Freshwater Biology (2005) **50,** 1594–1604 doi:10.1111/j.1365-2427.2005.01431.x

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

MARTIN T. DOKULIL AND KATRIN TEUBNER
Institute of Limnology, Austrian Academy of Sciences, Mondsee, Mondseestrasse, Austria

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

Correspondence: Martin T. Dokulil, Institute of Limnology, Austrian Academy of Sciences, A-5310 Mondsee, Mondseestrasse 9, Austria.
E-mail: martin.dokulil@oeaw.ac.at

tration 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

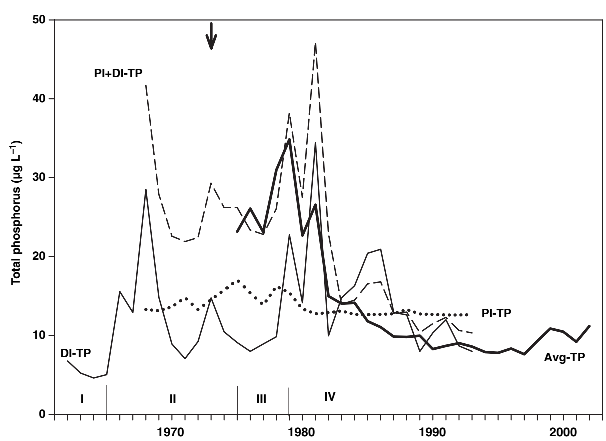

Fig. 1 Time-series of total phosphorus (TP) concentrations in Mondsee from 1962 to 2002. Avg-TP, Annual average epilimnetic TP concentration; DI-TP, Diatom-inferred TP concentration reconstructed from sediment cores according to Bennion *et al.* (1995); PI-TP, TP concentration approximated from *Planktothrix*; 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.

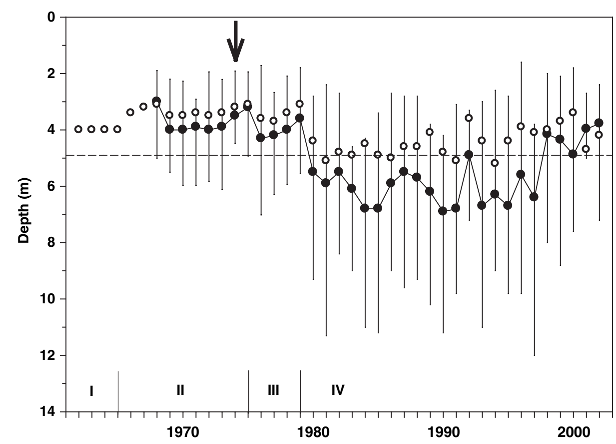

Fig. 2 Secchi-disc readings in Mondsee from 1962 to 2002. Open symbols show average summer values for June to September. Filled symbols refer to annual averages, with ranges depicted as vertical bars. The dashed horizontal line indicates the annual average for the period 1968–2002. The four periods discussed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

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.

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

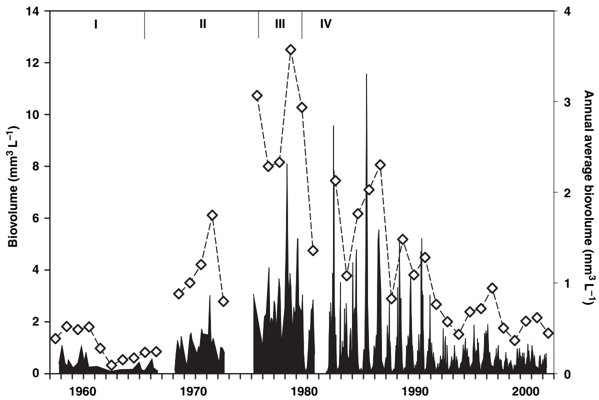

Fig. 3 Dynamics of phytoplankton biovolumes from 1958 to 2001 (black bars) and annual average biovolumes (diamonds) for the same period, both averaged over 0–20 m. The four periods discussed in the text are indicated as I–IV. Tertiary sewage treatment started in 1974.

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

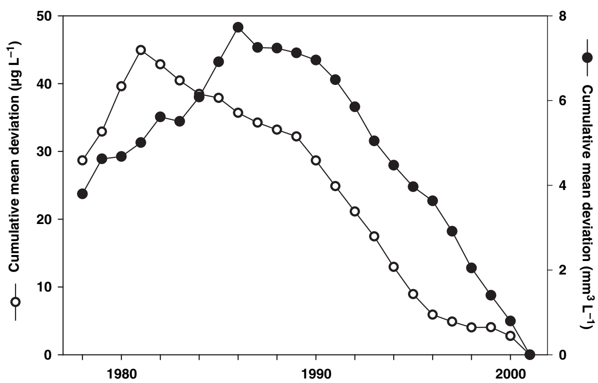

Fig. 4 Cumulative mean deviations (residuals) from the long-term annual average TP concentration (open circles) and phytoplankton biovolume (solid circles) for 1978–2001.

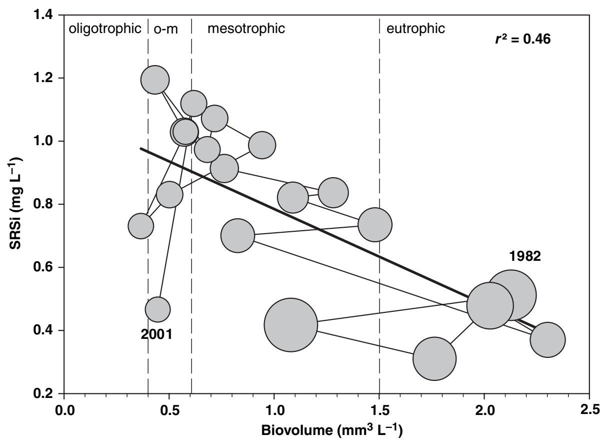

Fig. 5 Phytoplankton biovolume versus soluble reactive silica (SRSi) concentration for 1982 to 2001. Diameters of the symbols are proportional to TP concentrations.