and chlorophyll *a* concentration were higher in 1994 than in 1995 (TP: 65 and 48 µg l^{-1}; TN: 1.48 and 1.31 mg l^{-1}; chl *a*: 17 and 14 µg l^{-1}).

4.3 Plankton

Phytoplankton structure differed greatly between the two years studied (Fig. 8a).

The maximum biomass in 1994 was observed in the summer and was caused by the cyanobacterium *Aphanizomenon flos-aquae* (L.) RALFS. *Chlamydomonas* sp. and *Fragilaria crotonensis* KITTON were codominant. In summer 1995, *Peridinium* spp. and *Pandorina smithii* CHODAT dominated with low biomass whereas *Aphanizomenon flos-aquae* only predominated for a short period in mid October 1995 during a time of thermal stratification (Fig. 4).

In 1995, two biomass maxima due to diatoms were apparent. In late winter and early spring just following the short period of ice cover, *Stephanodiscus minutulus* (KÜTZ.) CLEVE & MÖLLER was dominant. In autumn 1995, *Aulacoseira ambigua* (GRUN.) SIMONSEN was by far the most important phytoplankton species when the water column was not stratified. In late winter and early spring 1994 after the lake had been covered by ice and snow for three weeks, flagellates (*Cryptomonas* spp. and *Chlamydomonas* spp.) prevailed whereas the share of diatoms on phytoplankton biomass was insignificant. In autumn 1994, despite of relatively high DSi concentration (Fig. 7g) the diatom *Asterionella formosa* HASSALL was only subdominant and *Cryptomonas* spp. became abundant.

The biomass of autotrophic picoplankton (only measured in 1995) was solely comprised of cyanobacteria and was always less than 10% of total phytoplankton biomass except on 4 dates in June/July and August/September 1995 when shares between 14 and 32% were observed. During that periods, however, absolute phytoplankton biomass was minimal (Fig. 8a).

The analysis of the horizontal distribution of phytoplankton on May 26th 1995 showed a higher phytoplankton

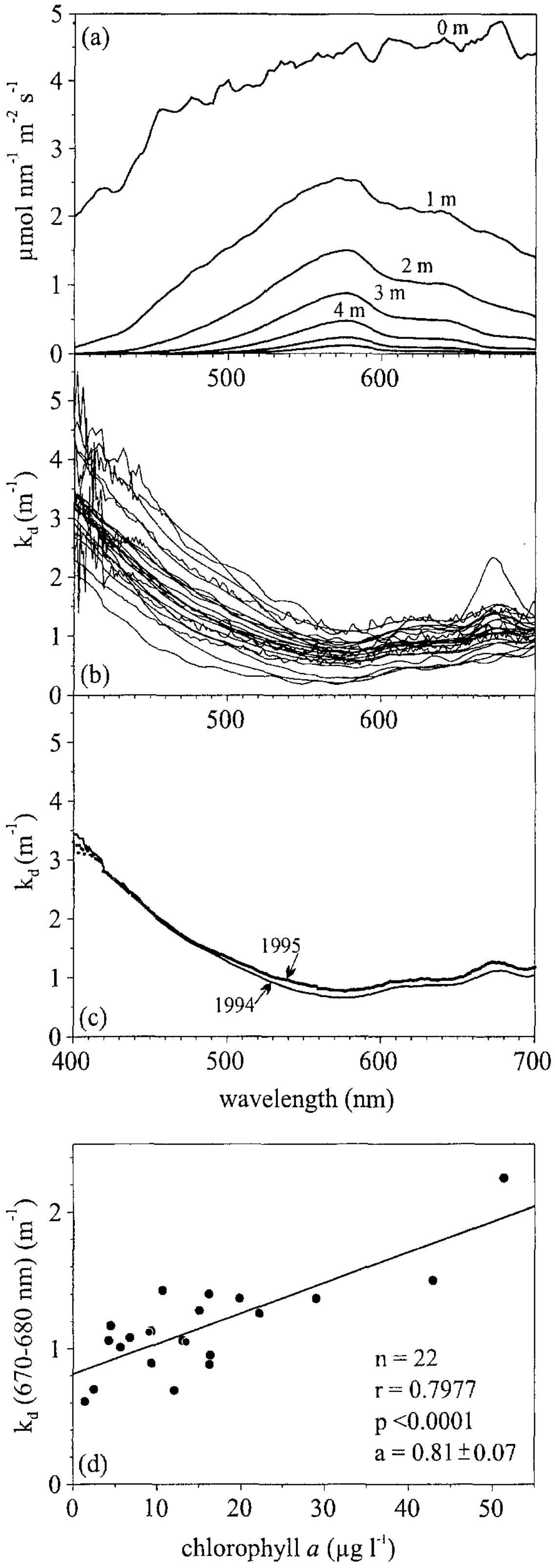

Fig. 6. (**a**) Typical pattern of the downward photon flux density versus wavelength in different depths of Grimnitzsee (0 to 6 m in 1 m intervals) on 28 June 1994. (**b**) Vertical attenuation coefficient (k_d) between 1 m and 2 m depth versus wavelength on 11 days throughout 1994 and 12 days throughout 1995. (**c**) Annual means of the epilimnetic k_d between 1 m and 2 m depth versus wavelength. (**d**) Relationship between the epilimnetic k_d (mean from 670 to 680 nm) and the epilimnetic chlorophyll *a* concentration. The line is the result of a linear regression.

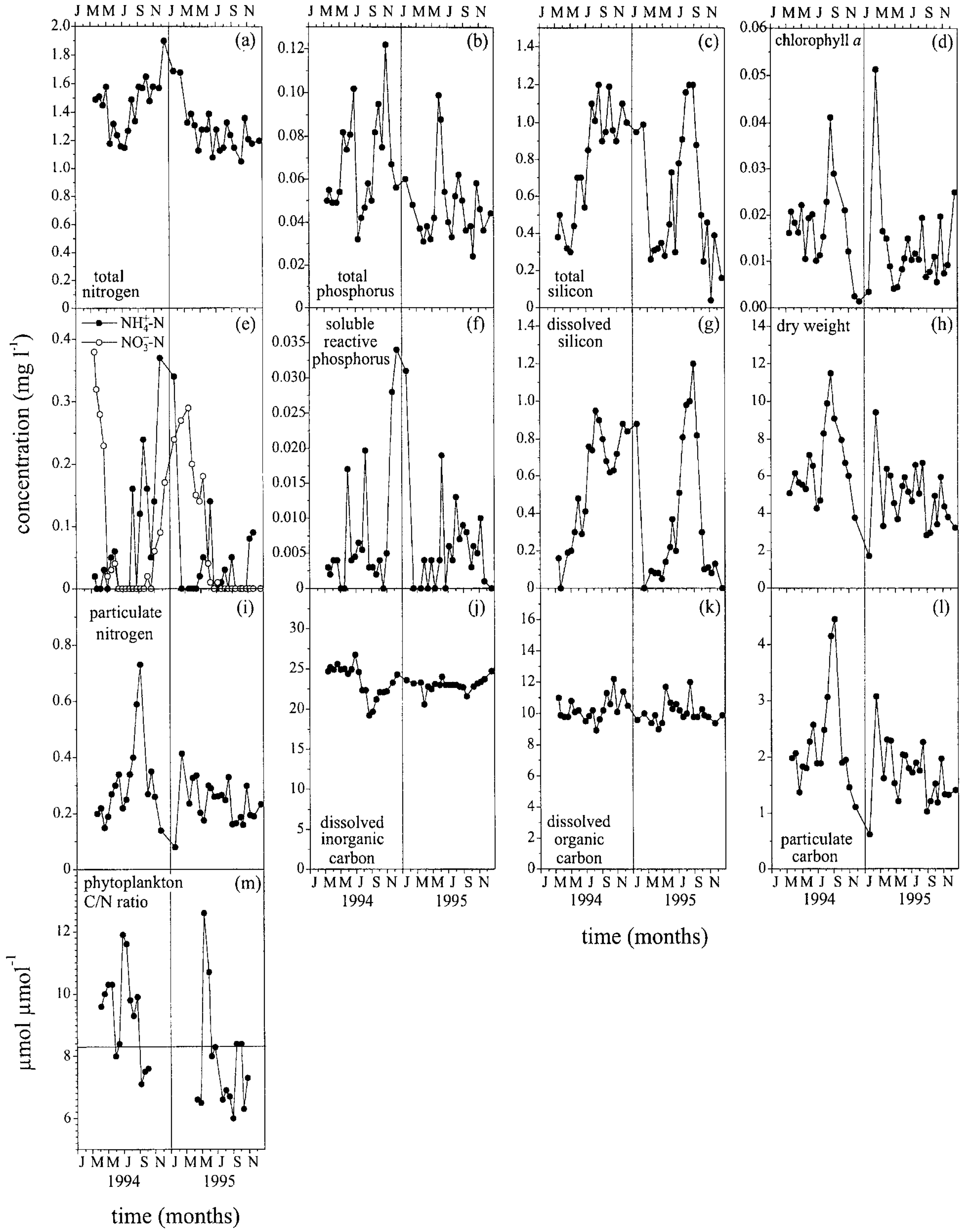

Fig. 7. Annual course of the concentrations of different hydrochemical variables as integral values over the water column of Grimnitzsee in 1994 and 1995 (**a–l**). Annual course of the molar C/N ratio of the phytoplankton (m), the horizontal line in (m) marks a ratio of 8.3 above which the growth of phytoplankton is N deficient according to HECKY et al. (1993). All y-axes in mg l^{-1} except in (**m**).

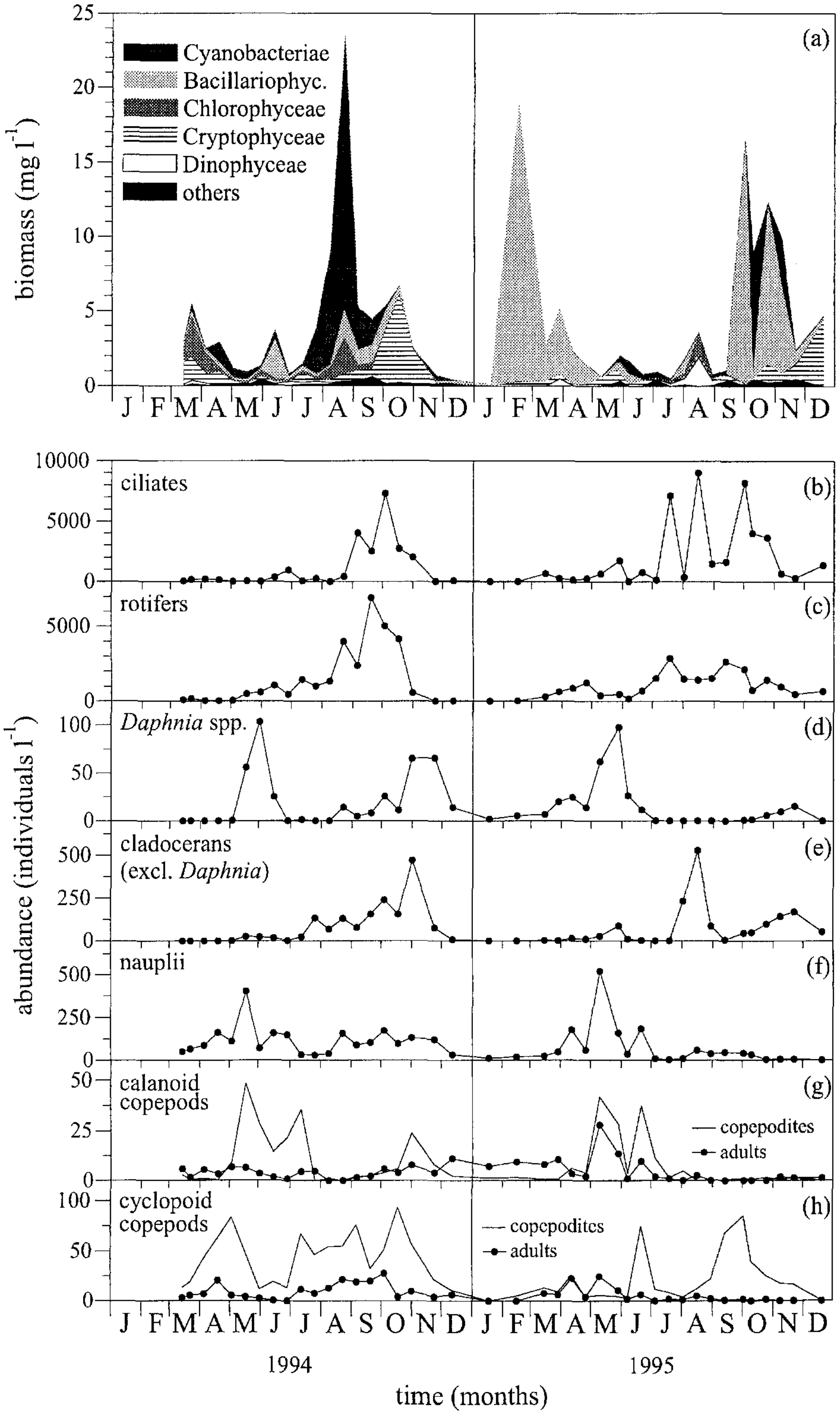

Fig. 8. Cumulative presentation of the annual course of the biomass of different groups of phytoplankton (a) and of the abundance of different groups of zooplankton (b–h) in Grimnitzsee 1994 and 1995.

biomass towards the lake shores along both tracks (Fig. 9). The relative contribution of the different phytoplankton species did not significantly change along the tracks except that an increase of the biomass of *Anabaena lemmermannii* P. Richter was observed in the north-west part of the lake (Fig. 9a, c). Wind was predominantly blowing westward during the time of sampling (Gervais, unpublished data recorded at the shore of the lake Müggelsee, 70 km southwest of Grimnitzsee).

Zooplankton development of Grimnitzsee (Fig. 8b–h) was characterized by abundance maxima of ciliates and rotifers (mainly *Keratella cochlearis* Gosse, *Synchaeta* spp. and *Polyarthra dolichoptera* Idelson) in late summer and autumn (Fig. 8 b-c).

Daphnia spp. (Fig. 8d) reached high abundances in May and June (*D. cucullata* Sars and *D. galeata* Sars in 1994; *D. hyalina* Leydig, *D. galeata* and *D. cucullata* in 1995). The high cryptophyte biomass in autumn 1994 (Fig. 8a) was followed by large abundances of *D. cucullata, D. hyalina* and *D. galeata*, whereas in autumn 1995 only low abundances of *D. galeata* were observed (Fig. 8d).

Smaller cladocerans were represented by *Chydorus sphaericus* O. F. Müller from May to August 1994 and by *Eubosmina coregoni thersites* Poppe from August to December 1994. In 1995, *C. sphaericus* was abundant in May and, together with *E. c. thersites*, from October to December. *Bosmina longirostris* O. F. Müller was the most important zooplankton species in August 1995 (Fig. 8e).

Calanoid copepods (*Eudiaptomus graciloides* Lilljeborg and with minor abundance *Eudiaptomus gracilis* Sars) and their copepodites and nauplii were es-

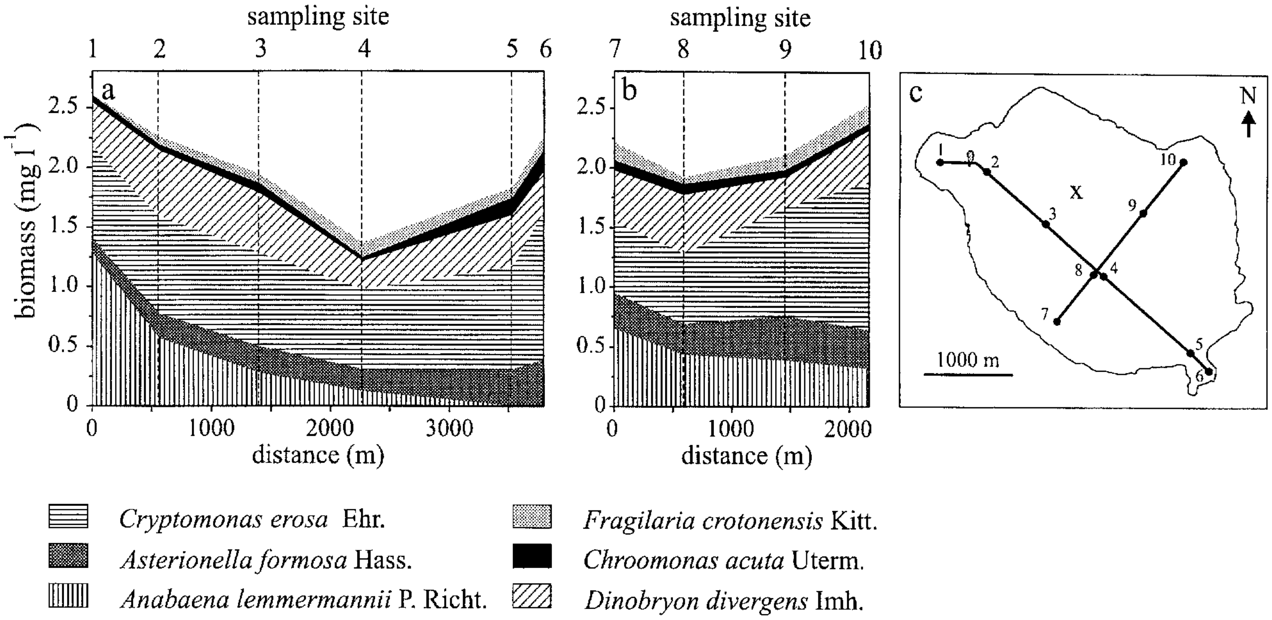

Fig. 9. Cumulative epilimnetic biomass of the most abundant phytoplankton populations at different sampling sites (1–10) in Grimnitzsee on May 26th 1995 (**a, b**). Location of the sampling sites 1–10 (**c**; see Fig. 2). The position of the point of routine sampling is indicated in c (x).

pecially abundant in May and June (Fig. 8g). Cyclopoid copepods and their copepodites were more frequently observed in 1994 than in 1995. When abundance maxima of adults occurred, *Mesocyclops leuckarti* CLAUS often was the most important species, but other species (*Cyclops vicinus* ULJANIN, *Diacyclops bicuspidatus* CLAUS, *Thermocyclops oithonoides* SARS, *Thermocyclops crassus* FISCHER, or *Acanthocyclops robustus* SARS) were often codominant.

Table 2. Mean relative abundance of the most abundant littoral diatoms in Grimnitzsee on April 17th 1995 and total phosphorus (TP) optimum, TP tolerance and TP stenoecy factor (SF) of the species.

Taxon	Relative abundance (%)	TP optimum (µg l^{-1})	TP tolerance (µg l^{-1})	SF
Cymbella silesiaca BLEISCH	20.5	54	22–135	2
Fragilaria capucina var. *vaucheriae* (KÜTZING) LANGE-BERTALOT	8.0	90	39–211	2
Stephanodiscus minutulus (KÜTZING) CLEVE & MÖLLER	7.2	54	23–128	2
Achnanthes minutissima KÜTZING var. *minutissima*	3.9	22	10–49	1
Fragilaria pinnata EHRENBERG f. *pinnata*	3.5	39	14–110	1
Fragilaria brevistriata GRUNOW	3.0	43	15–128	0
Cocconeis pediculus EHRENBERG	3.0	50	20–125	1
Gomphonema olivaceum (HORN.) BRÉBISSON var. *olivaceum*	2.7	69	30–159	3
Asterionella formosa HASSALL	2.7	64	24–173	0
Stephanodiscus hantzschii GRUNOW	2.6	113	54–240	2
Fragilaria capucina var. *rumpens* (KÜTZING) LANGE-BERTALOT	2.5	55	27–111	3
Cocconeis placentula var. *lineata* (EHRENBERG) VAN HEURCK	2.5	44	15–126	0
Fragilaria capucina DESMAZIÉRES var. *capucina*	2.1	74	32–174	2
Cymbella caespitosa (KÜTZING) BRUN	1.9	24	11–54	1
Diatoma moniliformis KÜTZING	1.9	21	10–44	1
Fragilaria construens (EHRENBERG) GRUNOW f. *construens*	1.7	45	16–125	0
Fragilaria ulna (NITZSCH) LANGE-BERTALOT var. *ulna* sensu lato	1.7	86	33–225	0
Aulacoseira granulata (EHRENBERG) SIMONSEN	1.2	158	89–280	3
Cavinula scutelloides (W. SMITH) MANN	1.2	50	23–109	2
Nitzschia dissipata var. *media* (HANTZSCH) GRUNOW	1.1	50	20–126	0

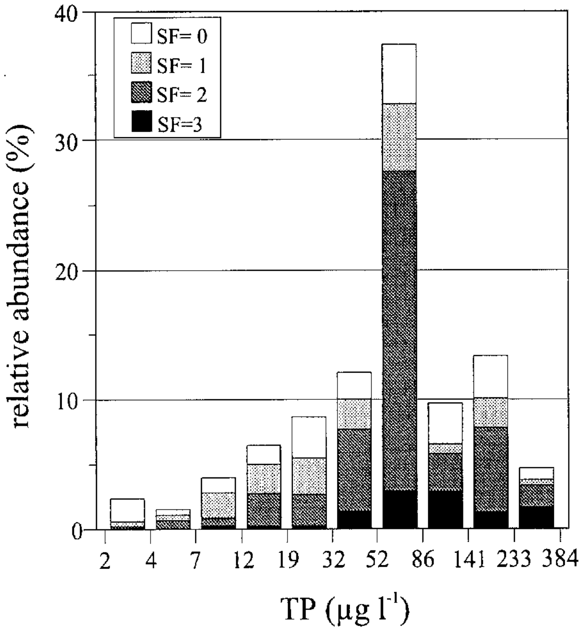

Fig. 10. Cumulative preference spectrum of the littoral diatom assemblage of lake Grimnitzsee on April 17th 1995. SF = stenoecy factor. The x-axis is divided into 10 TP ranges which are equidistant when transformed to ln values.

4.4 Littoral diatoms

Of the 113 diatom taxa found in the littoral of Grimnitzsee in April 1995, the 20 most frequent taxa (Table 2) comprised more than 75% of the individuals counted. The most abundant taxon was *Cymbella silesiaca* Bleisch (Table 2). Most of the taxa with high abundance have a TP optimum in the TP classes between 32 and 86 µg TP l^{-1} (Table 2, Fig. 10). When adding the preference spectra of all diatom species, the greatest relative abundance was found in the TP range between 52 and 86 µg TP l^{-1} (Fig. 10, Table 2). Highly stenoecious species (SF=3) were only observed in the upper TP range (Fig. 10).

5. Discussion

5.1 Mixing conditions, nutrient release from the sediment, retention time and horizontal distribution

In the sense of Nixdorf & Deneke (1997), Grimnitzsee is neither shallow ($z_{max} < 5$ m) nor deep ($z_{max} > 15$ m) but of intermediate type. This type of lakes is common in northern Germany and represents dimictic as well as polymictic lakes (Nixdorf & Deneke 1997). To be able to predict mixing conditions from basin morphology, a new approach was proposed by Nixdorf & Deneke (1997). According to this classification, Grimnitzsee belongs to the medium shallow lakes that are polymictic with short stratification periods because it is characterized by $z_{max} > z_{epi}$ and $z_{90} < z_{epi}$ (Table 1). The basin (large area, large effective fetch, medium depth) of Grimnitzsee is similar to that of the polymictic lake Großer Müggelsee (60 km south of Grimnitzsee; Driescher et al. 1993). In general, stratification events in Müggelsee lasted 1 or 2 weeks (Behrendt et al. 1993). From 1979 to 1990 only 5 stratification periods with a duration between four and five weeks were observed (Behrendt et al. 1993). Up to 7 alternations of mixing and stratification events occurred in Müggelsee from April to October (Behrendt et al. 1993). In 1994 and 1995 extraordinary long periods of uninterrupted summer stratification (6 weeks in 1994, 7 weeks in 1995) were evident in Müggelsee (Gervais, unpublished results, based on weekly measurements). The long periods of continuous summer stratification in Grimnitzsee in 1994 and 1995 (about 7 to 8 weeks from mid June to mid August; Fig. 4a) were analogous to the unusual situation in Müggelsee and were very likely due to the outstanding high input of solar energy in those summers. The global radiation registered in Berlin-Dahlem (70 km southwest of Grimnitzsee) was 13% and 17% higher in July/August 1994 and 1995 than the July/August-mean from 1975 to 1995, only three further years during that period showed similar high values (Berliner Wetterkarte 1975–1995). Stratification resulted in oxygen depletion and nutrient accumulation above the sediment of Grimnitzsee. As an increase in sulphate concentration in lakes is responsible for an increase in the rate of P-release from the sediment (Caraco et al. 1993), the high sulphate concentration in Grimnitzsee (annual means between 0.74 and 1.02 mmol l^{-1}) was probably an important contributory factor for the internal nutrient loading of the lake. In the polymictic lake Müggelsee, P-release from the sediment due to oxygen depletion was of great importance for the internal P-loading of the lake (Behrendt et al. 1993; Kleeberg & Kozerski 1997). Future studies of Grimnitzsee should therefore focus on sediment-water interactions and consider the importance of the duration of weather-mediated stratification periods for the nutrient budget of the lake.

Vietinghoff (1995) calculated a retention time of 6.9 years for Grimnitzsee. This estimate was based on modelled values of inflow, precipitation, evaporation and discharge and on the assumption of a lake volume of $22.8 \cdot 10^6$ m^3 (Vietinghoff 1995). Taking into account the lake volume that was calculated in the present study ($35.3 \cdot 10^6$ m^3) a considerably higher retention time of 10.7 years results from the hydrological parameters determined by Vietinghoff (1995).

The present study tries to characterize Grimnitzsee on the basis of analyses of one sampling location near the centre of the lake. This is a concession to the practicability of the study that has to be evaluated in the light of horizontal patchiness. The horizontal distribution of planktonic organisms can vary considerably as a response to lake basin size, vertical behaviour of the dominant species and wind action (Barthel-

MES 1960; REYNOLDS 1984: 112; WEBSTER & HUTCHINSON 1994). The accumulation of *Anabaena lemmermannii* at the downwind shore observed in Grimnitzsee (Fig. 9) was very likely due to advective patchiness (*sensu* REYNOLDS 1984: 108) of this buoyant organism. Nevertheless the stations nearest to the routine sampling station (3 and 9 in Fig. 9c) gave a representative picture of phytoplankton species composition as well as phytoplankton biomass (Fig. 9a, b). Even in the much larger Lake Constance, EHINGER (1994) was not able to detect systematic horizontal heterogeneity in the pelagic zone and concluded that results originating from one sampling point are representative for the whole lake. Considering the relatively small basin dimensions, the regular basin morphology and the minor importance of inflowing waters, it is unlikely that systematic horizontal heterogeneity will occur in the pelagic zone of Grimnitzsee. Therefore, the results of the central sampling station were generalized, bearing in mind that the situation near the different lake shores might have been somewhat different dependent on velocity and direction of the wind.

5.2 Light climate

The annual means of the vertical attenuation coefficient (k_d) in Grimnitzsee (0.8 and 1 m^{-1}) are typical values of eutrophic lakes *sensu* KLAPPER (1992). Whereas in deep and stratified lakes a high correlation between k_d(PAR) and chlorophyll *a* concentration and between particulate dry weight and chl *a* concentration was observed (SCHANZ 1985; TILZER & BEESE 1988) the correlation of these variables was less pronounced in Grimnitzsee. This was probably due to abiotic particulate material being dispersed in the water column due to wind action in that shallow lake. The maximum light transmission in Grimnitzsee between 565 and 585 nm indicates that its gilvin (*sensu* KIRK 1994) status is moderate (WATRAS & BAKER 1988), i.e. Grimnitzsee is not strongly coloured by humic substances. Compared with other eutrophic lakes in Brandenburg which have DOC concentrations between 5.5 and 14.9 mg DOC l^{-1} (means of the vegetation period in 1994, NIXDORF et al. 1995), the DOC content in Grimnitzsee (annual means: 10.3 and 10.0 mg l^{-1}, Fig. 7 j) was fairly high. This suggests that besides suspended non-photosynthetic particles, dissolved humic substances were responsible for the high background attenuation of PAR in Grimnitzsee.

The ratio of z_{eu}/z_{mix} was >1 only in periods of distinct thermal stratification (July 1994, June 1995; Figs 4a and 5b). Especially in summer, the ratio often was <1 so that algae circulating in the well-mixed water column encountered pronounced light/dark fluctuations.

5.3 Water chemistry and trophic state

Grimnitzsee is a calcareous hard-water lake which is well buffered around pH 8 due to the bicarbonate buffering system. Compared to other lakes of eastern Brandenburg its specific conductivity is rather high (VIETINGHOFF 1995) probably reflecting the former input of sewage.

The silicon status of the lake was strongly influenced by the incorporation of silicon by diatoms and their subsequent sedimentation in 1995 (Figs 7c, g and 8a). In general, the particulate silicon of settled diatoms is recycled to dissolved silicon in the hypolimnion or in the sediment (SOMMER 1988). In stratified lakes, the concentration of dissolved Si in the euphotic zone only gradually rises after the spring diatom maximum as mixing depth increases in the course of the year (LAMPERT & SOMMER 1997: 306). Unlike this, in Grimnitzsee silicon concentration had recovered within 3 months after its spring minimum. The higher temperature at the sediment surface of shallow lakes (FRIEDRICH 1982) and the polymictic properties of Grimnitzsee were the obvious reasons.

According to the fixed boundary system of the OECD (1982) all parameters (TP, chl *a* and Secchi depth) clearly characterize Grimnitzsee as an eutrophic lake. Applying the OECD (1982) open boundary system, all relevant parameters (TP, TN, chl *a*, Secchi depth) were within 1 standard deviation of the corresponding group means of the eutrophic category. The lakes in Brandenburg were classified by the water authorities with the help of the system TGL 27885/01 (KLAPPER 1992). According to this index which defines 5 different trophic states (oligo-, meso-, eu-, poly- and hypertrophic), the status of Grimnitzsee was between eutrophic (oxygen conditions, light climate, TP in 1994, phytoplankton biomass in 1994) and mesotrophic (SRP, DIN, TP in 1995, phytoplankton biomass in 1995). Recently a new classification system of the trophic state of Brandenburg's lakes has been proposed (MIETZ 1996 a) and expanded to German lakes of glacial origin (MIETZ 1996 b). This empirical system distinguishes 4 lake types differing in area and mixing conditions and is based on the mean summer chlorophyll *a* concentration, the TP concentration in spring and summer and the Secchi depth in summer (MIETZ 1996 b). The different trophic states characterized by this classification are named analogous to the classification by KLAPPER (1992, see above). According to MIETZ (1996 b), the trophic index of Grimnitzsee was 2.7 in 1994 and 2.2 in 1995 which characterizes the lake as being eutrophic (index 2–3).

In general in 1992–1994, 50% of the lakes in Brandenburg were eutrophic, whereas 37% were polytrophic and just 10% were mesotrophic [classification by WÖBBECKE (1996) who used the system of KLAPPER (1992)]. There are only very few shallow, polymictic lakes in the region of Berlin and Brandenburg which are as large as Grimnitzsee. Comparison with those lakes reveals that Grimnitzsee has a significantly higher retention time and also the lowest trophic state (Großer Müggelsee: DRIESCHER et al. 1993; Wolziger See: NIXDORF et al. 1995, VIETINGHOFF 1995; Breitlingsee: ROHDE 1995; Gülper See: KALBE 1993, KNÖSCHE 1995; Schwielowsee: KALBE 1993, MIETZ & VIETINGHOFF 1994; Großer Schwielochsee: RIPL et al. 1995).

5.4 Plankton

In contrast to many other shallow lakes of Brandenburg characterized by a higher trophic state (ARP & RIEMER 1996; RÜCKER et al. 1997), the phytoplankton of Grimnitzsee was not dominated by filamentous cyanobacteria of the Oscillatoriales. In the sense of SCHEFFER et al. (1997), the TP level of Grimnitzsee was probably too low to enable the dominance of these onerous planktonic algae.

In stratified lakes, the importance of physical factors for the interactions within the plankton is greatest in autumn and winter (SOMMER et al. 1986). The larger influence of physical factors (especially weather-mediated frequent mixing of the water column) in polymictic lakes like Grimnitzsee makes it even more difficult to predict plankton dynamics. The most obvious features of the phytoplankton in Grimnitzsee were the great differences in species composition between 1994 and 1995, especially the irregular appearance of diatoms and the short bloom of *Aphanizomenon flos-aquae* in summer 1994.

5.4.1 Winter/spring situation

In February 1995, small centric diatoms were favoured by high silicon concentration and were able to build up a huge population (Fig. 8a) as ice break was early and herbivorous zooplankton was scarce (Fig. 8c–g). After the later ice break in 1994, diatoms were not able to compete as little silicon was available (Fig. 7g). Instead, the biomass of phytoflagellates increased (Fig. 8a) that had solely been able to cope with the three weeks of stratification under the ice. In both years, the biomass of the spring populations reached a minimum in May as the abundance of herbivorous *Daphnia* spp. increased (Fig. 8a, d). Silicon limitation of biomass was an important reason for the decline of diatoms in spring 1995 (Fig. 7g). Although *Daphnia* abundance was maximal in May/June grazing was not strong enough to cause a distinct clear water phase (Fig. 5 and Fig. 8d).

5.4.2 Summer situation

Although the summer stratification of Grimnitzsee was much shorter than in dimictic lakes, typical summer species (*sensu* SOMMER et al. 1986 and REYNOLDS 1996) dominated (*Aphanizomenon flos-aquae* in 1994; *Peridinium* spp. and *Pandorina smithii* in 1995). The competitive advantage of the cyanobacterium *A. flos-aquae* in summer 1994 was probably its ability to fix atmospheric nitrogen, as the C/N ratio of the phytoplankton indicated quite strong N limitation in July 1994 (Fig. 8m). In July 1994, the highest input of global radiation in all months of the period from 1975 to 1995 was observed (Berliner Wetterkarte 1975–1995). This resulted in an extraordinary high water temperature (Fig. 4a) which might have improved the growth conditions of *A. flos-aquae* even more.

Just in the sense of the PEG-model of plankton succession (SOMMER et al. 1986) the large species of *Daphnia* were replaced by small cladocerans (*Chydorus sphaericus* in 1994, *Bosmina longirostris* in 1995) in summer. These smaller species are generally better able to take up food in the presence of large inedible algae (that were abundant in Grimnitzsee in summer) than larger species (SOMMER et al. 1986).

Higher abundance of rotifers was only observed when *Daphnia* spp. were rare (Fig. 8c, d) which is a general phenomenon due to competition between these groups (LAMPERT & ROTHHAUPT 1991; FUSSMANN 1996). In summer 1994, the abundance of smaller cladocerans was much lower than in summer 1995 (Fig. 8e) which might have enabled rotifers to build up high numbers in late summer 1994 (Fig. 8c).

The fact that cyanobacterial autotrophic picoplankton comprised 16% of the total phytoplankton biomass on average (and more than 30% on single days) in summer 1995 is quite unusual as eutrophic lakes generally tend to have lower contributions of APP (SØNDERGAARD 1991; STOCKNER 1991). These results suggest that it is necessary to consider this group of organisms in future studies of similar lakes.

5.4.3 Autumn situation

In autumn 1995, large inedible diatoms *(Aulacoseira ambigua)* grew due to favourable mixing, light and Si conditions (Fig. 4, 5, 7g, 8a). In October 1995 a 10 day period of low wind speed (GERVAIS, unpublished observations) caused thermal stratification of the lake (Fig. 4). Diatoms almost vanished (Fig. 8a), very likely due to sedimentation. When the water column was mixed again at the end of October (Fig. 4) the same diatom species dominated again until the breakdown of its population probably due to silicon limitation of biomass (Fig. 7g and 8a). It is very likely that *A. ambigua* survived the period of stratification at the sediment surface and was resuspended when mixing started as TSI but not DSi concentration increased at the same time as the diatom biomass at the end of October (Fig. 7c, g). Resting cells of *Aulacoseira granulata* (EHRENBERG) RALFS have been shown to be able to survive even in anoxic sediments for very long periods (SICKO-GOAD et al. 1986). DAVEY (1987) argued that the succession of sedimentation and resuspension is part of the survival strategy of *Aulacoseira granulata.*

In late summer and autumn 1994, diatoms were not able to outcompete the other algal groups (Fig. 8a) despite a relatively high level of DSi concentration (Fig. 7g). Under the condition of a very unfavourable light climate ($z_{eu}/z_{mix} < 0.5$, Fig. 5b) cryptophytes were more successful. In contrast to autumn 1995 when inedible diatoms prevailed, the high cryptophyte biomass supported an abundance maximum of *Daphnia* spp. and *Eubosmina coregoni thersites* (Fig. 8a, d, e).

5.5 Littoral diatoms

The TP concentration derived from the littoral diatom assemblage indicated a eutrophic state of Grimnitzsee sensu MIETZ (1996 b). The actual TP concentration in the lake at the time the diatom samples were taken (April 1995) was lower than the concentration range that was maximally represented by the littoral diatoms (Fig. 7c and 9). Assuming a slow rate of species succession in winter, the diatom assemblage (which also included dead cells) was probably more representative of the conditions at the end of 1994 when higher TP concentrations prevailed (Fig. 7c).

5.6 Eutrophication of Grimnitzsee

Only a few reports exist on the trophic state of Grimnitzsee in the course of this century. While submerged vegetation (esp. Charophytes) inhabited the lake with great biomass before 1930 (SCHIEMENZ 1932), the submerged plants declined in 1930–1932 (SCHIEMENZ 1932) but were still present in small amounts in 1938 (PANKNIN 1941). In 1970–1973 submerged macrophytes were no longer observed (BARTHELMES 1974). In 1938, the phytoplankton of Grimnitzsee was dominated by *Asterionella formosa* in spring and winter and by *Microcystis aeruginosa* in summer; a conspicuous bloom of *Aphanizomenon flos-aquae* was observed in July and August (PANKNIN 1941). Secchi depth ranged from 15 cm (during a *Microcystis* bloom) to 2 m in 1938 (PANKNIN 1941). PANKNIN (1941) measured chloride and sulphate concentrations around 22 and 30 mg l^{-1}, respectively. These values indicate that a considerable increase in the concentration of these ions occurred from 1938 to 1994/1995. Between 1949 and 1973 Secchi depth was measured in Grimnitzsee on 22 days (SCHARF 1969, 1971; BARTHELMES 1974). In that period, Secchi depths larger than 2 m were only observed in winter or spring. In summer 1968, there was an extended period of extraordinary low (0.5–0.8 m) Secchi depths (SCHARF 1969). The lake was assessed to be polytrophic in 1981/82 by SUCCOW & KOPP (1985).

Other shallow lakes in Brandenburg showed comparable changes of their trophic state leading to the decline of submerged macrophytes (Galenbecker See: KALBE 1984; Wolziger See, Gülper See: KALBE 1993). Grimnitzsee is one of the lakes of the biosphere reserve "Schorfheide-Chorin" that experienced the highest anthropogenic influence (MAUERSBERGER & MAUERSBERGER 1996). Its eu- or polytrophication was caused by sewage input and runoff from agricultural areas and also by very intense fish farming and temporary duck farming (SCHARF 1969; ANWAND 1971; BARTHELMES 1974, 1994, MAUERSBERGER & MAUERSBERGER 1996). At the beginning of the 1990s, fishing intensity in Grimnitzsee was reduced (MAUERSBERGER & MAUERSBERGER 1996). A sewage treatment plant with phosphorus removal that drains into Grimnitzsee (about 300 m^3 per day in 1995, pers. comm. of the Zweckverband für Wasserversorgung und Abwasserentsorgung Eberswalde) has been in operation since 1994/1995. Observations from 1991–1994 showed that the lake has been recolonized by submerged macrophytes (MAUERSBERGER & MAUERSBERGER 1996). A comparison of the results of the present study with the summer values of Secchi depth, TP, NH_4^+-N and chl *a* observed in Grimnitzsee by VIETINGHOFF (1995) in 1993 indicate that the trophic state of the lake was higher in 1993 than in 1994. As the trophic index again declined from 1994 to 1995 future studies should investigate whether this is a trend or just a sign of interannual variability. Due to its comparatively low degree of eutrophication and its favourable location within a biosphere reserve, Grimnitzsee will very likely be one of the first of the larger shallow lakes in Brandenburg in which a continuous recolonization by macrophytes will take place provided that the efforts toward the reduction of nutrient inputs are continued. Future studies should document the process of recovery of submerged vegetation and analyse its significance for the functioning of medium shallow lakes like Grimnitzsee.

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