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Do phytoplankton communities correctly track trophic changes? An assessment using directly measured and palaeolimnological data

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SUMMARY

1. Measurements of total phosphorus (TP) concentrations since 1975 and a 50-year time series of phytoplankton biovolume and species composition from Lake Mondsee (Austria) were combined with palaeolimnological information on diatom composition and reconstructed TP-levels to describe the response of phytoplankton communities to changing nutrient conditions.
2. Four phases were identified in the long-term record. Phase I was the pre-eutrophication period characterised by TP-levels of about 6 $\mu g\ L^{-1}$ and diatom dominance. Phase II began in 1966 with an increase in TP concentration followed by the invasion of *Planktothrix rubescens* in 1968, characterising mesotrophic conditions. Phase III, from 1976 to 1979, had the highest annual mean TP concentrations (up to 36 $\mu g\ L^{-1}$) and phytoplankton biovolumes (3.57 $mm^3\ L^{-1}$), although reductions in external nutrient loading started in 1974. Phases II and III saw an expansion of species characteristic of higher nutrient levels as reflected in the diatom stratigraphy. Oligotrophication (phase IV) began in 1980 when annual average TP concentration, Secchi depth and algal biovolume began to decline, accompanied by increasing concentrations of soluble reactive silica.
3. The period from 1981 to 1986 was characterised by asynchronous trends. Annual mean and maximum total phytoplankton biovolume initially continued to increase after TP concentration began to decline. Reductions in phytoplankton biovolume were delayed by about 5 years. Several phytoplankton species differed in the timing of their responses to changing nutrient conditions. For example, while *P. rubescens* declined concomitantly with the decline in TP concentration, other species indicative of higher phosphorus concentrations, such as *Tabellaria flocculosa* var. *asterionelloides*, tended to increase further.
4. These data therefore do not support the hypotheses that a reduction in TP concentration is accompanied by (i) an immediate decline in total phytoplankton biovolume and (ii) persistence of the species composition characterising the phytoplankton community before nutrient reduction.

Keywords: long-term trends, oligotrophication, peri-alpine lake, phosphorus, recovery, trophic state

Introduction

Eutrophication of freshwater ecosystems is accompanied by unidirectional changes in diversity and abundance of the phytoplankton, ultimately leading to the dominance of a single species, usually of cyanobacteria (Dokulil & Teubner, 2000). Each level along the continuum from oligotrophic to hypereutrophic conditions can be characterised by the succession and composition of the algal communities (Reynolds *et al.*, 2002), an observation that has been expanded towards a classification of freshwater phytoplankton using functional groups (Kruk

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et al., 2002; Reynolds *et al.*, 2002). Phytoplankton responses to the reverse process, oligotrophication, is often considerably delayed (Sas, 1989). While parameters such as phosphorus concentration and Secchi depth closely track external or internal restoration measures, backward shifts in taxonomic composition tend to lag behind. Composition and succession of communities, therefore, often do not adequately reflect the chemically determined nutrient status of a waterbody during oligotrophication. This hysteresis in community behaviour is not well understood.

Long-term direct observations of phytoplankton from a peri-alpine lake were combined with palaeolimnological data to provide information on an otherwise poorly represented but important period. By doing so, we sought to improve our understanding of the changes in phytoplankton community structure taking place during eutrophication and oligotrophication. Our hypothesis was that a reduction in total phosphorus (TP) concentration is accompanied by a decline in total phytoplankton biovolume, whereas composition of the phytoplankton community remains unchanged for several years.

Methods

Site description

The study lake, Mondsee, is a deep peri-alpine lake (surface area 14.2 km^2, maximum depth 68.3 m, average theoretical retention time 1.7 years) located in Austria's lake district east of the city of Salzburg. Like many other lakes in the world, Mondsee underwent cultural eutrophication in the 1970s but nutrient loading has considerably decreased since sewage treatment began in 1974. After oligotrophication, the lake's trophic state can now be classified as oligo-mesotrophic. More detailed information on Mondsee and similar lakes in the region can be obtained from Livingstone & Dokulil (2001) and Dokulil & Teubner (2002).

Sampling

Phytoplankton has been regularly monitored since 1978. Data prior to 1978 were extracted from Findenegg (1965, 1969), Müller-Jantsch (1977, 1979), Oberrosler (1979) and Schwarz (1979, 1981). The sampling interval ranged from weekly to monthly, but was biweekly most of the time. Sampling depths varied somewhat over the years. An integrated sample from the top 20 m was taken on all occasions since autumn 1981 (Züllig Co.; Schröder, 1969). Samples for phytoplankton enumeration were preserved in brown 100-mL glass bottles with 200 μL Lugol's solution added and stored in the dark at 4 °C until analysis.

Cell numbers were estimated with an inverted microscope using the sedimentation technique developed by Utermöhl (1958) and a computerised counter (Hamilton, 1990). Cell dimensions were measured with an image analysis system (Lucia, V 3.1, Prague) and cell volumes calculated using simple geometric approximations (Rott, 1981). Species abundance was then converted to biovolume.

Water transparency was estimated on each sampling occasion with a white Secchi disc (Ø 25 cm). Depth-integrated water samples or samples from discrete depths were analysed for TP and soluble reactive silica (SRSi) following standard analytical techniques (Greenberg, Clesceri & Eaton, 1992).

Palaeolimnological data

Diatom-inferred TP data (DI-TP) and sediment-derived diatom species abundance were taken from Klee & Schmidt (1987); Schmidt (1991), and Bennion, Wunsam & Schmidt (1995).

Data analysis

In the present study, results from integrated samples (0–20 m) are reported. When only data from discrete depths were available, mean phytoplankton biovolume for the 0–20 m zone was calculated from the profile by depth-weighted averaging. Monthly data were calculated from weekly or biweekly data, then annual averages from monthly data. The cumulative sums method was used to display the long-term trend of annual averages as described in Ibanez, Fromentin & Castel (1993) and Fromentin & Ibanez (1994). We added cumulatively the successive residuals calculated from the differences between annual values and the mean of the series from 1978 to 2001. Whenever conversion from chlorophyll *a* (Chl *a*) concentrations to biovolume was necessary, a phytoplankton Chl *a* content of 0.5% fresh mass was assumed. TP concentration was inferred from *Planktothrix* biovolume (PB) using the regression equation PB = 1.54 TP + 12.8 ($r^2 = 0.42$, $n = 638$; K. Teubner, unpublished data).

Results

Four developmental stages of the lake are reflected in the time series of directly measured or phytoplankton-inferred TP concentrations and Secchi depth (periods I–IV in Fig. 1). Diatom-inferred TP concentrations from sediment cores (Bennion *et al.*, 1995) show little change prior to 1965, with values around 6 µg L^{-1}. Values then increased markedly to 28 µg L^{-1} in 1968 (Fig. 1, period I). The stage of pre-eutrophication in the lake can also be identified from Secchi-disc readings (Fig. 2). Prior to 1969 Secchi depth values were only available for summer. The pre-eutrophication values of about 4 m in summer were higher than summer values during periods II and III. The lowest annual average transparency of 3 m recorded in 1968 coincided with the inferred TP concentration peak in Fig. 1 and the first appearance of *Planktothrix rubescens* (DC ex. Gom) Anagn. et Kom. (Findenegg, 1969). This early eutrophication period was followed by a period of moderate and stable Secchi depths during the eutrophic phase lasting until 1975; TP concentrations reconstructed from diatoms were moderate during this time (period II in Figs 1 & 2). The third period began in 1976 with an increase in mean annual Secchi depth because of the start of tertiary sewage treatment. It lasted until 1980 when Secchi depth further increased (Fig. 2). In this period, however, TP concentrations reconstructed from diatom communities dropped to approximately 10 µg L^{-1}, although direct chemical measurements indicated P concentrations well above 20 µg L^{-1} (Fig. 1). TP values inferred from *P. rubescens* (PI-TP) ranged from 13 to 17 µg L^{-1}, and also failed to match the results from chemical measurements of P concentrations (Fig. 1). Period IV was characterised by a substantial drop in TP concentrations from 34.9 to 24.5 µg L^{-1} between 1979 and 1980 and a further decline afterwards to 7.6 µg L^{-1} (Fig. 1), concomitant with a pronounced increase in water transparency (Fig. 2). The years from 1980 until 1997 were characterised by annual mean Secchi depths >6 m and summer values around 5 m. Starting in 1998, Secchi depth decreased again.

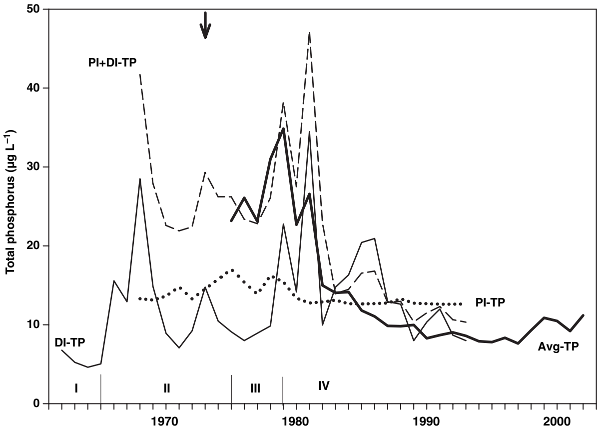

Fig. 1 Time-series of total phosphorus (TP) concentrations in Mondsee from 1962 to 2002. Avg-TP, Annual average epilimnetic TP concentration; DI-TP, Diatom-inferred TP concentration reconstructed from sediment cores according to Bennion *et al.* (1995); PI-TP, TP concentration approximated from *Planktothrix*; PI + DI-TP, TP concentration calculated from combined diatom- and *Planktothrix*-derived data. The four periods discussed in the text are indicated as I–IV. The arrow indicates the year 1974 when tertiary sewage treatment started.

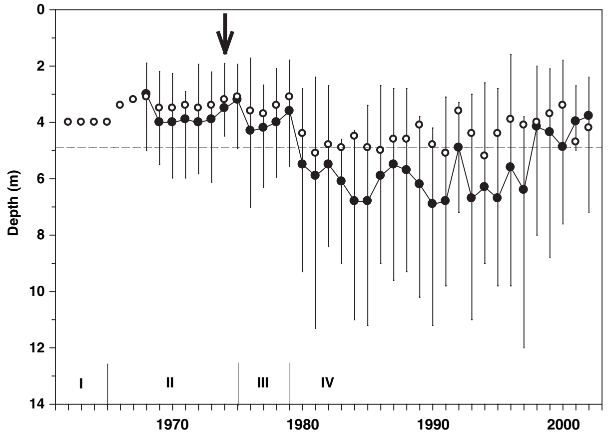

Fig. 2 Secchi-disc readings in Mondsee from 1962 to 2002. Open symbols show average summer values for June to September. Filled symbols refer to annual averages, with ranges depicted as vertical bars. The dashed horizontal line indicates the annual average for the period 1968–2002. The four periods discussed in the text are indicated as I–IV. The arrow indicates the start of tertiary sewage treatment in 1974.

The 50-year time series of total phytoplankton biovolume (Fig. 3) ran largely parallel with the data shown in Figs 1 & 2. Average pre-eutrophication values ranged from 0.17 to 0.52 mm^3 L^{-1} between 1958 and 1966. Mean phytoplankton biovolume markedly increased to 0.88 mm^3 L^{-1} in 1968 when the filamentous blue-green species *P. rubescens* invaded the lake. Average values tended to increase, thereafter

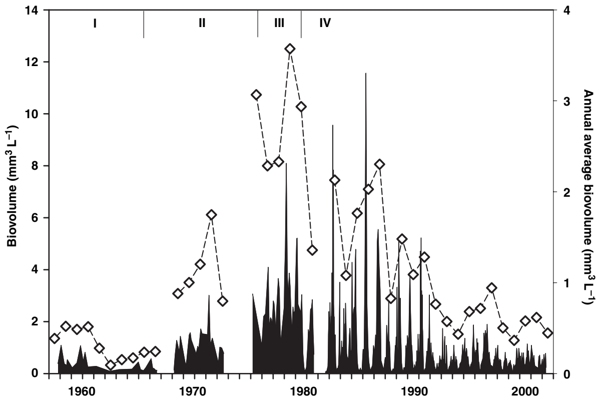

Fig. 3 Dynamics of phytoplankton biovolumes from 1958 to 2001 (black bars) and annual average biovolumes (diamonds) for the same period, both averaged over 0–20 m. The four periods discussed in the text are indicated as I–IV. Tertiary sewage treatment started in 1974.

reaching 3.57 mm^3 L^{-1} in 1978. Between 1968 and 1978 biovolumes were high for most of the year because of the large amounts of *P. rubescens* present with little seasonality and peaks occurring during summer and early fall (Fig. 3). Annual average total phytoplankton biovolume declined steadily from 1978 with occasional periods of increasing values (e.g. 1983–86). Maximum biovolume during summer rapidly declined from almost 12 mm^3 L^{-1} in 1985 to 0.8 mm^3 L^{-1} in 2001.

The trends of TP concentration and phytoplankton biovolume during the oligotrophication phase (period IV in Figs 1, 2 & 4) are displayed as the cumulative mean deviation from the long-term average 1978 to 2001 (Fig. 4). The gradual increase of the residuals of the TP concentration illustrates the trend of increasing P from 1978 to 1981 (Fig. 4). The decreasing residuals from 1981 onwards show a gradual decline of TP concentration from year to year. The period of increasing biovolume of phytoplankton is indicated by a positive slope from 1978 to 1986, followed by a decrease. The period from 1981 to 1986 is therefore identified by asynchronous trends: a continued increase of phytoplankton biovolume although TP concentration had already started decreasing. Hence, the response of phytoplankton biovolume to reduced TP was delayed by 5 years.

During the oligotrophication phase, average biovolume declined from 3.57 mm^3 L^{-1} in 1978 to 0.37 mm^3 L^{-1} in 1999 (Fig. 3), concomitant with decreasing epilimnetic TP concentrations ($n = 24$, $r^2 = 0.52$, $P < 0.001$) and increasing annual average concentrations of SRSi (Fig. 5; $n = 20$, $r^2 = 0.46$, $P \leq 0.001$).

The changes from the oligotrophic phase prior to 1968, through the period of increased nutrient loading and finally the recovery during oligotrophication are clearly reflected in the composition of phytoplankton communities (Fig. 6). Dominated by small centric diatoms during the 1950 and 1960s, the phytoplankton community became strongly dominated by *P. rubescens* in 1968 for about 10 years. During this period, diatoms were subdominant and their species composition changed (Fig. 6). In the course of oligotrophication, the dominant algal groups shifted from cyanobacteria to dinoflagellates and later back to

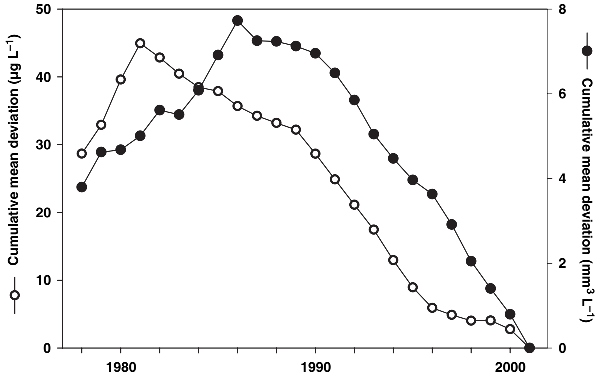

Fig. 4 Cumulative mean deviations (residuals) from the long-term annual average TP concentration (open circles) and phytoplankton biovolume (solid circles) for 1978–2001.

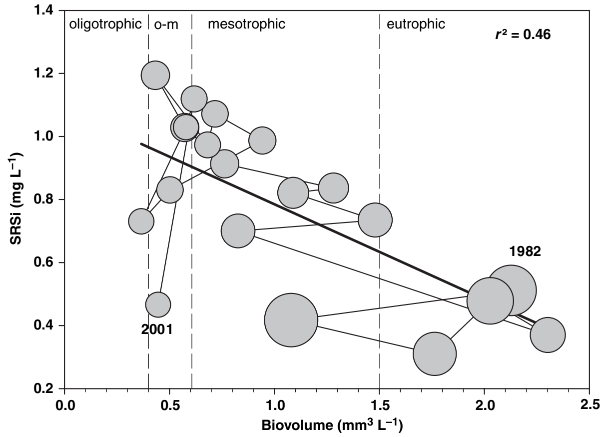

Fig. 5 Phytoplankton biovolume versus soluble reactive silica (SRSi) concentration for 1982 to 2001. Diameters of the symbols are proportional to TP concentrations.

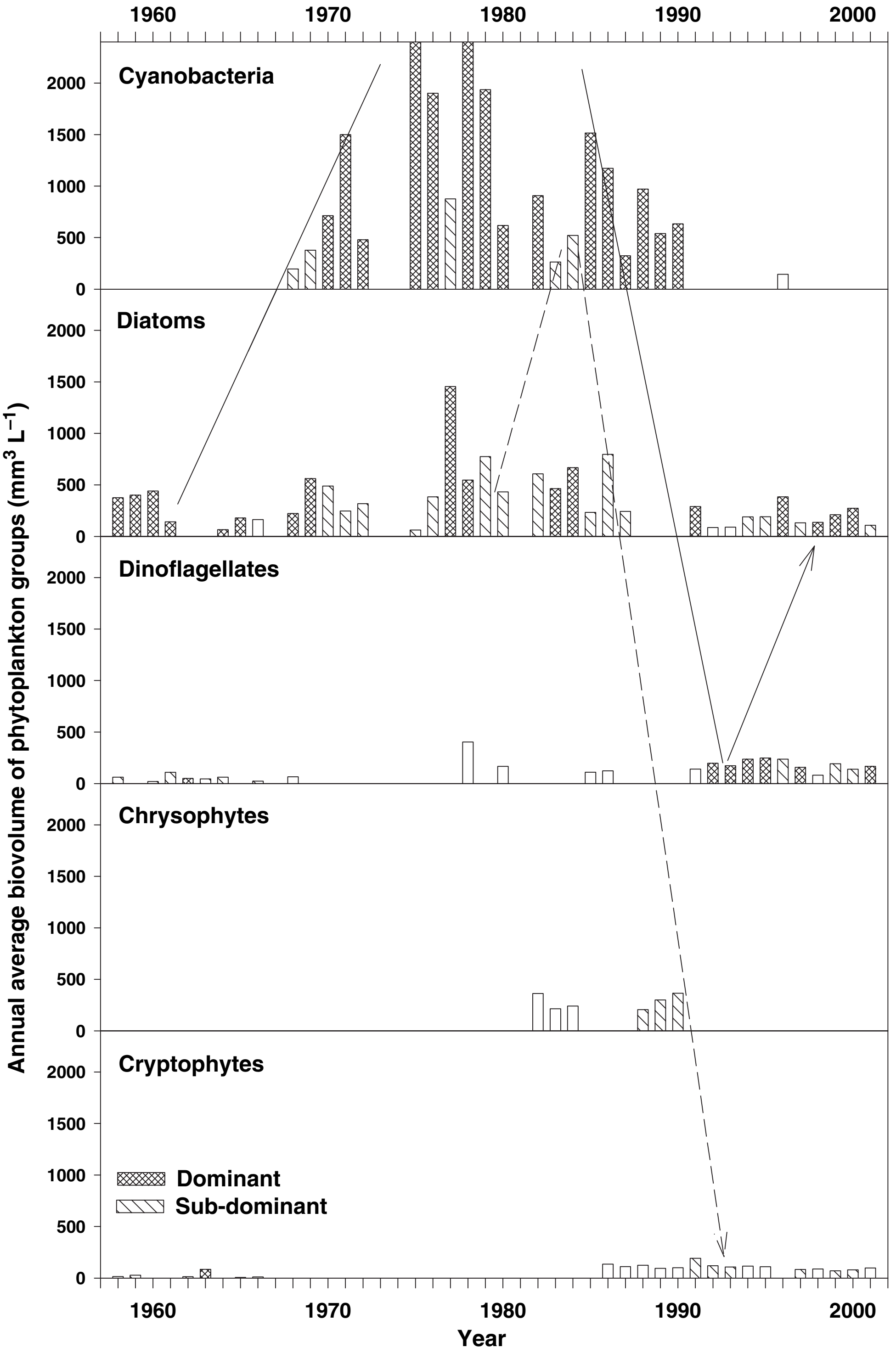

Fig. 6 Dynamics of phytoplankton groups from 1958 to 2001 given as annual average biovolume for each year and group. Dominant, subdominant and other groups are indicated by different hatching. The changes in the dominance pattern from diatoms in the 1960s, cyanobacteria in the 1970s, to dinoflagellates in the early 1990s and back to diatoms in the late 1990s is depicted by a solid line. Similarly, the dashed line indicated the subdominant groups.

diatoms. Similarly, subdominant algal groups followed the sequence from cyanobacteria in 1983/84, through diatoms (1985–87), chrysophytes (1988–90), cryptophytes (1991–93) to dinoflagellates during later years.

The long-term changes of the five dominant algal taxa differed in their timing of increases and declines (Fig. 7). *Planktothrix rubescens* decreased concomitantly with the decline of TP concentration after 1980, as indicated by a decrease of the cumulative annual mean deviations. In contrast, the biovolume of the dominant diatom *Tabellaria flocculosa* var. *asterionelloides* Grunow and the chrysophyte *Dinobryon sociale* Ehrenb. increased significantly until 1987 and 1990, respectively, but declined afterwards as well. The dinoflagellate *Gymnodinium helveticum* Pernard and the cryptophyte *Cryptomonas pusilla* Bachm. decreased during the first phase of oligotrophication until 1985 and 1990, respectively, but recovered in recent years as indicated by the gradual increase in Fig. 7. These examples illustrate that the long-term dynamics of individual species' abundance differed and were not necessarily in phase with the onset of nutrient reduction.

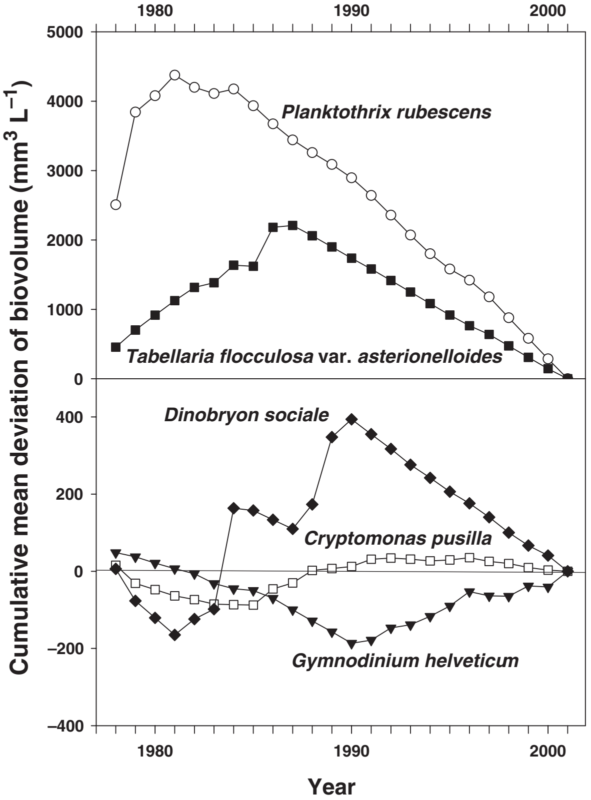

Fig. 7 Cumulative annual mean deviations (residuals) for dominant species of cyanobacteria (*Planktothrix rubescens*), diatoms (*Tabellaria flocculosa* var. *asterionelloides*), dinoflagellates (*Gymnodinium helveticum*), chrysophycean (*Dinobryon sociale*) and cryptophyceans (*Cryptomonas pusilla*).

As exemplified by the five dominant algal taxa shown in Fig. 7, the succession of individual species responded to P reduction in a non-synchronous pattern during the course of lake oligotrophication. The early oligotrophic phase was characterised by dominance of centric diatoms as evidenced from records in Findenegg (1959). Diatom remains from sediment cores indicate dominance by the centric diatoms *Stephanodiscus alpinus* Hustedt and *Cyclotella bodanica* Grunow in Schneider prior to 1950 (Schmidt, 1991). While *C. bodanica* disappeared with increasing nutrient concentrations and did not re-appear during oligotrophication, *S. alpinus* (Kütz.) Cleve et Möller has been gradually replaced by *Stephanodiscus neoastraea* Håkanson et Hickel at reduced P concentrations. The *Cyclotella comensis* Grunow group, together with *C. distinguenda* var. *unipunctata* Hustedt and *Fragilaria crotonensis* Kitton, was most abundant in the early 1960s as evidenced from the sediment record. Subdominant taxa include dinoflagellates such as *Ceratium hirundinella* (O.F. Müller) Dujardin during summer and a variety of cryptophycean species (Findenegg, 1959; Fig. 6).

Before and during eutrophication, *Cyclotella* taxa declined while expansion of other diatom species such as *T. flocculosa* var. *asterionelloides*, *Stephanodiscus parvus* Stoermer et Håkanson and *Aulacoseira subarctica* (O. Müller) Haworth indicated more nutrient-rich conditions (Bennion *et al.*, 1995). *Tabellaria flocculosa* var. *asterionelloides* maintained a high abundance throughout the *Planktothrix* phase and began to decline in the early 1990s (Dokulil & Kofler, 1995). The sudden expansion of *P. rubescens* in 1968 completely dominated the phytoplankton community for about a decade. These long-term developments are schematically summarised in Fig. 8.

With the onset of oligotrophication in the mid-1980s phytoplankton biovolume began to decline, leading to more pronounced peaks, greater seasonality and shifts in species composition. Species from the *Microcystis* complex and *Gomphosphaeria* began to replace much of the cyanobacterial biovolume formerly contributed by *Planktothrix*. Chrysophyte species, mainly *D. sociale* and *D. divergens* Imhof, and a variety of

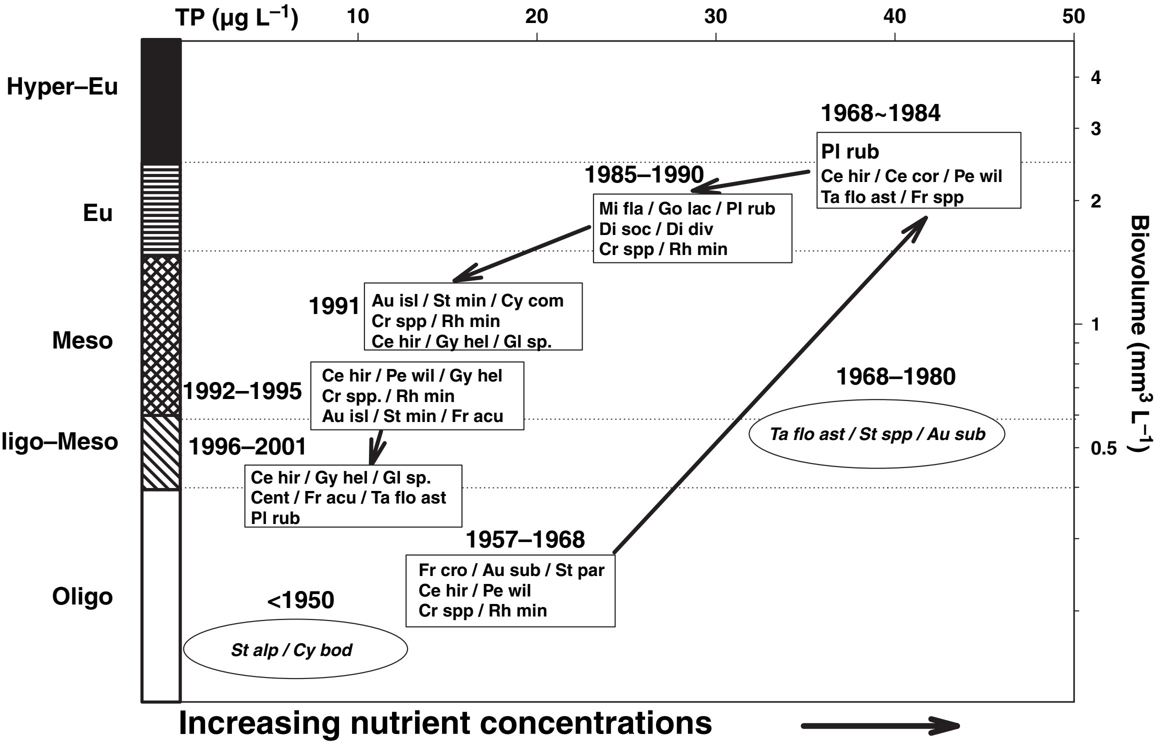

Fig. 8 Schematic diagram of long-term changes in phytoplankton species composition in Mondsee projected into the TP-biovolume space, based on directly measured (squares) and palaeolimnological (ellipses) data. Mi fla, *Microcystis flos-aquae* Kütz.; Go lac, *Gomphosphaeria lacustris* Chod.; Pl rub, *Planktothrix rubescens*; St alp, *Stephanodiscus alpinus*; St par, *S parvus*; St spp., different *Stephanodiscus* species; St min, *S minutulus*; Cy bod, *Cyclotella bodanica*; Cy com, *C. comta*; Cent, different centric diatoms; Au sub, *Aulacoseira subarctica*; Au isl, *A. islandica*; Fr cro, *Fragilaria crotonensis*; Fr acu, *F. acus*; Fr spp., species of *Fragilaria*. Ta flo ast, *Tabellaria flocculosa* var. *asterionelloides*; Cr spp., different *Cryptomonas* species; Rh min, *Rhodomonas minuta* Skjua; Ce hir, *Ceratium hirundinella*; Ce cor, *C. cornutum*; Pe wil, *Peridinium willei* Huitfeld-Kass.

cryptophyte species became more prominent (Fig. 8). Within the diatoms, *Aulacoseira subarctica* (Müller) Haworth was replaced by *A. islandica* (Müller) Simonsen during the 1980s and a number of small centric diatoms appeared (Dokulil, 1993). Finally dinoflagellates became dominant in the summer phytoplankton community while diatoms prevail in spring and fall.

Discussion

The P concentrations in the lake prior to 1975, when direct chemical measurements started, could only be indirectly inferred from diatom-transfer functions (Bennion *et al.*, 1995). These estimates show good agreement with chemical measurements of P concentrations at the onset of eutrophication (1969) and for the years 1981–93 after sewage treatment started, but they deviate considerably from chemically determined values during the 1975–79 period with high P concentrations. One reason for the discrepancy between chemically measured and diatom-inferred P data for 1975–79 may be the predominance of *P. rubescens* in the plankton throughout these years (Fig. 6), substantiated by profiles of phytoplankton biovolume taken from the lake in 1975–78 (Müller-Jantsch, 1977; Oberrosler, 1979; Schwarz, 1979). Moreover, large amounts of the *Planktothrix*-specific carotenoid oscillaxanthin were found in sediment cores in the layers dated 1969 to 1977 (Schultze, 1985). At low nutrient concentrations this opportunistic species forms metalimnetic layers while it extends its growth into the epilimnion when nutrients are abundant (Zimmermann, 1969; Findenegg, 1973). Diatom-inferred TP concentrations may therefore underestimate real TP values in the water column under such conditions because *Planktothrix* can compete for phosphorus and suppress diatom growth which, in addition, can be limited by SRSi concentrations.

To get a second, independent estimate for TP, an equation was derived from the relationship between *Planktothrix* biomass and TP concentration, allowing calculation of TP concentration from *Planktothrix* biomass (PI-TP). Values derived in this way gave rather constant values over the whole period but were not significantly higher than those inferred from diatoms. The best fit to the chemically determined P concentrations between 1968 and 1982 was obtained when both diatom and *Planktothrix*-inferred estimates were added together (DI + PI-TP in Fig. 1). The rationale underlying this approach is that a substantial fraction of TP is incorporated into *Planktothrix* biomass which develops during spring overturn and subsequently moves downwards into the metalimnion when the lake becomes stratified. As a result of this stripping process, P concentrations to which diatoms are exposed in the euphotic zone are lower than real P concentrations during overturn. Therefore, diatom-inferred TP concentrations derived form training sets of lakes lacking a migrating *Planktothrix* population would underestimate TP-concentrations in the epilimnion of lakes where a metalimnetic *Planktothrix* population is present, the difference being explained by the P locked up in *Planktothrix* biomass. From 1983 onwards, average DI and PI values matched better, possibly because *P. rubescens* retreated into the metalimnion where it survives isolated during the summer (Dokulil, 1987).

As biovolumes declined during oligotrophication, SRSi concentrations increased, substantiating our hypothesis of reversed Si-depletion during oligotrophication. Given that 0.5 mg Si L^{-1} is the threshold concentration for diatoms to become Si-limited (Sas, 1989), the years 1982–86 with annual average concentrations between 0.31 and 0.51 mg L^{-1} were at least seasonally Si-depleted (Fig. 5). The period 1986–99 showed a steady seasonal increase in SRSi concentrations. Following the reappearance of diatoms in 1999, depletion of silica became apparent again in 2001 (Fig. 6).

Although mainly controlled by P concentration, the phytoplankton community showed a high degree of resistance to changing nutrient supply. Compensatory changes in biovolume or species composition of phytoplankton lagged behind reductions in TP and Chl *a* concentration as well as in Secchi depth. As a result, phytoplankton community structure did not adequately track the improvement in water quality (Dokulil & Teubner, 2003). A similar inertia in species replacement to reduced P loading was evident on both an annual and seasonal basis in Lake Constance, a large peri-alpine lake (Gaedke, 1998). Likewise, delayed response to reduced loading was held responsible for deviations in trajectories or unexpected behaviour of phytoplankton in four large lakes in Sweden (Wilander & Persson, 2001).

The decrease in Secchi depth in recent years is possibly a response to changes in climatic conditions enhancing calcite precipitation in summer (Koschel, 1997). The long-term average of 4.9 m closely corresponds to the 5.5 m estimated from early light measurements in August 1934 by Eckel (1935).

The *Planktothrix*-dominated phase in Mondsee was particularly long-lasting and can be interpreted as resistance of the community to changing environmental conditions (Sas, 1989). In fact, *P. rubescens* typically has its maximum in mesotrophic conditions (10–25 TP $\mu g\ L^{-1}$) but is able to develop considerable amounts of biomass even at TP concentrations well below 10 $\mu g\ L^{-1}$, which indicate oligotrophic conditions (Schanz & Thomas, 1981; Konopka, 1982; Teubner *et al*., 2003a,b).

One of the most interesting observations from the long-term phytoplankton data from Mondsee, is the mass occurrence of an evidently mixotrophic genus, *Dinobryon*, in 1989 and 1990 (Dokulil & Skolaut, 1991; Dokulil, 2000). Under P-depleted conditions, ingestion of bacteria can provide an additional P-source for mixotrophic algae (Nygaard & Tobiesen, 1993), as has been demonstrated for *Dinobryon* (Psenner & Sommaruga, 1992; Gaedke, 1998).

Beginning in 1985, cryptophycean species gained importance especially during summer, which is in agreement with observations on Lake Constance (Sommer, Gaedke & Schweizer, 1993). Contrary to observations in Sweden where the proportion of small and intermediate-sized species increased during oligotrophication (Willén, 2001), the dominant species in Mondsee during the mid-1990s were large-sized dinoflagellates. In Lake Constance, cell sizes increased during the spring bloom, but the size distribution during summer and autumn remained constant (Gaedke & Schweizer, 1993).

In contrast to records collated by Willén (2001), there was no increase in evenness of the phytoplankton community in Mondsee although development of strong dominance by single species or bloom formation has decreased dramatically since TP concentrations fell below 10 μg L^{-1} in 1990 (results not shown). Taxon richness, however, has remained relatively stable throughout the investigation period because of species replacement within the community. Reasons for species replacements other than oligotrophication include changing contributions to different functional groups, shifting nutrient requirements, and grazing pressure (Dokulil & Teubner, 2003).

In conclusion, analysing changes in phytoplankton community structure over half a century has yielded valuable information on phytoplankton species dynamics in response to increasing and later decreasing P concentrations in lake water. This analysis benefited from information from sediment archives that provide data on diatom species composition and P reconstruction for an important period which was otherwise poorly represented by directly monitored data. In contrast to our original hypothesis, phytoplankton biovolume did not immediately decline as TP concentration was reduced. Further, although the composition of phytoplankton communities changed, these changes were not in agreement with the trophic level indicated by chemically determined TP concentration during the early phase of oligotrophication.

Acknowledgments

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