

# Interactions of temperature and nutrient changes: effects on phytoplankton in the Piburger See (Tyrol, Austria)

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## SUMMARY

1. Contemporary limnological and palaeolimnological data from Piburger See (Eastern Alps, Austria) allowed the reconstruction of its trophic state since the late 19th century and the assessment of changes in phytoplankton biomass and species composition in relation to selected environmental parameters.

2. A radiometrically dated sediment core from Piburger See was analysed for geochemical parameters, spheroidal carbonaceous particles (SCPs), bacterial and algal pigments, and diatoms. The low SCP sediment inventory assigns Piburger See to the 'cleaner' sites in Europe with respect to fossil-fuel related air pollution. The sedimentary pigment and diatom record reveals moderate eutrophication during the 20th century, followed by a slow re-oligotrophication since the mid-1980s because of lake restoration starting in 1970.

3. Epilimnetic temperature for Piburger See was reconstructed using air temperature records. A pronounced temperature increase has been recorded during the mid-1940s and since the late-20th century, both promoting algal growth and changes in species composition (e.g. increase in centric diatoms and recent bloom of *Asterionella formosa*).

4. Climate scenarios project additional substantial warming for this mountain lake by the end of the 21st century which will be most pronounced during the growing season. The predicted change in lake water temperature and thermal dynamics represents a key driver for the trophic and ecological status of Piburger See in the future.

*Keywords:* diatoms, eutrophication, mountain lake, sediment, temperature

## Introduction

In the 20th century, many freshwater lakes experienced eutrophication by direct discharge of domestic sewage and by diffuse pollution from changing land use (Schindler, 2006). Fundamental studies and field experiments (e.g. Vollenweider, 1968, 1976; Schindler, 1971, 1977; OECD, 1982; Carpenter *et al.*, 1995) revealed the importance of phosphorus as a key factor limiting primary production in fresh waters, which resulted in improved sewage treatment, point-source control and reduction of phosphorus, and its replacement in laundry detergents by

aluminium silicates (Allen, Haing Cho & Neubecker, 1983). At present, cultural eutrophication still represents a major human impact on lakes at a worldwide scale (Smol, 2008), but climate-related factors affect nutrients and temporal phytoplankton and zooplankton dynamics in lakes in several regions (e.g. Huber, Adrian & Gerten, 2008; Manca & DeMott, 2009; Nöges *et al.*, 2010), particularly in mountain ranges (e.g. Saros *et al.*, 2003; Rühland, Paterson & Smol, 2008). Climate change may shift the baseline of previously defined reference conditions by altering boundary conditions (Battarbee *et al.*, 2005), which in turn may require a re-definition of lake

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restoration targets, particularly for temperate lakes (Smol, 2008).

Piburger See is a small mountain lake in the Eastern Alps (Austria) and was part of the OECD study on eutrophication (OECD, 1980). This lake experienced cultural eutrophication during several decades in the 20th century. In the 1950s and 1960s, recreational activities increased with a concurrent rise in tourism, and increasing amounts of fertilisers were used on nearby fields (Pechlaner, 1968). This resulted in enhanced primary production and rising hypolimnetic oxygen depletion in the lake (Pechlaner, 1979). Lake restoration started in 1970 by exporting anoxic and nutrient-rich hypolimnetic waters with an Olszewski tube (Pechlaner, 1971, 1979). External nutrient loading was reduced by altering fertiliser application and by diverting sewage from a public bath (Psenner, Pechlaner & Rott, 1984). After the installation of the Olszewski tube in June 1970, phytoplankton biomass increased, accompanied by an increase in chlorophyll *a* and total phosphorus (TP) (Rott, 1983; Tolotti & Thies, 2002). The period from 1970 until 1988 was characterised by a marked increase in the filamentous cyanobacterium *Oscillatoria limosa* C.A. Agardh, which became the dominant algal taxon in the lake and contributed up to 40% to the mean annual phytoplankton biovolume (Rott, 1976; Wolf, 1991). The response of phytoplankton biovolume to lake restoration was delayed by two decades and re-oligotrophication of Piburger See began during the late-1980s (Pechlaner, 1979; Rott, 1983; Pipp & Rott, 1995). At present, Piburger See is oligo-mesotrophic (Tolotti & Thies, 2002). Since the early 2000s, chlorophyll *a* and phytoplankton biovolume values suggest a reversing trend in lake trophic status with a rising contribution of diatoms including blooms of *Asterionella formosa* (Tolotti *et al.*, 2005).

Here, we address the response of Piburger See to environmental conditions from the late 19th to the early 21st century with an emphasis on the period of cultural eutrophication and recovery. We intend to bridge monitoring gaps during the late 20th century and to interpret recent changes in diatom species composition and biomass (Battarbee *et al.*, 2005; Saros, 2009). The combination of palaeo- and neolimnological approaches helps to assess reference conditions and the lake's susceptibility to future climate change impacts (Bennion & Battarbee, 2007).

## Methods

### Study site

Piburger See is a mountain lake situated in the Oetz Valley in the Central Eastern Alps (47°11' N, 10°53' E,

Tyrol, Austria). The catchment of 1.59 km<sup>2</sup> covers an elevation range from 913 to 2400 m. Coniferous forest dominates on granite and gneiss bedrock up to c. 2000 m asl. The lake has an area of 0.17 km<sup>2</sup>, and its mean and maximum depths are 14 and 24 m, respectively. The lake water retention time is about 2 years. Piburger See is meromictic during spring and develops hypolimnetic anoxia during summer. Holomixis can occur in autumn, but lasts for a few days only. In the 1970s, the lake used to be ice-covered from early December to early April, while in recent years, the ice-cover period has been reduced by about 2 weeks. Piburger See has been a protected site since 1929 and is part of a Natural Reserve since 1983. Apart from a single house, there is no settlement in the catchment.

### Sediment core sampling and radiometric dating

This study focuses on the upper 16 cm of a sediment core, which was taken at Piburger See with a Kajak corer on 12 June 2004, and extruded in consecutive 0.5-cm increments in the field. Sediment samples were analysed for <sup>210</sup>Pb, <sup>226</sup>Ra, <sup>137</sup>Cs and <sup>241</sup>Am by direct gamma assay in the Bloomsbury Environment Isotope Facility at University College London, using an ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector. <sup>210</sup>Pb was determined via its gamma emissions at 46.5 keV, and <sup>226</sup>Ra by the 295 and 352 keV gamma rays emitted by its daughter isotope <sup>214</sup>Pb following 3 weeks storage in sealed containers to allow radioactive equilibration. <sup>137</sup>Cs and <sup>241</sup>Am were measured by their emissions at 662 and 59.5 keV. The absolute efficiencies of the detector were determined using calibrated sources and sediment samples of known activity. Corrections were made for the effect of self-absorption of low-energy gamma rays within the sample. <sup>210</sup>Pb (half-life 22.3 years) is a naturally produced radionuclide, derived from atmospheric fallout (termed unsupported <sup>210</sup>Pb). <sup>137</sup>Cs (half-life 30 years) and <sup>241</sup>Am (half-life 432 years) are artificially produced radionuclides, introduced to the study area by atmospheric fallout from nuclear weapons testing and nuclear reactor accidents. Chronological data were calculated using the constant rate of supply (CRS) dating model (Appleby & Oldfield, 1978; Appleby *et al.*, 1986; Appleby, 2001).

### Spheroidal carbonaceous particles

Spheroidal carbonaceous particles (SCPs) are a component of fly ash. They are produced by the high temperature, industrial combustion of fossil fuels, such as coal and fuel oil, and are emitted to the atmosphere with flue

gases. There are no natural sources of SCPs, and consequently, they provide an unambiguous indicator of contamination from these industrial sources. The analysis of SCPs in the core of Piburger See followed the analysis by Rose (1994, 2008). SCP concentrations are converted to fluxes by use of the sediment accumulation rate data produced by the radiometric dating and are expressed in the form  $\text{no. cm}^{-2} \text{ year}^{-1}$ .

#### *Geochemistry and subfossil pigments*

Water content and organic matter (estimated as loss-on-ignition, LOI) in the sediment core were determined by drying 5–6 g of wet sediment at temperatures of 60 and 550 °C, respectively. Total carbon, nitrogen and sulphur were determined in dry sediment using a CNS analyser (Fisons, NA 1500; Fisons, Carlo Erba, NJ, USA). Total phosphorus was analysed on dry sediment samples after digestion with 96% sulphuric acid according to standard methods. Chlorophyll derivatives (CD) and total carotenoid (TC) were analysed in the sediment core according to Guilizzoni *et al.* (1983) and Züllig (1982). Specific pigments were determined by reverse-phase HPLC (DIO-NEX, Summit; Sunnyvale, CA, USA) after extraction in 90% acetone under nitrogen (Lami *et al.*, 1994). The 430 : 410 spectrophotometric absorbance ratios were calculated for each sediment layer to evaluate the level of preservation of pigments in the sediment (Guilizzoni, Lami & Marchetto, 1992; Guilizzoni & Lami, 2001).

#### *Subfossil diatoms*

Dried sediment was cleaned and mounted according to standard procedures (Battarbee *et al.*, 2001). For each sample, at least 500 valves were counted under an Olympus BX51 (Tokyo, Japan) light microscope ( $\times 1000$  magnification) equipped with differential interference contrast. Diatom identification to the lowest possible taxonomic level was based on the studies by Krammer & Lange-Bertalot (1986–1991) and Lange-Bertalot & Metzeltin (1996), Lange-Bertalot (2001), Reichardt & Lange-Bertalot (1991) and Reichardt (1997). Diatom data are presented as relative abundance of the total number of diatom valves counted in each sediment interval.

#### *Lake water chemistry and phytoplankton*

Lake water nutrients and chlorophyll *a* were analysed monthly in discrete water samples, which were collected with a Patalas-Schindler sampler (UWITEC, Mondsee, Austria) along a vertical profile at 3-m intervals from lake

surface to maximum depth at 24 m. Lake water nutrients have been analysed using standard methods since the mid-1970s (Pechlaner, 1979; Psenner *et al.*, 1984; Tolotti & Thies, 2002). Since 1973, chlorophyll *a* has been determined spectrophotometrically according to Jeffrey & Humphrey (1975). Phytoplankton biovolume was determined by Utermöhl's method (1958), and cell volumes were estimated according to the method described by Rott (1981). The earliest data on phytoplankton species composition and biovolume are available from 1966 (Findenegg, 1968). Monthly phytoplankton data are available for the 1970s and early 1980s (Rott, 1983), for the summer 1990 and 1991 (Prader, 1993), for the year 1998 (Tolotti & Thies, 2002) and for 2002–04.

#### *Temperature*

Air temperature at Piburger See was derived from the gridded HISTALP data set (Auer *et al.*, 2007), which is based on monthly homogenised long-term series of temperature and other meteorological variables for the so-called Greater Alpine Region (4–19°E, 43–49°N, 0–3500 m asl). The temperature record extends back to 1760 and thus completely covers the time period of the sediment record of Piburger See. Mean air temperature projected to the end of the 21st century was derived from the Regional Climate Model RCAO (Rossby Centre, SMHI, Sweden) (Räisänen *et al.*, 2004). RCAO was driven by two Global Climate Models, i.e. the HadAM3H (Hadley Centre, U.K.) and the ECHAM4/OPYC3 (Max Planck Institute, Germany) models, using SRES forcing scenarios A2 and B2 (Nakićenović *et al.*, 2000). RCAO model output data were downloaded from the web page of the PRUDENCE project (Prediction of Regional scenarios and Uncertainties for Defining European Climate change risks and Effects; <http://prudence.dmi.dk>) (Christensen *et al.*, 2007). The systematic bias of gridded RCAO output data and observed values in the control period (1961–90) was dealt with using the so-called delta change method. In particular, changes in temperature are estimated by comparing simulated future and simulated present-day climate, as any biases in the two simulations were assumed to cancel out (e.g. Räisänen, 2007; Graham, Andréasson & Carlsson, 2007). Lake water temperature profiles have been measured at monthly intervals since 1972. A time series of the upper epilimnetic water temperature (0–4.5 m) for the growing season (April through September) dating back to 1840 was built using the relationship between mean monthly air temperature and monthly volume-weighted water temperature. Schmidt stability was calculated according to Idso (1973)

for the whole lake water column of Piburger See using measured monthly lake water temperature data.

#### Data analysis of sedimentary biological composition

Diatom diversity was determined on the binary logarithm-based Shannon Index (Shannon & Weaver, 1949). Reconstruction of diatom-based TP (DI-TP) for each sedimentary interval was based on the weighted average regression model with inverse deshrinking applied to the Combined European training set, which includes modern samples from 477 European lakes (Battarbee *et al.*, 2001). DI-TP reconstruction was performed with transfer functions from the software ERNIE (<http://craticula.ncl.ac.uk/Eddi/jsp>) and was restricted to the 62 diatom taxa with minimum relative abundance of  $\geq 1\%$ . Model and training sets were selected according to regression coefficients, and low apparent and prediction errors (reflecting the ability to estimate measured TP and to predict TP, respectively). Measured lake volume-weighted average TP was compared to inferred DI-TP to test the accuracy of the model in inferring TP concentrations.

The gradient length of sedimentary biological composition (in terms of diatoms and pigments) was investigated by detrended correspondence analysis (DCA) using the software CANOCO for Windows version 4.5 (Ter Braak & Šmilauer, 2002). A gradient length shorter than 2 standard deviation units for both pigments and diatoms favours the application of the linear model of principal component analysis (PCA) to summarise major variation patterns. Data were  $\log(x + 1)$  transformed prior to analyses to equalise variance among data. Diatom multivariate analyses were restricted to the 56 taxa with minimum relative abundance of  $\geq 1\%$  and present in  $\geq 3$  samples, to minimise the effect of rare taxa. The relation of sediment biological composition and environmental drivers was explored by comparing the pigment and diatom PCA sample scores for each sediment level to monthly mean air temperature records and sediment SCPs, TC and DI-TP. A Kolmogorov–Smirnov distance test indicated Spearman's rank correlation as the most appropriate method.

## Results

#### Sediment core chronology

Total  $^{210}\text{Pb}$  activity reaches equilibrium with the supporting  $^{226}\text{Ra}$  at a depth around 12 cm in the sediment core. Total  $^{210}\text{Pb}$  activities were higher than the supporting  $^{226}\text{Ra}$  activities in 18–20 cm depth. This may be due to errors arising from relatively high  $^{226}\text{Ra}$  concentrations related to

a strong natural radon source in the Oetz Valley (Purtscheller *et al.*, 1995). The variation in  $^{226}\text{Ra}$  concentrations in the core implies changes in sediment properties. In general, unsupported  $^{210}\text{Pb}$  activities, calculated by subtracting  $^{226}\text{Ra}$  activity from total  $^{210}\text{Pb}$  activity, decline with depth, but there is a possible non-monotonic feature in the  $^{210}\text{Pb}$  record, suggesting that sedimentation rates in this core were not uniform (Fig. 1). The  $^{137}\text{Cs}$  activity profile has two relatively well-resolved peaks; one in the 6.5–7-cm sample at  $273 \text{ Bq kg}^{-1}$  and the other in the 2.5–3-cm sample at  $442 \text{ Bq kg}^{-1}$  (Fig. 1). These identify the years 1963 (i.e. nuclear weapons fallout peak) depth and 1986 (i.e. Chernobyl nuclear accident), respectively. The 1963 depth was confirmed by the detection of  $^{241}\text{Am}$ . The CRS model places 1963 and 1986 at about 7 and 3 cm, respectively, in good agreement with the dates indicated by the  $^{137}\text{Cs}$  record (Fig. 1). This chronology suggests that the sediment accumulation rate increased from the 1880s by reaching a maximum of about  $0.010 \text{ g cm}^{-2} \text{ year}^{-1}$  in the 1980s before declining slightly in the two most recent decades (Fig. 1).

#### Spheroidal carbonaceous particles

The first presence of SCPs is observed in the 1880s. A rapid increase in SCP input starts in c. 1960 and concentrations peak in the mid 1970s with about  $6000 \text{ g DW}^{-1}$ .

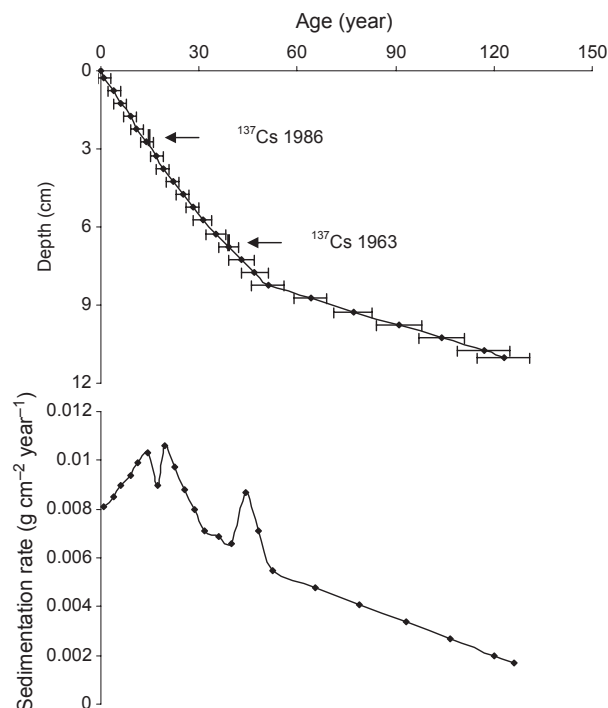


Fig. 1 Radiometric chronology of Piburger See sediment core showing CRS model  $^{210}\text{Pb}$  dates and sedimentation rates, together with the 1986 and 1963 depths indicated by the  $^{137}\text{Cs}$  record.



From this point, SCP concentrations decline to the sediment surface where the concentration is about  $1300 \text{ g DW}^{-1}$ . Converting the concentrations to SCP fluxes does not significantly alter the profile (Fig. 2). The peak SCP flux is  $55 \text{ cm}^{-2} \text{ year}^{-1}$ .

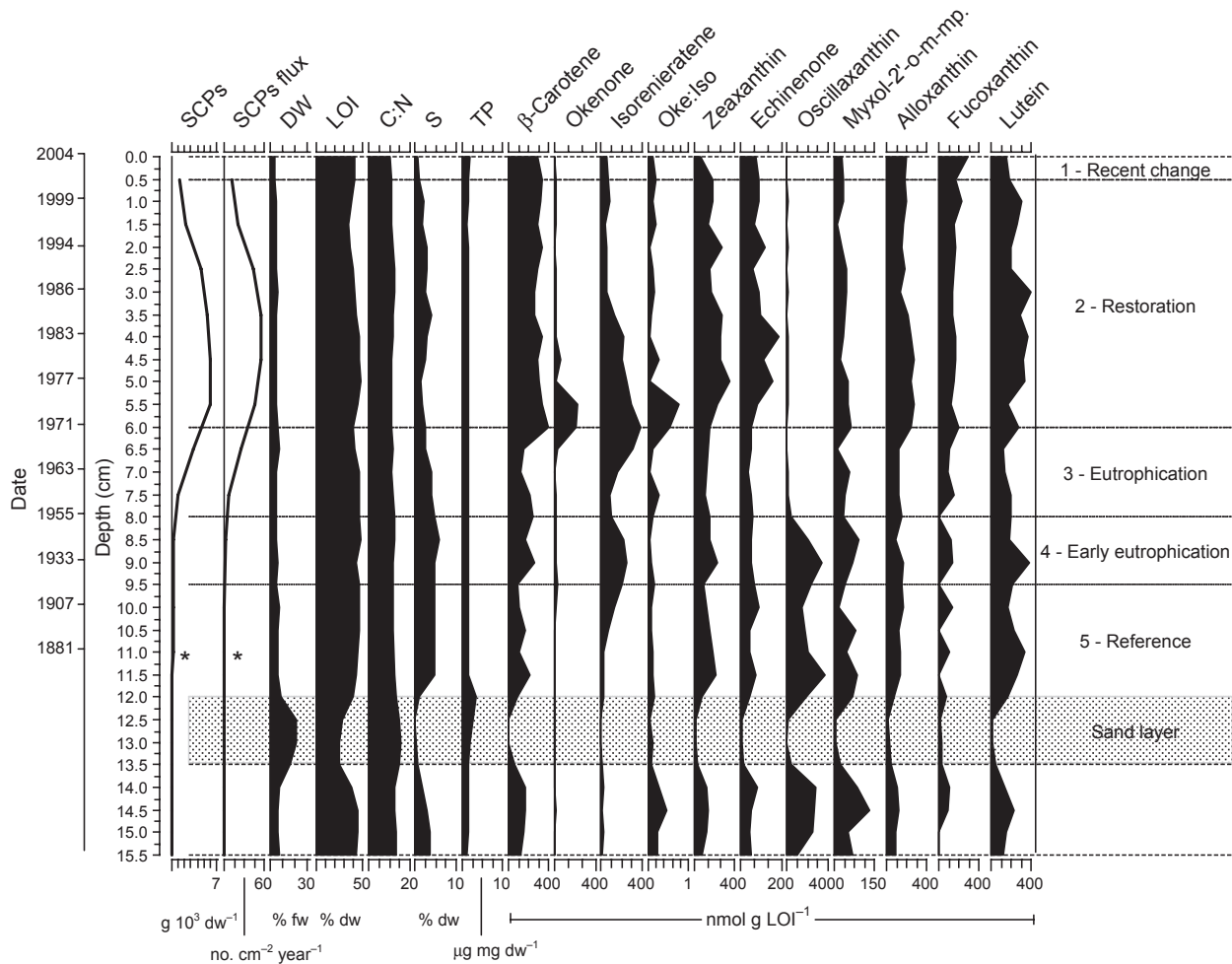
#### Geochemistry and subfossil pigments

The upper 10 cm of the sediment core is characterised by high water content with dry weight contributing <10% of fresh weight. Mean LOI is about 40%, C:N ratios are up to 10 and TP is below  $2 \mu\text{g mg}^{-1}$  dry sediment (Fig. 2). In the 1880s, sulphur amounts to 5% of dry weight and declines to values below 1% in the most recent sediment layers. At a sediment depth of 12.0–13.5 cm, there is a sand layer with different geochemical characteristics, e.g. sulphur near detection limit, LOI approximately 30%, dry weight

up to 20%, C:N ratio up to 16 and TP up to  $3.5 \mu\text{g mg}^{-1}$  dry sediment.

The 430 : 410 spectrophotometric absorbance ratios (not shown) range from 0.9 to 1.0 along the sediment core indicating a good preservation of pigments in the sediment. This is supported by the occurrence of the labile carotenoid fucoxanthin (Leavitt, 1993).  $\beta$ -carotene, one of the most stable carotenoids present in all algal taxa (Swain, 1985; Guilizzoni & Lami, 2001), ranges around  $150 \text{ nmol g LOI}^{-1}$  in the pre-1900 period (Fig. 2), increases during the late 1960s, peaks during the early 1970s at almost  $400 \text{ nmol g LOI}^{-1}$  and then declines to around  $300 \text{ nmol g LOI}^{-1}$  in the top sediment layers (Fig. 2).

Pigments of cyanobacterial carotenoids, i.e. zeaxanthin (abundant in several filamentous and coccal taxa of *Oscillatoriales* and *Chroococcales*) and echinenone (abundant



**Fig. 2** Geochemistry and algal pigments in the upper 16 cm of the Piburger See sediment core. SCP, spheroidal carbonaceous particles; DW, dry weight; LOI, loss of ignition; S, sulphur; TP, total phosphorus; myxol-2'-om-mp, myxol-2'-o-methyl-methylpentoside; DI-TP, diatom total phosphorus inferred according to the Combined European diatom calibration set (Battarbee *et al.*, 2001; oke:iso – ratio of okenone to isorenieratene. \*Denotes earliest detection of SCPs.

in all cyanobacteria), show a maximum occurrence in the late-1970s. Myxol-2'-o-methyl-methylpentoside, a pigment specific to *O. limosa* (Züllig, 1982), is present at low concentrations throughout the whole sediment core. Higher pigment values above 100 nmol g LOI<sup>-1</sup> occurred in the late-19th and in the first half of the 20th century, followed by an overall decline. Oscillaxanthin, the marker carotenoid pigment of *Oscillatoria rubescens* = *Planktothrix rubescens* (DeCandolle ex Gomont) Anagnostidis & Komárek (1988), dominated in Piburger See from the deeper core sections until the mid 1950s with maximum values up to 3700 nmol g LOI<sup>-1</sup>. Oscillaxanthin has strongly declined from the 1950s onwards.

Okenone indicates the presence of purple sulphur bacteria (*Chromatium* sp.) during pronounced anoxic periods (Züllig, 1985) and is barely present in the sediment core except for the 1970s with maximum values up to 218 nmol g LOI<sup>-1</sup> between 1965 and 1975 (Fig. 2). Isorenieratene, the marker for green sulphur bacteria (*Chlorobium* sp.) living under strictly anoxic conditions, shows a major peak of 384 nmol g LOI<sup>-1</sup> in the early

1970s (Fig. 2). A secondary maximum of isorenieratene of 250 nmol g LOI<sup>-1</sup> occurred during the 1940s (Fig. 2). The ratio okenone/isorenieratene as a proxy for water transparency (Brown, McIntosh & Smol, 1984) indicates a decrease of water transparency during the second half of the 20th century, being most pronounced during the 1970s. Alloxanthin, a pigment of cryptophytes, and lutein, a pigment of chlorophytes, both increased slightly in the 1970s.

Fucoxanthin, a pigment of diatoms and chrysophytes, shows oscillating values up to 150 nmol g LOI<sup>-1</sup> in the deepest sediment layers, and an increase since the onset of lake restoration (1970) up to c. 300 nmol g LOI<sup>-1</sup> in the most recent sediment layers (Fig. 2). Within a sand layer at 12.0–13.5 cm sediment depth, all pigments exhibited very low values.

#### Subfossil diatoms

Sediment diatom assemblages between 15.5 and 9.5 cm depth (c. pre-1900 AD, Fig. 3) are diverse (mean Shannon

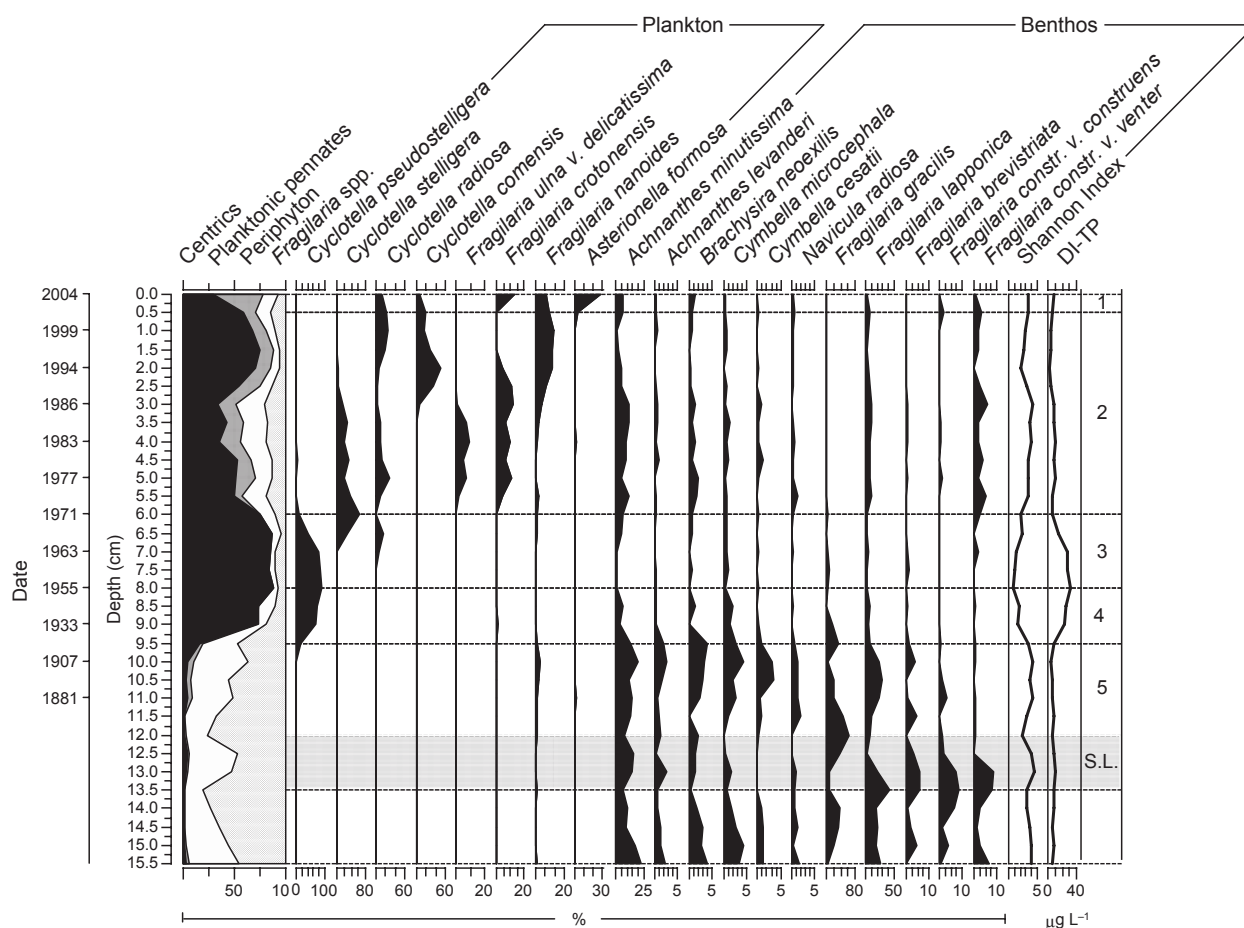


Fig. 3 Relative abundances of key diatom taxa of the Piburger See sediment core.

Index = 3.6) and dominated by periphytic genera (70–98%), namely *Achnanthes* (e.g. *A. minutissima* Kützing, *A. levanderi*, *A. marginulata* Grunow), *Cymbella* spp. [e.g. *C. microcephala*, *C. cesatii*, *C. gracilis* (Ehrenb.)] Kützing, *Brachysira neoexilis*, *Navicula radiosa* and several *Fragilaria* taxa commonly found in oligotrophic alpine lakes [e.g. *Fragilaria lapponica*, *Fragilaria brevistriata*, *Fragilaria contruens* var. *construens*, *Fragilaria capucina* var. *vaucheriae* (Kütz.) Lange-Bertalot, *Tabellaria flocculosa* (Roth) Kützing]. Centric diatoms are almost absent in the pre-1900 period (except for sporadically occurring *Cyclotella pseudostelligera* and *Cyclotella comensis*), while the tychoplanktonic *Fragilaria gracilis* reaches an abundance up to 65% at 12 cm depth (Fig. 3).

The diatom assemblages in the top 10 cm of the sediment core show a lower diversity (mean Shannon Index = 2.9) and are dominated by planktonic diatoms (52–89%, Fig. 3, Table 1). *Cyclotella* species were particularly abundant (up to 88%) from early 1900s to early 1970s and during the most recent two decades. *Cyclotella* species exhibit a clear shift from stelligeroid species (i.e. *C. pseudostelligera* followed by *C. stelligera*), dominating until approximately 1970 AD, to *Cyclotella radiosa* during the

late-1970s and the late-1990s, and finally to *C. comensis* complex (i.e. *C. comensis sensu stricto* and different *C. aff. comensis sensu* Wunsam, Schmidt & Klee, 1995) in the upper 3 cm, with a maximum of about 50% during the early-to mid-1990s. Planktonic pennates were mainly represented by *Fragilaria crotonensis* with abundances up to c. 12% since the 1970s and a decrease during the 1990s (Fig. 3). Other planktonic *Fragilaria* species include *F. ulna* var. *delicatissima*, which reached 10% during the 1980s, and *F. nanoides*, which increased up to c. 13% during the late-1990s (Fig. 3). The relative abundance of centric diatoms has decreased again since the early-2000s, when the planktonic pennate *F. crotonensis* and *A. formosa* became dominant (Fig. 3).

Benthic taxa remain scarce in the upper 10 cm of the sediment core and are mainly represented by *Achnanthes minutissima*, *F. lapponica*, *F. construens* var. *venter*, followed by *B. neoexilis*, *Cymbella microcephala* and by the less frequent *Nitzschia alpina* Hustedt, *Nitzschia bryophylla* and *Nitzschia lacuum* Lange-Bertalot. Nevertheless, several of these periphytic taxa show a certain recovery with respect to their low relative abundances between early 1900s and beginning of lake restoration in the 1970s.

**Table 1** Diatom taxa used for DI-TP reconstruction and multivariate analyses occurring in  $\geq 3$  sediment samples

| Taxon  | Code  | No. | Mean RA (%) | Max RA (%) | TS  | TP op ( $\mu\text{g L}^{-1}$ ) |
|--|-------|-----|-------------|------------|-----|--------------------------------|
| <i>Achnanthes levanderi</i> Hust.                              | Ac-le | 27  | 0.8         | 2.8        | o   | 13.2                           |
| <i>Achnanthes minutissima</i> Kütz.                            | Ac-mi | 32  | 9.0         | 22.5       | i   | 24.6                           |
| <i>Asterionella formosa</i> Hass.                              | As-fo | 16  | 1.2         | 27.8       | m-e | 44.0                           |
| <i>Brachysira neoexilis</i> (Bréb.) Grun.                      | Br-ne | 27  | 1.4         | 4.1        | o   | 12.2                           |
| <i>Cyclotella comensis</i> group Grun.                         | Cy-co | 32  | 8.4         | 61.7       | –   | 13.7                           |
| <i>Cyclotella pseudostelligera</i> Hust.                       | Cy-ps | 27  | 14.8        | 88.1       | e   | 39.8                           |
| <i>Cyclotella radiosa</i> (Grun.) Lemm.                        | Cy-ra | 28  | 5.9         | 28.3       | e   | 30.4                           |
| <i>Cyclotella stelligera</i> (Cleve & Grun.) V. Heu.           | Cy-st | 23  | 8.6         | 65.1       | –   | 18.5                           |
| <i>Cymbella affinis</i> Kütz.                                  | Cm-af | 12  | 0.2         | 1.2        | e   | 17.0                           |
| <i>Cymbella cesatii</i> (Raben.) Grun.                         | Cm-ce | 21  | 0.6         | 3.3        | o   | 14.0                           |
| <i>Cymbella helvetica</i> Kütz.                                | Cm-he | 10  | 0.2         | 1.4        | m   | 16.9                           |
| <i>Cymbella microcephala</i> Grun.                             | Cm-mi | 30  | 1.3         | 4.2        | m-e | 19.8                           |
| <i>Fragilaria brevistriata</i> Grun.                           | Fr-br | 19  | 1.2         | 6.3        | i   | 38.1                           |
| <i>Fragilaria capucina</i> var. <i>vaucheriae</i>              | Fr-co | 6   | 0.2         | 2.0        | e   | 52.8                           |
| <i>Fragilaria construens</i> v. <i>construens</i>              | Fr-cc | 17  | 1.3         | 8.5        | m-e | 56.4                           |
| <i>Fragilaria construens</i> v. <i>venter</i> (Ehre.) Hust.    | Fr-ve | 26  | 2.2         | 8.8        | m-e | 51.7                           |
| <i>Fragilaria crotonensis</i> Kitt.                            | Fr-cr | 12  | 2.5         | 13.6       | m   | 30.9                           |
| <i>Fragilaria gracilis</i> (Østr.) Hust.                       | Fr-gr | 30  | 11.8        | 65.2       | o-m | 22.2                           |
| <i>Fragilaria lapponica</i> Grun.                              | Fr-la | 32  | 11.5        | 42.0       | –   | 16.6                           |
| <i>Fragilaria nanoides</i> Lange-B.                            | Fr-na | 25  | 2.6         | 12.2       | o*  | 8.0                            |
| <i>Fragilaria pinnata</i> Ehre.                                | Fr-pi | 19  | 0.6         | 3.3        | i   | 34.6                           |
| <i>Fragilaria robusta</i> (Fusey) Mang.                        | Fr-ro | 24  | 1.8         | 7.2        | –   | 14.9                           |
| <i>Fragilaria ulna</i> v. <i>angustissima</i> (Nitz.) Lange-B. | Fr-ua | 11  | 1.1         | 9.3        | i   | 65.8                           |
| <i>Navicula radiosa</i> Kütz.                                  | Na-ra | 25  | 0.6         | 2.0        | m-e | 30.4                           |

Code, species abbreviations; No, number of sediment subsamples, where each taxon was identified; Mean and Max RA, mean and maximum relative abundance within the data set; TS, trophic preference according to Van Dam *et al.* (1994); \*trophic preference according to Lange-Bertalot & Metzeltin (1996); o, oligotrophic; o-m, oligo-mesotrophic; m, mesotrophic; m-e, meso-eutrophic; e, eutrophic; i, indifferent; TP op, total phosphorus optima according to the Combined European calibration set (Battarbee *et al.*, 2001).

*Diatom-based total phosphorus reconstruction*

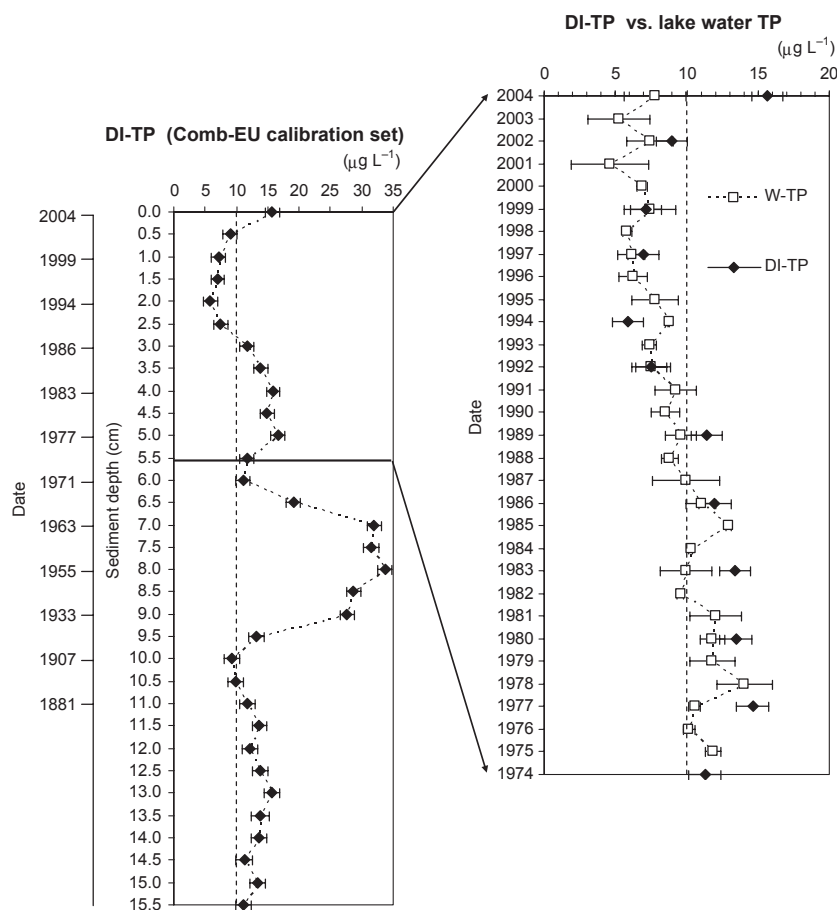
Cumulative relative abundances of diatoms which were used for DI-TP reconstruction range between 73 and 97% (average = c. 86%), with minimum values for the sand layer (as a consequence of higher proportion of very rare taxa) and maximum values for the samples dominated by a few taxa. Of 62 taxa, 55 could be used for the DI-TP reconstruction. The remaining seven taxa were all periphytic and rare, with a maximum relative abundance of c. 3.5% for *N. bryophyla*. The regression coefficient, root mean squared error and bias of estimation (Table 2) are highly comparable with the performance of the transfer function based on the whole Combined European training set (i.e. 0.637, 0.334 and 0.719, respectively), thus indicating that diatom assemblages of the analysed core section are well represented in the training set. The average standard error of reconstructed DI-TP values is  $2.3 \mu\text{g L}^{-1}$  ( $2.2\text{--}2.8 \mu\text{g L}^{-1}$ ), corresponding to an error of 19%. DI-TP

shows a significant relation with mean summer lake water TP (Fig. 4, Pearson's  $r = 0.7$ ,  $P < 0.02$ ,  $N = 11$ ). In general, DI-TP overestimates measured lake water TP, with an average absolute difference of c. 25%. The maximum difference (51%) has been found in the top sediment layer (Fig. 4) and is related to the high TP optima attributed to *A. formosa* and *F. crotonensis* by the Combined European training set. By contrast, the smallest differences (c. 9%)

**Table 2** Errors of estimation (apparent) and of prediction (jackknife) relative to the lake TP concentrations reconstructed from sediment diatoms (DI-TP) through the inverted weighted averaging procedure applied at the Combined European training set (Battarbee *et al.*, 2001)

|              | Apparent errors           | Jackknife error |
|--------------|---------------------------|-----------------|
| $r^2$        | 0.710                     | 0.637           |
| RMSE         | 0.299                     | 0.334           |
| Average bias | $-1.636 \text{ e}^{-007}$ | 0.003           |
| Max. bias    | 0.625                     | 0.720           |

RMSE, root mean squared error.



**Fig. 4** Diatom-inferred TP concentrations (DI-TP) based on weighted averaging with inverse deshrinking method applied to the Combined European calibration set (Comb-EU, Battarbee *et al.*, 2001) in the upper 16 cm of the Piburger See sediment core (left panel) and comparison (right panel) between DI-TP (black diamonds) and measured summer volume-weighted averages of lake water TP (W-TP, open squares) from 1975 to 2004. Standard deviations shown for both data series.



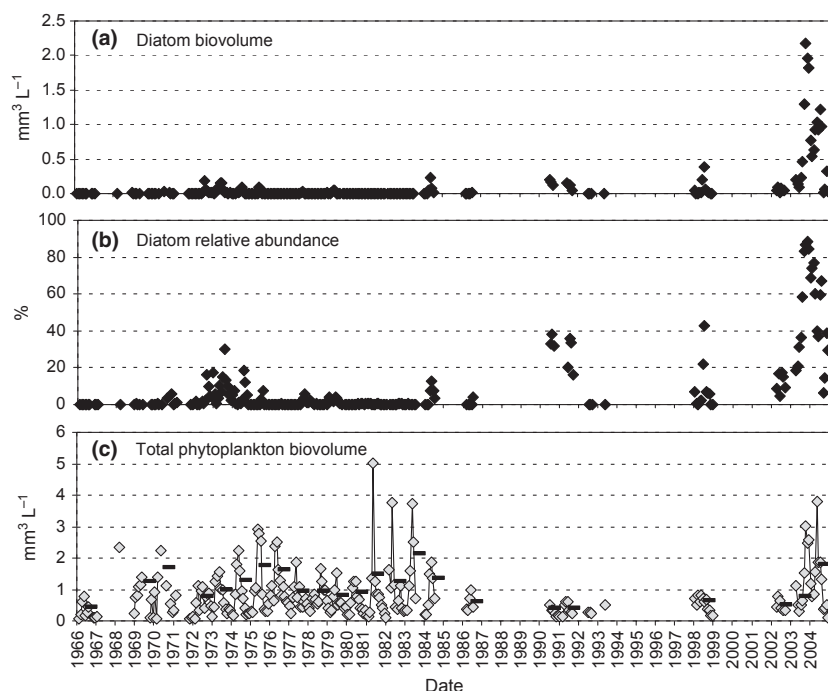
between DI-TP and measured concentrations were found in samples of the 1990s dominated by *C. comensis*.

The reconstructed DI-TP concentration combined with sediment chronology and post-1970 records of lake trophic development allows the discrimination of five periods of varying trophic status in Piburger See (Figs 2 & 3). A reference period corresponds to a period around the turn of the 19th to the 20th century with DI-TP values between 10 and 15  $\mu\text{g L}^{-1}$  TP. The early eutrophication period started in the first decades of the 20th century with increasing DI-TP, and culminated during the eutrophication period in the 1950s and 1960s, with DI-TP values up to 34  $\mu\text{g L}^{-1}$  TP. The progressive decrease in DI-TP during a restoration period started in 1970, and resulting values of <10  $\mu\text{g L}^{-1}$  in the 1980s and 1990s agree with the slow recovery from eutrophication indicated by recorded water TP levels. Increasing DI-TP values in the early 2000s (up to 16  $\mu\text{g L}^{-1}$  in 2004) suggest a recent change in trophic level, which however is not confirmed by almost unchanged lake water TP concentrations.

### Phytoplankton

In the 1970s and early-1980s, lake volume-weighted annual averages of chlorophyll *a* ranged from 3 to 5  $\mu\text{g L}^{-1}$ , corresponding to mesotrophic conditions (OECD, 1982). Maximum annual chlorophyll *a* values up

to c. 17  $\mu\text{g L}^{-1}$  occurred in spring, particularly in years of high planktonic biovolume of *O. limosa*. From the late 1980s to the late 1990s, chlorophyll *a* decreased to oligotrophic levels (i.e. annual mean <2.5  $\mu\text{g L}^{-1}$ : OECD, 1982) with spring chlorophyll *a* values of <8  $\mu\text{g L}^{-1}$ . In the early-2000s, spring chlorophyll *a* values rose again with values up to 12  $\mu\text{g L}^{-1}$  in May 2004. During the late 1960s, lake volume-weighted averages of phytoplankton biovolume for the growing season were about 0.5  $\text{mm}^3 \text{L}^{-1}$  (Fig. 5c). After lake restoration in the 1970s, lake volume-weighted monthly averages of phytoplankton biovolume reached up to 5  $\text{mm}^3 \text{L}^{-1}$ , e.g. in spring 1981 (Fig. 5c). Effects of lake restoration on phytoplankton biovolume appear to have been delayed until the mid-1980s, when growing period averages fell below 1.0  $\text{mm}^3 \text{L}^{-1}$  (Fig. 5c). Phytoplankton biovolume increased again since 2003 and reached in 2004, a spring maximum of c. 4  $\text{mm}^3 \text{L}^{-1}$  and a growing season average close to eutrophic levels of the 1970s and 1980s (i.e. >2  $\text{mm}^3 \text{L}^{-1}$ ) (Fig. 5c). Between the late-1960s and the 1980s, flagellate algae (cryptophytes, chrysophytes and dinoflagellates) dominated the phytoplankton with a mean annual average between 22 and 66%, and gelatinous coccal green algae reached up to 45% in the summer epilimnion (Findenegg, 1968; Rott, 1983; Prader, 1993). Phytoplankton species composition revealed minor changes since the lake restoration, except for the occurrence of *O. limosa*, *A. formosa* and



**Fig. 5** Volume-weighted averages of (a) planktonic diatom biovolume, (b) percentage of planktonic diatom to total phytoplankton biovolume and (c) total phytoplankton biovolume in Piburger See from 1966 to 2004. Black horizontal bars: seasonal weighted averages (April to September).

*F. crotonensis*. The filamentous cyanobacterium *O. limosa* dominated spring–summer phytoplankton in the 1970s and 1980s with an average annual abundance of up to 40%, disappeared in the late 1980s, and was rediscovered in summer 2010 on the lake sediment surface. Even though the availability of phytoplankton data became limited in the late 1980s, data indicate an increase in biovolume and relative abundance of planktonic diatoms (Fig. 5a–c). Increasing diatom abundances of up to 50% of total phytoplankton biovolume were caused by epilimnetic summer assemblages of *Cyclotella* spp. and meta- to hypolimnetic assemblages of *A. formosa* and *F. crotonensis* in 2003 and in 2004. This development contrasts to the 1970s and 1980s, when diatoms were reported to be <10%.

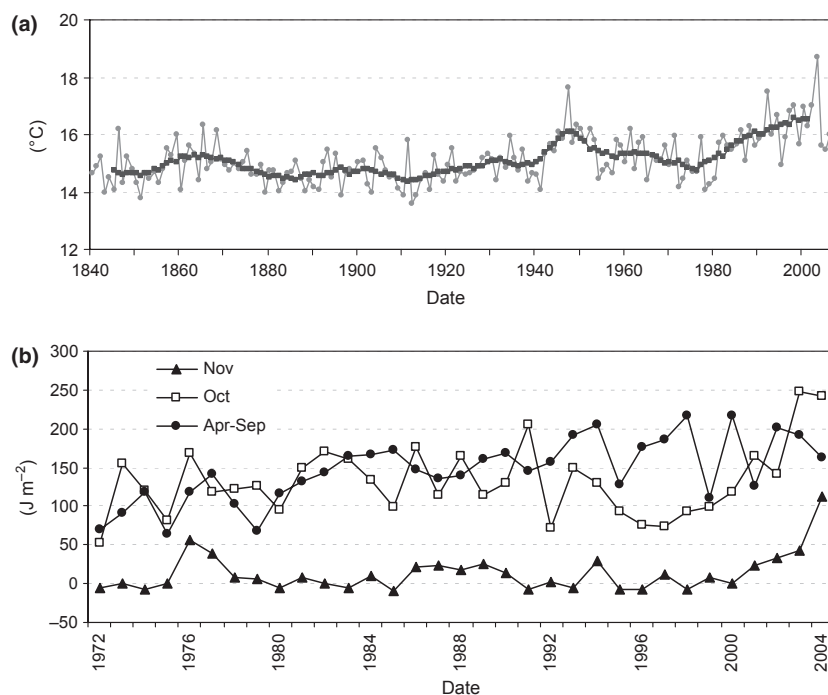
#### Lake water

From 1840 to 2004, epilimnetic water temperatures in Piburger See ranged between 14 and 16 °C (Fig. 6a). The 10-year running average shows warmer periods around the 1860s, the 1940s and an increase since the 1980s. The absolute maximum lake water temperature occurred in summer 2003. Calculated Schmidt stability for the whole water column of Piburger See reveals the most pronounced stable autumn periods in 2003 and 2004 with values of up to 250 J m<sup>-2</sup> (Fig. 6b). During the past two

decades, average Schmidt stability increased during the growing season (i.e. from April to September) by more than 50% when compared to the 1970s. Total phosphorus in Piburger See shows volume-weighted average values of 10–20 µg L<sup>-1</sup> during the eutrophication period in the 1970s and 1980s (Fig. 7a, Tolotti & Thies, 2002). In the late-1980s, TP declined to values below 10 µg L<sup>-1</sup> and TP was <5 µg L<sup>-1</sup> in the mid-1990s (Fig. 7a). Since then, TP has ranged between 5 and 10 µg L<sup>-1</sup>. Dissolved inorganic nitrogen (DIN) analyses in Piburger See started in 1975 (with a gap from 1977 to 1986, Fig. 7b). Volume-weighted averages range from <50 to 300 µg L<sup>-1</sup>, with minimum values in late autumn and maxima in spring. DIN reached recent peak values in the late 1990s and decreased since the early 2000s (Fig. 7b). Dissolved reactive silica (i.e. SiO<sub>2</sub>-Si) is available only for the past decade. Volume-weighted monthly averages range from c. 1000 µg L<sup>-1</sup> Si in the late 1990s to almost 3000 µg L<sup>-1</sup> Si in the years 2001–02 (Fig. 7c). Since 2003, silica has strongly decreased to 1000 µg L<sup>-1</sup> Si.

#### Air temperature

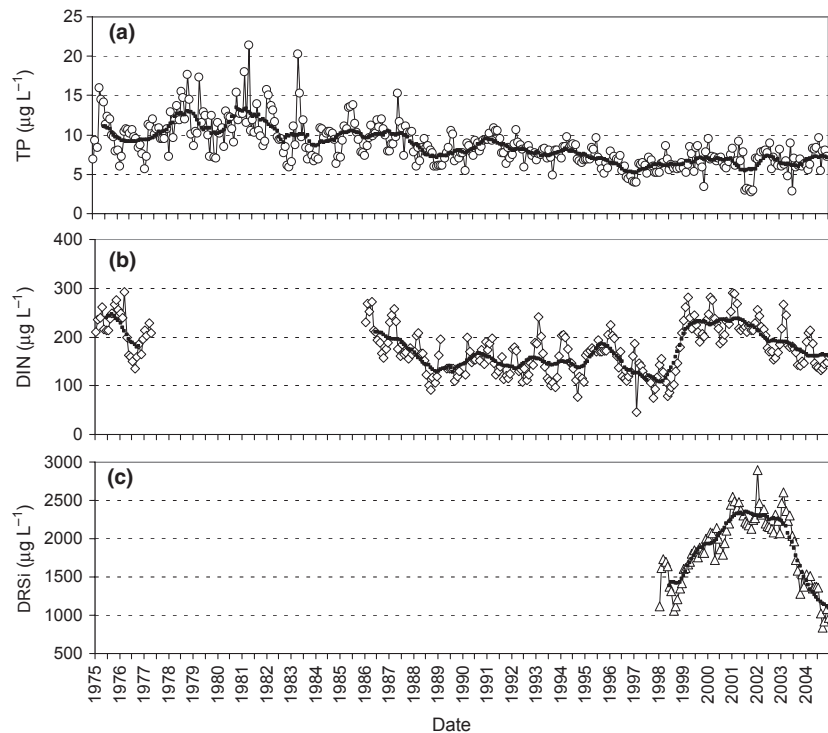
Mean annual air temperature at Piburger See, derived from the HISTALP data set (Auer *et al.*, 2007), increased by about 2 °C through the time period of the sediment



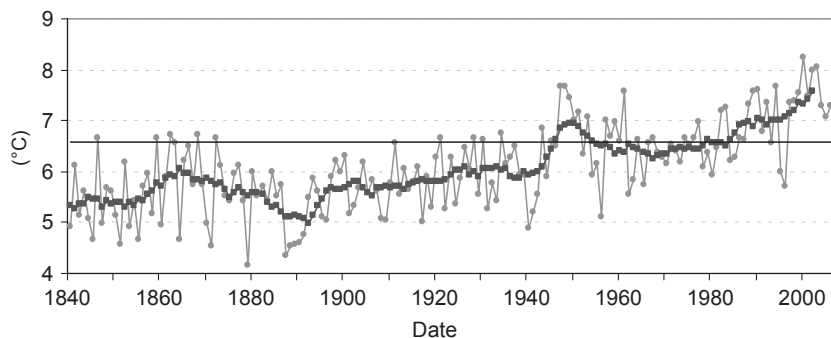
**Fig. 6** (a) Volume-weighted epilimnetic water temperature during growing season (April–September mean, 0–4.5 m depth): 1840–1971, calculated from the relation between air and water temperature; 1972–2004, *in-situ* measured values; Bold line: 10-year running average; (b) Schmidt stability for the lake water column.

record. Minima of annual air temperatures were in the 1890s, relative maxima in the 1860s and 1950s, and since the 1980s, a positive trend in mean annual air temperature has been observed (Fig. 8). Regional anomalies are highly correlated within the European Alps (Böhm *et al.*, 2001). Mean annual air temperature at Piburger See was 6.6 °C in the reference period 1961–90 and increased by 0.6 °C for 1991–2004. The rise in annual air temperature revealed a pronounced seasonal variability with values of 0.6 in winter (December–February), 0.9 in spring (March–May) and 1.1 °C in summer (June–August), but almost no change in autumn (September–November).

Prior to the 1940s, mean annual air temperature remained well below the 1961–90 average (Fig. 8). Changes in mean annual air temperature, which are simulated to the end of this century, are up to three times higher than those in the period of the sediment record. The projected increase in air temperature ranges from 3 to 6 °C depending on the GCM and SRES scenario and is projected to be highest in summer (Fig. 9). The HadAM3H model generally shows a smaller increase than the ECHAM4/OPYC3 model, and the increase is about 2 °C higher for the A2 scenario compared to the annual mean under B2.



**Fig. 7** Monthly volume-weighted average nutrient concentrations in the water column of Piburger See, (a) TP: total phosphorus, (b) DIN: dissolved inorganic nitrogen, (c) DRSi: dissolved reactive silica. Bold lines: 12-month running average.



**Fig. 8** Mean annual air temperature at Piburger See (1840–2004), bold line: 10-year running average. Horizontal line: 1961–90 mean (6.6 °C).

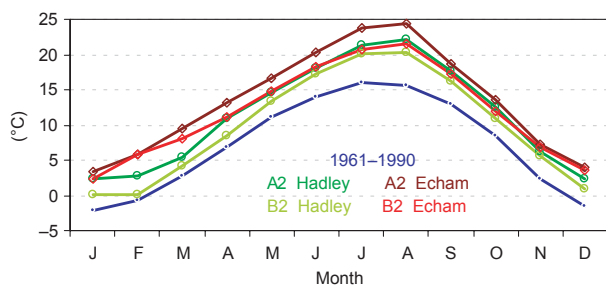


Fig. 9 Mean monthly air temperature at Piburger See for the control period 1961–90 and the scenario period 2071–2100 using the GCMs HadAM3H (Hadley Centre, U.K.) and ECHAM4/OPYC3 (Max Planck Institute, Germany) and the emission scenarios A2 and B2.

### Multivariate analysis

The distribution of sediment samples within the PCA biplot according to subfossil pigments is mainly driven by the variability of fucoxanthin and oscillaxanthin (Fig. 10a). Consequently, most samples from the upper 10 cm of the sediment core are located within the upper left quadrant of the ordination space, while the samples

from the reference period group in the lower right quadrant (Fig. 10a). A subgroup along axis 1 reflects high concentrations of Myxol-2'-o-methyl-methylpentoside since the start of lake restoration. Samples from the sand layer (No. 25–28) are located in the upper right quadrant corresponding to the lowest pigment concentrations in the sediment.

The sediment diatom PCA biplot (Fig. 10b) shows two species groups at each end of the first axis which clearly separates samples corresponding to the reference period from samples of the post-restoration period. Several periphytic *Fragilaria*, *Achnanthes*, *Cymbella* and *Navicula* species group in the lower left quadrant of the ordination space. The most abundant *Cyclotella* spp. and planktonic *Fragilariaceae*, such as *F. crotonensis* and *A. formosa*, group into the positive extreme of axis 1. Samples corresponding to eutrophication period (sample No. 13–19) are completely separated because of the high abundance of *C. pseudostelligera* and the scarcity of benthic taxa (Fig. 10b). Diatom and pigment PCA sample scores on axis 1 show striking changes in pigment and diatom assemblages during the eutrophication period in the

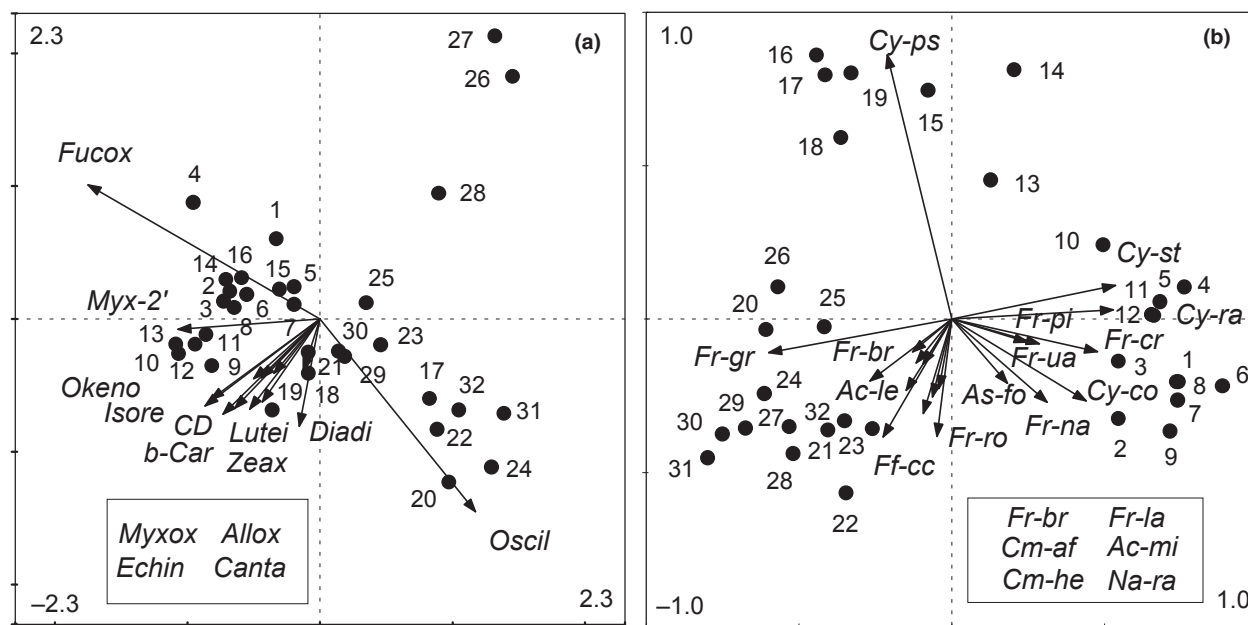


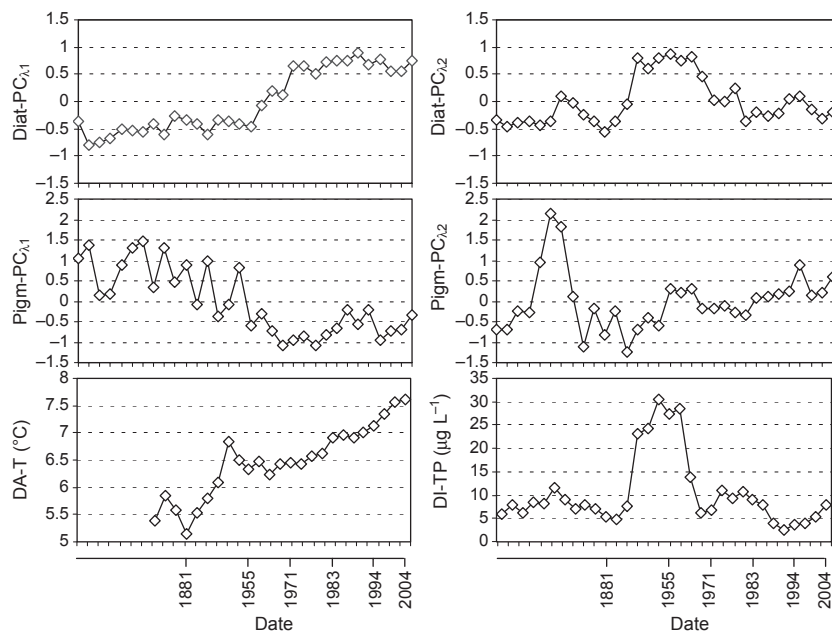
Fig. 10 (a) PCA ordination of subfossil pigment concentrations measured in the upper 16 cm of the Piburger See sediment core. Downcore variation in the principal and second component of the pigment assemblages ( $PC_1$  and  $PC_2$ ) capture 42 and 26% of the pigment assemblage variability. CD, chlorophyll derivatives (Guilizzoni *et al.*, 1983); b-car,  $\beta$ -carotene; Fucox, fucoxanthin; Oscil, oscillaxanthin; Myx-2', myxol-2'-o-methyl-methylpentoside; Allox, alloxanthin; Lutei, lutein; Echin, echinenone; Zeaxa, zeaxanthin; Myxox, myxoxanthophyll; Canta, Cantaxanthin; Okeno, okenone; Isore, isorenieratene. Abbreviations in the inset refer to pigments with minor variability, as indicated by the short arrows pointing to the lower left quadrant of the ordination space. (b) PCA ordination of the 46 subfossil diatom taxa identified in  $\geq 3$  of the analysed sediment samples with a relative abundance  $\geq 1\%$ . Downcore variation in the principal and second component of the pigment assemblages ( $PC_1$  and  $PC_2$ ) capture 32 and 18% of the diatom assemblage variability. Plot is restricted to the 19 taxa with minimum fit  $\geq 34\%$ . Taxa abbreviations as in Table 2. Abbreviations in the inset refer to diatoms with minor variability, as indicated by the short arrows pointing to the lower left quadrant of the ordination space. Numbered dots in plot A and B refer to the 32 sediment layers (each 0.5 cm thick) analysed from the core top (Nr. 1) to the bottom (Nr. 32).

1950s. Pigment PCA sample scores show a higher variability before the 1950s compared to the 1980s. Diatom and pigment changes occur after a period of increasing air temperature in the 1940s (Fig. 8). Diatom PCA sample scores on axis 2 show a first major change during the early 20th century, followed by a relative stable period during eutrophication until the 1960s, and a second phase of pronounced change in the 1970s after the start of lake restoration. Variability in diatom assemblages on PCA axis 2 corresponds to changes in DI-TP. Pigment PCA sample scores on axis 2 show a moderate increase since the late 19th century apart from a peak in the reference period related to the sand layer (Fig. 10a). Diatom PCA sample scores on axis 1 (Fig. 11) are significantly correlated with air temperature, in particular with decadal annual means. Correlation with autumn and winter temperature means reflects the impact of ice-cover duration and the onset of autumnal mixing (Table 3), while no significant correlation was found with spring and summer mean temperature. Diatom sample scores on axis 2 (Fig. 11) are significantly correlated only with DI-TP and TC and indicate a positive relation between diatom variability and lake trophic status. The pigment PCA sample scores on axis 1 (Fig. 11) are less correlated with air temperature than diatom PCA sample scores. All tested diatom species correlate with decadal annual and winter mean air temperature, apart from *C. pseudostelligera*, *A. formosa*, *F. construens* var. *construens* and *F. lapponica*.

Only *C. pseudostelligera*, *C. comensis* and *F. nanoides* are significantly correlated with DI-TP. Fucoxanthin correlates positively with decadal annual and winter mean air temperature, and TC, while oscillaxanthin is correlated negatively with temperature.

## Discussion

The analysis of lake sediment and contemporary limnological data, supported by multivariate analysis, allows the discrimination of key phases of lake trophic state during the last c. 130 years. The pre-1900 period is considered a reference period prior to major anthropogenic impacts. Higher concentrations of the pigment oscillaxanthin relate to dense *P. rubescens* populations and indicate mesotrophic conditions (Konopka, 1982; Dokulil & Teubner, 2005), while sediment organic matter content is generally >40%, and C:N ratios >10 indicate important allochthonous contribution (Smol, 2008). However, an increase in the bacterial carotenoid isorenieratene indicates the establishment of deep-water anoxia and slightly increasing lake productivity (Züllig, 1985) already occurring during the late 19th century. The elevated phosphorus and increased dry weight values in the lake sediment occurring in a sand layer at 12.0–13.5 cm depth (i.e. prior to 1881) cannot be related to major landslides, land-use changes (Forestry department Oetz, pers. comm.) or to building activities (i.e.



**Fig. 11** Principal (PC<sub>1,1</sub>) and second (PC<sub>1,2</sub>) component for the full record of subfossil pigments and diatoms. DA-T°: synthetic decadal averages of annual mean air temperature since 1840 (Böhm, ZAMG, pers. comm.); DI-TP: concentrations according to the Combined European diatom calibration set (Battarbee *et al.*, 2001). Temporal scaling according to sediment radiometric dating.



**Table 3** Relations of pigments and diatoms species scores on the first two PCA axes, synthetic averages of annual mean temperatures, key geochemical sediment variables, and most variable pigment and diatoms

|              | D1          | D2          | P1          | DA T°       | OND T°      | JFM T°      | DI-TP  | TC          |
|--------------|-------------|-------------|-------------|-------------|-------------|-------------|--------|-------------|
| D1           |             | n.s.        | -0.73       | <b>0.76</b> | <b>0.72</b> | <b>0.73</b> | n.s.   | <b>0.49</b> |
| D2           |             |             | -0.43**     | n.s.        | n.s.        | n.s.        | 0.43** | <b>0.58</b> |
| P1           |             |             |             | -0.57*      | -0.59       | -0.63       | n.s.   | -0.68       |
| Dec T°       |             |             |             |             | <b>0.93</b> | <b>0.88</b> | n.s.   | 0.39**      |
| <i>Cy-co</i> | <b>0.67</b> | n.s.        | n.s.        | <b>0.54</b> | 0.48**      | 0.47**      | -0.62  | n.s.        |
| <i>Cy-ps</i> | n.s.        | <b>0.68</b> | n.s.        | n.s.        | n.s.        | n.s.        | 0.45** | n.s.        |
| <i>Cy-ra</i> | <b>0.77</b> | n.s.        | -0.69       | 0.55**      | 0.56**      | <b>0.61</b> | n.s.   | 0.42*       |
| <i>Cy-st</i> | <b>0.76</b> | n.s.        | -0.78       | 0.42*       | 0.44**      | 0.48**      | n.s.   | 0.50**      |
| <i>Fr-cc</i> | -0.52       | -0.70       | -0.56       | -0.52**     | -0.50**     | -0.47*      | n.s.   | -0.61       |
| <i>Fr-cr</i> | <b>0.78</b> | n.s.        | -0.50**     | 0.50**      | 0.49**      | 0.52**      | n.s.   | 0.46**      |
| <i>Fr-gr</i> | -0.86       | n.s.        | <b>0.73</b> | -0.83       | -0.80       | -0.82       | n.s.   | 0.54**      |
| <i>Fr-la</i> | n.s.        | -0.84       | 0.43**      | n.s.        | -0.42*      | n.s.        | n.s.   | -0.42*      |
| <i>Fr-na</i> | <b>0.63</b> | n.s.        | n.s.        | -0.44*      | n.s.        | -0.47**     | -0.76  | n.s.        |
| <i>Fr-ua</i> | <b>0.66</b> | n.s.        | -0.50**     | 0.39*       | 0.44*       | 0.39*       | n.s.   | 0.36*       |
| Fucox        | <b>0.74</b> | n.s.        | -0.84       | <b>0.71</b> | <b>0.70</b> | <b>0.70</b> | n.s.   | 0.51**      |
| Oscil        | -0.64       | n.s.        | <b>0.58</b> | -0.50**     | -0.52**     | -0.55**     | n.s.   | n.s.        |

For each correlation Spearman's rank order  $r$  are shown; bold:  $P < 0.001$ , \*\*:  $P < 0.01$ , \*:  $P < 0.05$ . D1 and D2: diatom species scores on principal component analysis (PCA) axis 1 and 2; P1: pigment species scores on PCA axis 1; DA T°: synthetic decadal mean annual air temperature; JFM T° and OND T°: synthetic decadal mean air temperature for the periods January–March and October–December; DI-TP: TP concentrations according to the Combined European diatom calibration set (Battarbee *et al.*, 2001); TC = sediment total carotenoid concentrations (mg g LOI<sup>-1</sup>). Pigment and diatom abbreviations as in Fig. 10 and in Table 1, respectively.

just a single house in the catchment since early 1900s), but seems to be related to pronounced wet periods in the years 1867, 1876 and 1877 (Böhm, ZAMG, pers. comm.) causing enhanced catchment exports of inorganic matter and a dilution of lake organic matter, microbial and algal pigments. The reference sediment layers are dominated by small periphytic and tycho-planktonic *Fragilaria*, *Achnanthes*, *Brachisyrta*, *Cymbella* and *Navicula*, all considered as typical for nutrient-poor lakes in the Northern Hemisphere (e.g. Lange-Bertalot & Metzeltin, 1996; Kamenik *et al.*, 1999; Lotter & Bigler, 2000; Rühland & Smol, 2002; Schmidt *et al.*, 2004). The pronounced dominance of periphytic taxa and *Fragilaria* spp. in Piburger See during the pre-1880 period agree with lower than 1961–90 mean air temperatures. This is supported by several studies on temperate and alpine lakes showing a high ratio of benthic *Fragilaria* to planktonic diatoms during periods of long ice-cover duration and low summer temperature (Lotter & Bigler, 2000; Koinig *et al.*, 2002; Rühland *et al.*, 2008; Kirilova *et al.*, 2009).

The period between 1900 and 1970 is characterised by pronounced environmental changes in Piburger See indicating lake eutrophication. The sediment profile of  $\beta$ -carotene shows increasing algal biomass. The abrupt decrease in oscillaxanthin indicates a decline in *P. rubescens*, which is known as a mesotrophic species absent in strongly eutrophicated waters (Sommer, 1986).

Increasing lake productivity is supported by a rise in the bacterial carotenoid isorenieratene (Züllig, 1985), and its maximum concentration coincides with pronounced oxygen depletion in the whole water column in late 1960s. Okenone maxima in lake sediment core coincide with, and hence confirm, the increase in anoxic water volume observed in the late 1960s (Pechlaner, 1979). The rapid and abrupt increase in *C. pseudostelligera* and the concomitant decrease in benthic diatoms represent the major change in sediment diatom assemblage. This implies a shift towards a higher proportion of planktonic diatoms, which agrees with rising air temperature (Lotter & Bigler, 2000; Koinig *et al.*, 2002; Rühland *et al.*, 2008). PCA analysis confirm changes in air temperature as the dominant factor driving diatom variability in Piburger See while trophic-related factors play a secondary role. *Cyclotella pseudostelligera* and other small fast-growing *Cyclotella* species are reported to respond positively to increasing water temperature and thermal stability during the growing season (Baier *et al.*, 2004; Rühland *et al.*, 2008; Ampel *et al.*, 2010). This taxon is known to bloom in the summer metalimnion, and it may become dominant under conditions of a longer growing season and higher thermal stability during late-summer and autumn (Rautio, Sorvari & Korhola, 2000; Rühland *et al.*, 2008). Despite the prevailing role of temperature reflected in the PCA analysis, the increase in DI-TP is mainly because of the dominance of the eutraphentic *C. pseudostelligera* (Van Dam, Mertens & Sinkeldam, 1994;

Wunsam *et al.*, 1995; Schönfelder, 1997), whose optimum TP reported by the Combined European calibration set ( $39.8 \mu\text{g L}^{-1}$ , Battarbee *et al.*, 2001) is comparable to the highest DI-TP values from the 1930s to the 1960s (c.  $35 \mu\text{g L}^{-1}$ ).

The restoration period in Piburger See represents a phase of increasing sediment algal pigments, despite slowly decreasing lake water TP values. The increase in cyanobacterial pigments zeaxanthin and echinenone is because of a rise in meso-eutraphentic phytoplankton species like *Aphanothece clathrata* (West), *Chroococcus limneticus* Lemmermann and *Snowella littoralis* Chodat (Rott, 1983). After a mass development of *O. limosa* in the 1970s, this species was reported to have disappeared in the phytoplankton of Piburger See in the early 1990s (Rott, 1991) corresponding to the lowest pigment concentrations of myxol-2'-o-methyl-methylpentoside in top sediment layers. However, the presence of myxol-2'-o-methyl-methylpentoside in the whole sediment record suggests that this species has experienced major changes in its vertical distribution and possibly due to the deep-water withdrawal by the Olszowski tube (Rott, 1976).

The shift in *Cyclotella* and *Fragilaria* species has been found both in the sediment core and in phytoplankton samples (Rott, 1983; Prader, 1993; Tolotti & Thies, 2002), although centric diatoms are reported to be very scarce during the first 15 years after the start of lake restoration (Rott, 1983). The changes in *Cyclotella* and *Fragilaria* species composition in the lake sediment, which had already started during the 1960s, coincide with the slow reduction of reconstructed DI-TP and measured lake water TP down to oligotrophic levels in the 1990s. However, the distribution of the most abundant *Cyclotella* and planktonic *Fragilaria* species along the first PCA axis indicates a temperature-dependent response. The low but stable isorenieratene concentrations from the early 1990s onwards confirm the regularly anoxic conditions recorded in the hypolimnion despite improving oxygen content because of the deep-water withdrawal by the Olzewski tube (Pechlaner, 1979; Tolotti & Thies, 2002). The presence of myxol-2'-o-methyl-methylpentoside in the upper sediment core sections indicates a persistence of *O. limosa* in Piburger See. This has been confirmed by the rediscovery of living cells of *O. limosa* directly on the lake sediment surface by a diving expedition in summer 2010.

Fucoxanthin shows a pronounced increase in the uppermost sediment layer and is linked to a strong increase in *F. crotonensis* and *A. formosa* in growing seasons 2003 and 2004. Present inferred DI-TP values (c.  $15 \mu\text{g L}^{-1}$ ) overestimate lake water TP values by a

factor of about two. However, the dominance of *C. radiosa* and *C. comensis* among the centric taxa confirm present oligo-mesotrophic conditions of the lake. *Cyclotella radiosa* has often been recorded during re-oligotrophication stages of alpine lakes (Lotter & Bigler, 2000; Rühland *et al.*, 2008), while *C. comensis* is dominant in oligotrophic temperate lakes of high (Lotter & Bigler, 2000; Koinig *et al.*, 2002; Rühland & Smol, 2005) and low altitude (Wunsam *et al.*, 1995; Marchetto & Musazzi, 2001; Schmidt *et al.*, 2002; Barker *et al.*, 2005). The results of multivariate analysis show a positive temperature-related response for these oligotrophic taxa. Most recent DI-TP values in Piburger See are because of the high TP optima assigned to the most abundant planktonic taxa (i.e.  $44 \mu\text{g L}^{-1}$  for *A. formosa* and  $31 \mu\text{g L}^{-1}$  for *F. crotonensis*) by the calibration set adopted for the TP reconstruction in the present study (Battarbee *et al.*, 2001). In fact, both *A. formosa* and *F. crotonensis* are traditionally interpreted as indicators of enhanced P availability (Reynolds, 2006; Bigler *et al.*, 2007). However, recent field observations of both taxa in lakes of the Northern Hemisphere (Interlandi, Kilham & Theriot, 1999; Wolfe, Baron & Cornett, 2001; Saros *et al.*, 2005; Rühland *et al.*, 2008), as well as field and laboratory experiments (Tilman, Kilham & Kilham, 1982; Michel *et al.*, 2006), revealed a high affinity for phosphorus and low affinity for nitrogen and silica. As a consequence, both species can perform well even under depleted P availability, when combined with enriched nitrogen and silica. Despite the limited data set for lake DIN and silica in Piburger See, we assume that corresponding nutrient relations have changed and thus support recent high abundance of *A. formosa* and *F. crotonensis* as seen in 2003. We suggest that both diatom species are additionally favoured by a strong autumnal rise of Schmidt stability in Piburger See, which is supported by the high epilimnetic biovolume of *A. formosa* from June to November. *Asterionella formosa* and *F. crotonensis* can grow in the summer metalimnion because of their tolerance to low light intensity and sufficient stability to prevent entrainment into the aphotic zone (Rühland *et al.*, 2008).

The present study confirms that Piburger See experienced a period of moderate nutrient enrichment during the mid-20th century. Consequently, algal production slightly increased without blooms of toxic cyanobacteria. Our analyses reveal the predominant role of air temperature in controlling phytoplankton species composition and abundance in Piburger See.

In view of climate scenario projections for the end of the 21st century, water temperatures and thermal stability in Piburger See will increase during the growing season. This may favour the alteration in phytoplankton assemblages

and dominance of species like *A. formosa* as already occurred at the beginning of the 21st century.

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