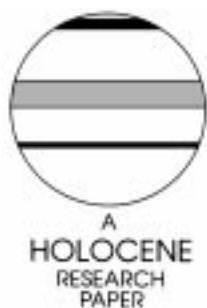# The recent eutrophication of Baldeggersee (Switzerland) as assessed by fossil diatom assemblages

André F. Lotter

(Geobotanical Institute, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland; and Swiss Federal Institute for Environmental Science and Technology (EAWAG), CH-8600 Dübendorf, Switzerland)

Abstract: Diatom analyses with an annual resolution were carried out on varves of the hypertrophic Baldeggersee (Central Swiss Plateau) for the timespan ad 1885 to 1993. They reveal seven major changes in the dominant planktonic diatoms. As a result of progressive nutrient enrichment, Baldeggersee changed in the 1910s from a *Cyclotella* to a *Tabellaria fenestrata* dominated assemblage, and eventually in the 1950s to a *Stephanodiscus parvus* dominated diatom assemblage. The timing and direction of diatom-assemblage changes in the varved sediment compare well with sedimentological and limnological observations. Partitioning of the variance in the diatom data revealed that TP is a stronger explanatory variable than temperature for these changes. A diatom-inferred total phosphorus (TP) reconstruction indicates three major steps in eutrophication, occurring at 1909, the mid-1950s and the mid-1970s. Comparison with TP measurements in the water column demonstrates that the diatom-TP inference model used is able to hindcast past TP concentrations reliably. The major steps in eutrophication led to decreases in diatom diversity and also resulted in a progressive increase of calcite grain-size. The lake restoration programme established since 1982 shows no direct impact on the composition of the diatom assemblages. However, the decrease in phosphorus loads since the mid-1970s is reflected in the diatom assemblages and in decreasing diatom-inferred TP concentrations.

Key words: Varves, laminated sediments, lacustrine sediments, lake eutrophication, human impact, diatom-inferred total phosphorus, diversity, Baldeggersee, Switzerland.

Introduction

Anthropogenically induced nutrient enrichment has become one of the major problems for aquatic ecosystems. Baldeggersee is a typical example of a Swiss Plateau lake that has undergone strong cultural eutrophication during this century. For water protection legislation and lake restoration purposes it is essential to have knowledge about the background values for important limnological variables and about their natural variability (Gächter and Imboden, 1985). Very few long observations on lakes exist that follow the development and the interannual variability of a limnic system over more than one or two decades (e.g. Maberly *et al.*, 1994; Bürgi, 1994). To assess the dynamic nature of lake development these time-series are often too short and their onset usually does not include pre-eutrophic conditions. Manipulation of whole lakes can provide insights into the mechanisms and dynamics of aquatic responses to nutrient enrichment (e.g. Schindler, 1985), but only palaeolimnological sediment studies are able to provide long time-series that help to assess the natural variability in aquatic systems (Anderson and Battarbee, 1994) as well as past

trophic states (Anderson, 1995). High-resolution analyses (e.g. Klee and Schmidt, 1987; Simola *et al.*, 1990; Leavitt *et al.*, 1993; Alefs *et al.*, 1996) of recent sediments provide a link between palaeo- and neolimnology. With its varved sediments (Lotter *et al.*, 1997c), Baldeggersee provides a unique opportunity to investigate its eutrophication history on a precise and high-resolution timescale that would allow an assessment of the timing and the rates of nutrient enrichment (see Wehrli *et al.*, 1997).

The aims of the present study are as follows. First, to investigate the dynamics and interannual variability of the diatom composition in the varved sediment of Baldeggersee on an annual basis and to compare it with historical phytoplankton data. Second, to compare diatom-inferred total phosphorus (TP) concentrations with measured TP values as a means of evaluating independently a phosphorus transfer function for the Alps (Lotter *et al.*, 1998). Third, to use the diatom-inferred TP reconstruction to reveal dates of phosphorus enrichment, and details of the eutrophication process in Baldeggersee over the last 110 years. Finally, to perform a quantitative assessment of the effects of nutrient loadings and of climate on the diatom assemblages as a

means of exploring the relative influence of these two factors on the composition of recent diatom assemblages in Baldeggersee.

Site

Baldeggersee ($47°10'$N, $8°17'$E) is located at an elevation of 464 m a.s.l. on the central Swiss Plateau, to the north of Lucerne (Figure 1). The lake has a simple basin with a maximum depth of 66 m and is of glacial origin. It has a surface area of 5.2 km^2, a volume of 0.173 km^3, and a water renewal time of 5.6 years. Its hydrological catchment is 67.8 km^2, of which 77% consists of intensively used agricultural land. The lake is protected from prevailing westerly winds by high hills (up to 400 m) to the east and west, thus inhibiting wind-induced mixing.

In the 1920s Nipkow (1927) discovered light and dark laminae in the topmost sediments of Baldeggersee and investigated the cyclicity of auxospore formation of different diatoms using these annual layers. He dated the onset of the uninterrupted annual lamination to the year 1885. Using modern sampling methods and thin-section analyses, Lotter *et al*. (1997c) verified the varved nature of the sediment and Nipkow's chronology.

Owing to strong anthropogenically nutrient enrichment, Baldeggersee has become hypertrophic in the course of this century and distinct blooms of *Oscillatoria rubescens* have been repeatedly reported (Adam and Birrer, 1943). Sedimentary fossil carotenoid analyses revealed changes in phytoplankton composition and abundance in historical time (Züllig, 1982). The increasing nutrient enrichment of Baldeggersee is also well documented by a drastic reduction in the Secchi disc depth, from an average of 4.9 m in 1910/11 to 2.5 m in 1938/39, and eventually to 1.6 m in 1957–59 (Züllig, 1982).

At the beginning of this century complete oxygen depletion was observed at water depths >60 m. In 1940 the water/sediment interface below 40 m, and in 1975 below 10 m, was anoxic (Niessen and Sturm, 1987). Since 1967 and 1975 sewage treatment plants have operated in the catchment. However, the lake receives its major phosphorus load of 10–18 tons P yr^{-1} (Wehrli and Wüest, 1996) from intensive agriculture in the catchment. Moreover, substantial P release from the sediment occurs (Gächter, 1987). Since 1982 a lake restoration programme has been established (Stadelmann, 1984). In order to enhance mixing of the water column and to fulfil the Swiss quality standard of 4 g $O_2 m^{-3}$ for natural lakes, oxygen (4.5 tons O_2 d^{-1}) during summer and air during winter are pumped into the deepest part of the lake. Since 1982 bioturbation has prevented varve formation above 55 m of water depth due to the better oxygen regimes at the water/sediment interface. Below this water depth mineralization of organic carbon is still causing oxygen depletion that

allows the formation and preservation of varves. The algal biomass is dominated by cyanophytes and has even increased since the onset of restoration (Bürgi, 1994) due to enhanced nutrient circulation.

Geochemical studies on the Baldeggersee varves showed a close correlation between Mn and oxygen availability. High values of Cr/Mg, Mo and Cr/V indicate periods of stable anoxic conditions (Schaller,1996). Stratigraphical analyses (Lotter *et al*., 1997c) have shown that before 1885 there are packets of 5–10 varves interrupted by massive, homogeneous marl beds (Figure 2; see also Züllig, 1982), indicating oscillating hypolimnetic oxygen levels, whereas in 1885 the bottom water definitely became anoxic. Between 1885 and 1905 varves are thin, with a low organic carbon content, whereas between 1905 and 1910 the varve thickness increased. At the onset of the 1960s, during the time of highest phosphorus concentrations in Baldeggersee, the total phosphorus concentrations in the sediments, as well as the varve thickness and the total accumulation rates, increased (Lotter *et al*., 1997c). Statistical analyses of the Baldeggersee varves (Lotter and Birks, 1997) indicate that the lake restoration programme installed in 1982 had a significant impact on the formation of the seasonal layers. Furthermore, variance partitioning revealed that trophic state explains only *c*. 5%, whereas climate accounts for about 28% of the variance in the varve thickness data between 1920 and 1981, before lake restoration had a strong impact on the varve formation. Annual precipitation was found to be a strong predictor of the thickness of both the dark layer and the total couplet thickness, whereas summer precipitation was important for the thickness of the light layer (Lotter and Birks, 1997).

Methods

In summer 1993 three freeze-cores were taken in the deepest part of the basin with a special freeze-corer (Lotter *et al*., 1997b). A varve chronology was established on the basis of thin-section analyses and successfully cross-checked by ^{137}Cs and ^{210}Pb dating of annual layers (Lotter *et al*., 1997c). In core BA93-C each single annual layer between 1993 and 1885 was scratched off the frozen sediment slab (Lotter *et al*., 1997b; 1997c). The freeze-dried sediment of these 109 layers was then used for a variety of biological and geochemical analyses (see Wehrli *et al*., 1997). An annual cycle in this varve chronology corresponds to a hydrological year rather than to a calendar year. Stratigraphically, the annual cycle starts with the spring calcite precipitation and ends at the top of the winter organic layer, before the next calcite precipitation occurs (see Lotter, 1989a; Lotter *et al*., 1997c).

For diatom analysis *c*. 0.5 g of freeze-dried sediment was treated with hot 10% HCl and 30% H_2O_2 before mounting on
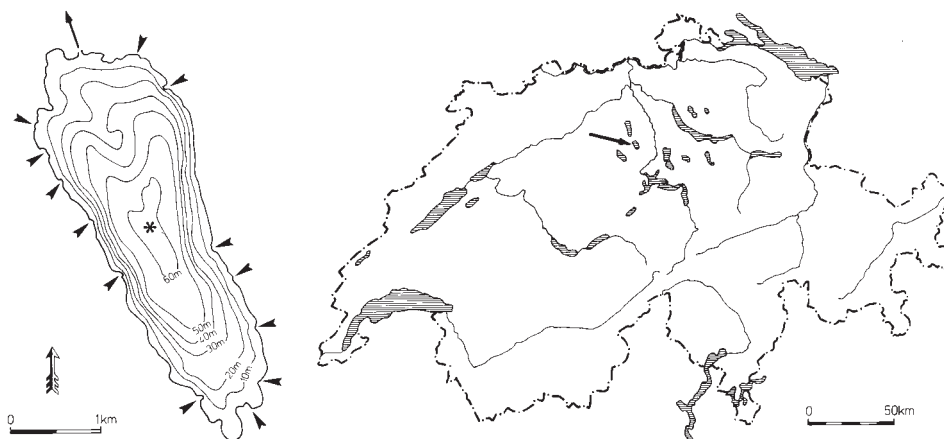
Figure 1 Location of Baldeggersee within Switzerland (marked by arrow) and bathymetric map indicating the location of the coring site (star).

Figure 2 Freeze-core taken in the deepest part of Baldeggersee at 66 m of water depth. The water/sediment interface represents autumn 1993.

slides with Naphrax®. A minimum of 250 valves was counted for each annual sample using a Leitz DM microscope with a magnification of 1250× and phase contrast. Diatom taxonomy follows Krammer and Lange-Bertalot (1986–1991).

Zonation of the diatom stratigraphical data was carried out on percentage data, using ZONE (Lotter and Juggins, 1991) which implements a variety of different numerical zonation methods (see, e.g., Birks and Gordon, 1985; Birks, 1986). The significant number of diatom assemblage zones (DAZ) was assessed by a broken stick model according to Bennett (1996). Rarefaction analysis (Heck *et al.*, 1975) was carried out using the program RAREPOLL (Birks and Line, 1992). Biostratigraphic rate-of-change analysis relied on the program RATEPOL (J.M. Line and H.J.B. Birks, unpublished program) with chord distance between adjacent samples used as the dissimilarity measure. Diatom-inferred TP values and sample-specific error estimates (500 simulations) were assessed using weighted-averaging partial least

squares (WA-PLS) calibration methods implemented by the program WAPLS (ter Braak and Juggins, 1993). Modern diatom assemblage analogue matching was carried out by the program MAT (S. Juggins, unpublished program). Squared chord distance was used as the dissimilarity coefficient (Overpeck *et al.*, 1985).

Because the floristic gradient in the diatom data (as assessed in a DCCA with sample age as the sole constraining variable) is greater than 2 SD, unimodal methods were used as recommended by ter Braak and Prentice (1988) and Birks (1995). For the variance partitioning analysis a series of partial Canonical Correspondence Analyses (CCA) were carried out using the program CANOCO 3.12 (ter Braak, 1987–1992) on square-root transformed percentage data of all taxa with a minimum number of four occurrences and an abundance of at least 1%. For CCA averaged monthly mean air temperatures (1885–1993) of the climate stations Zürich, Bern and Basel were used. Lake restoration was modelled as a binary variable, with a value of 1 designating

samples from the period between 1993 and 1982, and the value 0 being used for samples older than 1982. To model nutrients, measured mean spring circulation TP concentrations for the uppermost 15 m of the water column (seven measurements) back to 1958 were used. For the period before 1958 the TP concentrations have been assumed to decrease linearly by 2 μg l^{-1} yr^{-1} back to 1885.

Results and discussion

Diatom stratigraphy
Diatom analysis of the 109 annual layers from Baldeggersee (Figure 3) reveals a distinct succession, with sharp transitions between intervals characterized by specific dominant diatom taxa. As could be expected from a core taken in the deepest part of Baldeggersee the assemblages are dominated by planktonic taxa. The diagram was subdivided into seven statistically significant diatom assemblage zones (DAZ; Table 1). Their statistical significance was assessed by use of a broken-stick model (Bennett, 1996).

The stratigraphical grouping of taxa shows a succession found in many anthropogenically eutrophied hardwater lakes (e.g. Lotter, 1989b; Alefs *et al.*, 1996). After a long dominance of mesotrophic *Cyclotella* species (DAZ BA-1, but see also data from Züllig, 1982, going back to the fifteenth century), taxa with a high Si:P preference (van Donk and Kilham, 1990; Rosen, 1981) such as *Fragilaria crotonensis*, *Asterionella formosa*, and *Tabellaria fenestrata* (DAZ BA-2) become more important, indicating a first step in eutrophication around 1910. A marked increase in the percentages of *Stephanodiscus minutulus* and, to a minor extent, of *S. parvus* between the late 1920s and the mid-1940s (DAZ BA-3) was observed. *S. minutulus* has a very low Si:P optimum and this dominance change in the diatom assemblage may reflect further phosphorus enrichment.

Between 1945 and 1955 *F. crotonensis* and *F. ulna* var. *acus* become more important again (DAZ BA-4). *F. ulna* var. *acus* (*Synedra ulna*) is known to be Si-limited (Kilham, 1986; Kilham *et al.*, 1986). It temporarily disappeared from the record between 1960 and the early 1980s.

A final step in eutrophication can be inferred by the rapid expansion and dominance of the hypertrophic *S. parvus* (Kilham *et al.*, 1986; Anderson, 1990) between the mid-1950s and 1970s (BA-5). The appearance of *Aulacoseira granulata*, a species with high Si and P requirements (Kilham and Kilham, 1975; Rosen, 1981; Tilman *et al.*, 1982; van Donk and Kilham, 1990) in the 1970s (BA-6) coincided with the highest measured TP values in the water column (Wehrli *et al.*, 1997; see also Figure 5).

Since 1980 the diatom assemblages were again dominated by *S. parvus* (BA-7) and towards the top of the core *Cyclotella* species appear again in low percentages. As the onset of the lake restoration programme changed the circulation pattern in the lake substantially, changes in the diatom assemblages could be expected. Due to enhanced turbulent mixing (Lund, 1971), heavily silicified taxa, such as *A. granulata*, could be expected to stay longer in the water column and thus become more important in the assemblages. This is, however, not the case in the fossil record. The assemblages do not show a direct effect of the restoration programme. The decrease in phosphorus loading (Figure 5) may be inferred from gradual changes (e.g. decreases in *S. parvus* and *A. formosa*), with simultaneous increases in *F. crotonensis* and *Cyclotella* species.

These biostratigraphical results compare well with phytoplankton analyses carried out sporadically in Baldeggersee (Adam and Birrer, 1943; Bachofen, 1960; Durrer, cited in Züllig, 1982). Nipkow (1927) described the expansion of *Tabellaria fenestrata* and the major decline in abundance of *Cyclotella* spp. occurring in

1909. Besides the confirmation of the diatom stratigraphy, this agreement provides further evidence for the reliability of the varve chronology for core BA93-C. Sediment investigations by Züllig (1982) show a major change from centric to pennate diatoms occurring around 1910. This was accompanied by the first substantial increase in diatom accumulation rates, especially of pennate diatoms. Around 1965 he reported another strong increase in diatom accumulation rates, this time of both centric and pennate taxa, with maximum accumulation rates in 1977/78 (i.e. the years of highest TP concentrations, see Wehrli *et al.*, 1997).

Variance partitioning
Lotter and Birks (1997) were able to show that climatic variables (annual precipitation and summer temperature) as well as lake restoration accounted for most of the explained variance in the varve thickness in Baldeggersee. Using a similar approach, I have estimated the amount of variance in the diatom data explained independently by trophic state and climate. This provides information on the relative magnitude of factors controlling the recent diatom assemblage composition in Baldeggersee.

The variables used in the partial CCAs were measured (1958–1993; Figure 5) and extrapolated TP concentration (1885–1957) during spring circulation, presence (1982–1993) or absence of lake restoration (1885–1981), and yearly (1885–1993) values of mean spring air temperatures (March, April, May). An interaction term between TP concentrations and lake restoration was introduced because the changed mixing regime is thought to have had an influence on the nutrient cycling in the water column. Mean spring air temperatures were used because only spring temperature accounts for a statistically significant amount of the total variance (1.7%, p = 0.04 as assessed by 999 unrestricted Monte Carlo permutations) in CCAs with seasonal temperatures as the sole constraining variables.

The total variance of the diatom data was partitioned into four components (Table 2): (i) variance due to lake trophic state only (modelled by TP, lake restoration, and their interaction) independent of climate; (ii) variance due to climate only (modelled by mean spring air temperatures) independent of trophic state; (iii) covariance between trophic state and climate; and (iv) variance unexplained by this model.

Because of the strong temporal autocorrelation in the data, the diatom time-series was detrended by partialling out sample age as a covariable in all the analyses. Of the 14.2% (p = 0.01) of total variance explained by trophic state and climate (Table 2), a major but statistically insignificant part (12.6%, p = 0.06) is explained by TP concentration, presence of the lake restoration programme, and their interaction. Only a small, statistically insignificant part (1.1%, p = 0.08) of the variance is explained by mean spring air temperature.

Mean spring air temperatures may be used as a proxy for mean spring water temperatures (Livingstone and Schanz, 1994; Livingstone and Lotter, 1998). Warmer springs affect water temperatures and thus may allow an earlier diatom bloom which can have implications on the species composition of the vernal diatom bloom (Willén, 1991). Several studies indicate a close relationship between climate and the composition of diatom assemblages (Pienitz *et al.*, 1995; Wunsam *et al.*, 1995; McQuoid and Hobson, 1996; Lotter *et al.*, 1997a). Recent studies by Anderson *et al.* (1996) indicate a relationship between summer temperatures and diatom diversity in varved sediments of a Swedish lake. However, they observed a 20-year lag phase and therefore concluded that it was mainly climatically induced changes in the catchment that led to changes in the diatom assemblages. In Baldeggersee, however, the trophic signal seems to be the driving force for the changes in diatom assemblages. It could be speculated that climate may have a more significant influence on the composition of diatom assemblages in oligotrophic and mesotrophic lakes with less
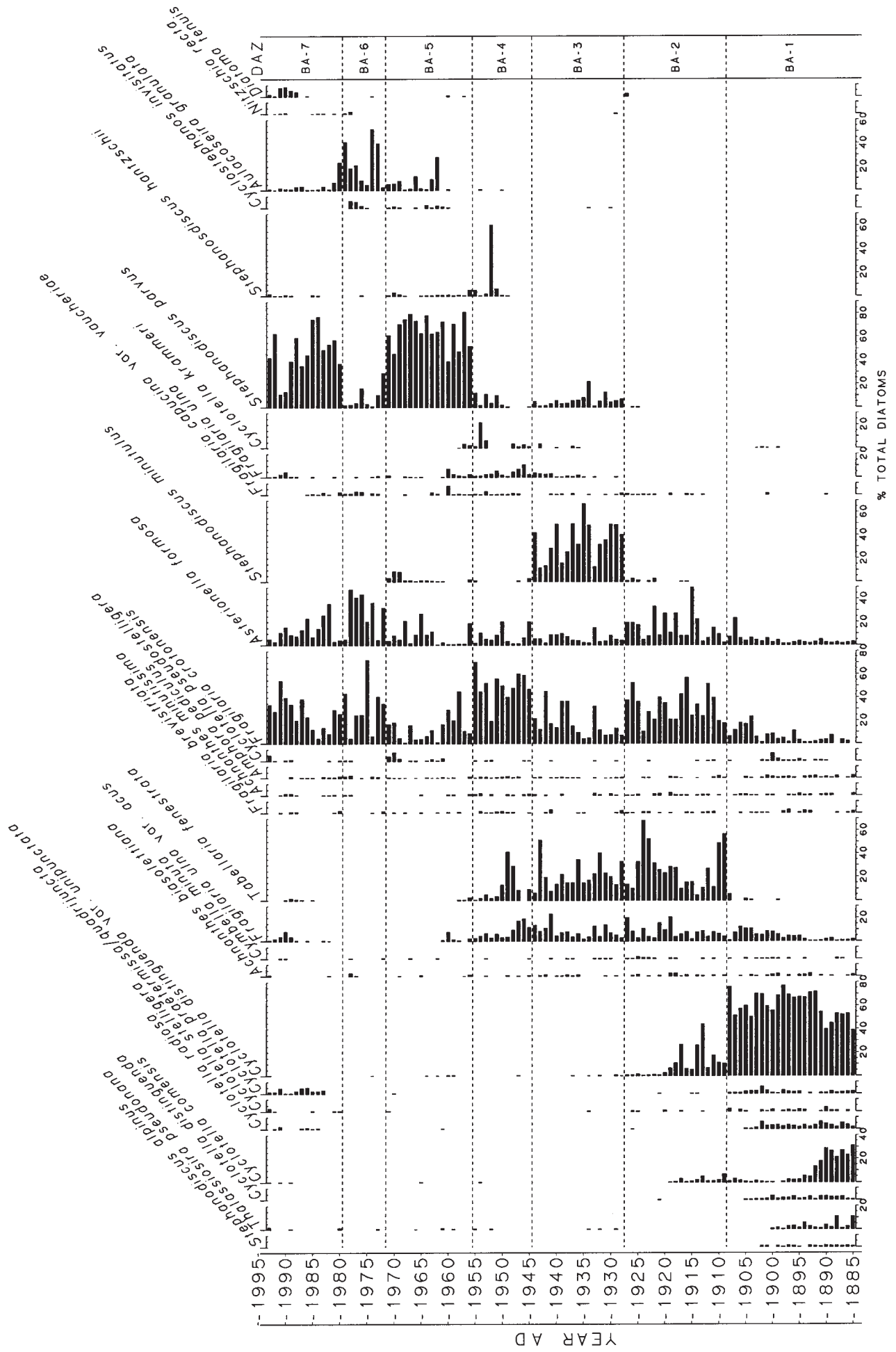
Figure 3 Diatom succession in Baldeggersee freeze-core BA93-C between 1885 and 1993. Only the major taxa are shown.

Table 1 Diatom assemblage zones (DAZ; Figure 3) in relation to chronology and taxonomic composition. The number of statistically significant zones has been assessed according to the broken-stick model (Bennett, 1996)

Zones	Chronology	Zone name (dominant taxa)	Taxonomic composition
BA-1	1885–1908	*Cyclotella distinguenda* var. *unipunctata* zone	with *C. comensis, C. radiosa, C. pseudostelligera, C. praetermissa/quadrijuncta, Thalassiosira pseudonana, Stephanodiscus alpinus, Fragilaria ulna* var. *acus, F. crotonensis, Asterionella formosa*
BA-2	1909–1927	*Tabellaria fenestrata-F. crotonensis* zone	with *A. formosa, F. ulna* var. *acus, C. distinguenda* var. *unipunctata, C. comensis*
BA-3	1928–1944	*Stephanodiscus minutulus* zone	with *T. fenestrata, F. crotonensis, F. ulna* var. *acus, S. parvus, A. formosa*
BA-4	1945–1955	*Fragilaria crotonensis* zone	with *T. fenestrata, F. ulna* and var. *acus, A. formosa, C. krammeri, S. hantzschii, S. parvus*
BA-5	1956–1971	*Stephanodiscus parvus* zone	with *F. crotonensis, A. formosa, Aulacoseira granulata, S. minutulus, S. hantzschii, C. pseudostelligera, Cyclostephanos invisitatus*
BA-6	1972–1979	*A. formosa-F. crotonensis-A. granulata* zone	with *S. parvus, C. invisitatus, F. capucina* var. *vaucheriae*
BA-7	1980–1993	*S. parvus-F. crotonensis-A. formosa* zone	with *C. praetermissa/quadrijuncta, F. ulna* and var. *acus, A. granulata, Nitzschia recta, Diatoma tenuis*

Table 2 (a) Partitioning of the variance in the diatom data of Baldeggersee core BA93-C

Response variable	Covariable(s)	Explanatory variable(s)	% variance explained	p[1]
diatoms	age	TP	4.3	0.16
diatoms	age	Restoration	5.6	0.45
diatoms	age	TP*Restoration	4.0	0.46
diatoms	age	Spring temperature	1.7	0.04•
diatoms	age	TP + Restoration + Spring temperature + TP*Restoration	14.2	0.01•
diatoms	age + Spring temperature	TP + Restoration + TP*Restoration	12.6	0.06
diatoms	age + TP + Restoration + TP*Restoration	Spring temperature	1.1	0.08

[1] exact Monte Carlo probability (999 permutations)
• significant at the 5% level

(b) Results of the variance partitioning of the diatom data in Baldeggersee core BA93-C using trophic state (TP, presence of lake restoration, and their interaction) and mean spring air temperature as explanatory groups of variables

Unexplained variance	85.8%
Effects of trophic state independent of spring temperature	12.6%
Effects of climate independent of trophic state	1.1%
Interaction due to covariation of trophic state and climate with age	0.5%

available nutrients than at Baldeggersee. Nevertheless, factors such as grazing, competition with other algae, mixing of the water column, vegetation and land use in the catchment should not be disregarded when assessing direct and indirect effects of climate on aquatic ecosystems.

Rates of change

Rate-of-change measures in biostratigraphical data are commonly expressed as dissimilarity measures between adjacent samples divided by a standard time unit (Jacobson and Grimm, 1986). As the yearly diatom stratigraphy from Baldeggersee represent an exceptional case of evenly spaced samples from a chronological viewpoint, the rate of change can be assessed by simple chord distance measures between samples. Ambiguities caused by chronological problems (e.g. Lotter *et al.*, 1992) are thus avoided.

As a result of the inherent natural interannual variability in dia-

tom composition, the rate-of-change curve (Figure 4) of the Baldeggersee diatom stratigraphy is very spiky. The highest rates of change occur between the following years: 1908/09, 1927/28, 1933/34, 1943/44, 1944/45, 1952/53, 1955/56, 1961/62, 1974/75 and 1978/79. Not surprisingly, most of these peaks coincide with boundaries of the diatom zones (Table 1), as the major changes in diatom assemblages take place at these levels. In contrast to the geochemical composition of the varves (Schaller, 1996; Lotter and Birks, 1997) the onset of restoration did not seem to directly influence the composition of the diatom assemblages.

Phosphorus

The annual resolution of the subfossil diatom record from Baldeggersee permits a comparison with the available water chemistry data. TP measurements from the water column are available since 1957 (Wehrli *et al.*, 1997) and, therefore, represent an excellent

Rarefaction

Rates of Change
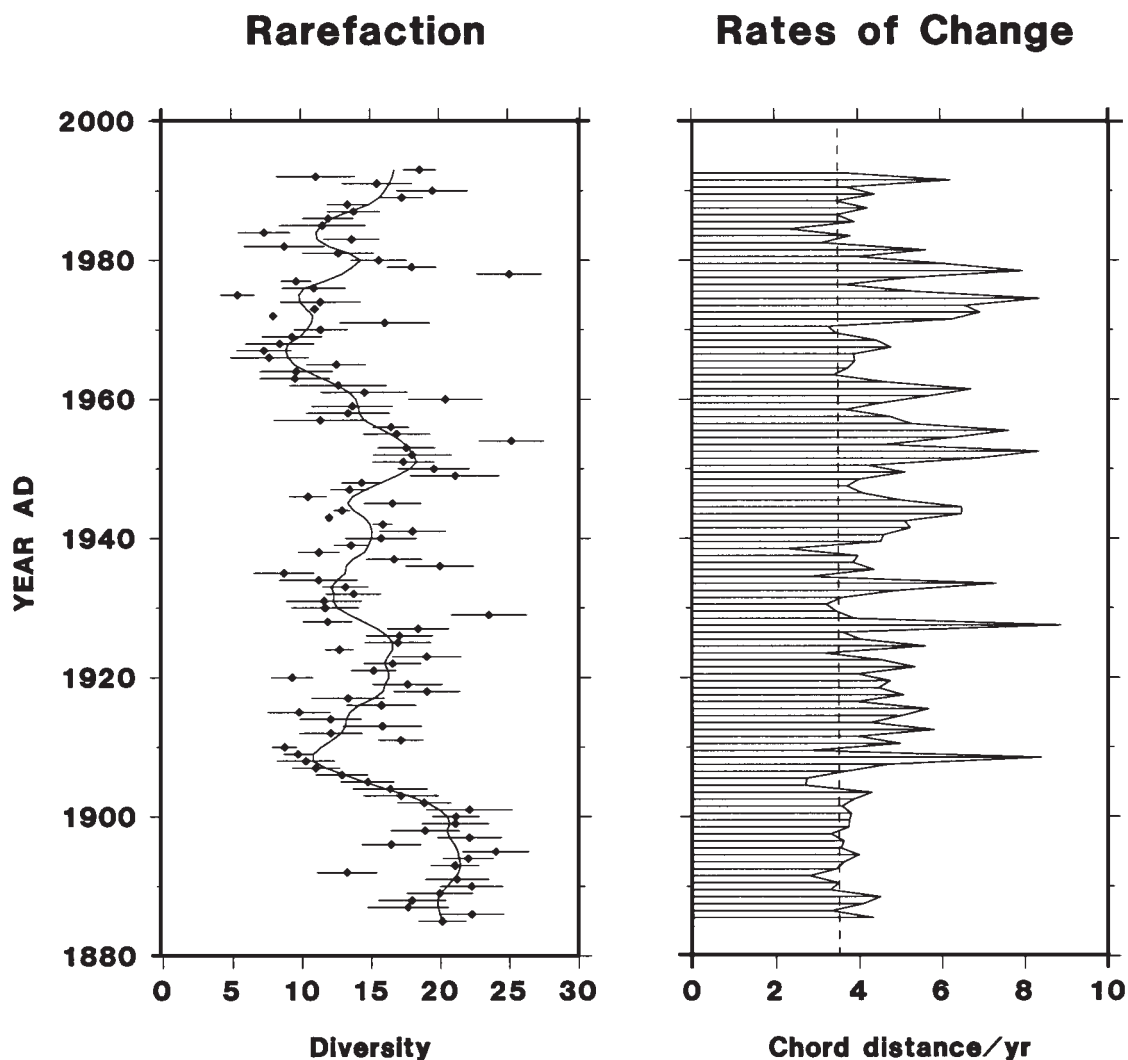
Figure 4 Diatom diversity as assessed by rarefaction analysis and rate of diatom assemblage change in the varved sediment of Baldeggersee between 1885 and 1993. The error bars in the rarefaction diagram represent the 95% confidence interval, whereas the dashed line in the rates of change diagram indicates the approximate significance level (2.5th percentile). The line through the rarefaction estimates is based on a LOWESS smoother.

opportunity for a comparison with the diatom-inferred TP reconstructions. Lotter *et al.* (1998) have developed a WA-PLS diatom-TP calibration set for the Alps, covering a surface-water spring TP gradient of 10–520 μg l^{-1}. This modern training set is characterized by a jack-knifed r^2 of 0.786 and a root-mean-squared-error-of-prediction (RMSEP) of 0.19 log$_{10}$ μg TP l^{-1} (for details on numerical methods see ter Braak and Juggins, 1993; ter Braak *et al.*, 1993; Birks, 1995).

The trend of the diatom-inferred WA-PLS TP reconstruction compares well with the measured spring TP concentrations (Figure 5) for the period where lake water chemistry monitoring data are available. The first major increase in inferred TP concentrations occurs in 1909 when the TP values shift from below 50 μg l^{-1} to over 100 μg l^{-1}. According to the classification of OCDE (1982) this would signify a change from eutrophic to hypertrophic conditions. The inferred TP values gradually increase with some fluctuations to 150–200 μg l^{-1} until the mid-1950s. In 1956 another step in inferred TP concentrations takes place, increasing to levels of 200–300 μg l^{-1}. The inferred TP concentrations reach a maximum in 1977, coinciding with the maximum measured TP values in the epilimnion, and subsequently decrease again. However, the inferred values are consistently lower than the measured ones during the years of highest TP concentrations (Figure 5). The diatom-inferred TP values display a higher interannual variability than the measured spring values. This may be attributed to the inherent interannual varia-

bility in the diatom data. Averaging several years, as suggested by Bennion *et al.* (1995), would, in fact, smooth the inferred TP curve and remove much of the scatter, but would not solve the problem of underestimating the maximum TP concentrations. Several studies have shown an overestimation of diatom-inferred TP concentrations compared to measured data (e.g. Anderson and Rippey, 1994; Bennion *et al.*, 1995) at the lower end of the TP gradient. Besides WA model-inherent problems, this has commonly been interpreted as a lack of suitable low TP sites in the training sets (e.g. Anderson and Rippey, 1994). In the present case, however, the modern training set with its median TP concentration of 31 μg l^{-1} (see Lotter *et al.*, 1998) is likely to be biased towards low and medium TP sites and the model thus generally underestimates high TP values (Lotter *et al.*, 1998). This is in contrast to the study by Marchetto and Bettinetti (1995) on Northern Italian lakes, where their WA model overestimated the higher end of TP concentrations. There is also considerable annual variability in epilimnetic TP (e.g. Gibson *et al.*, 1996). Considering this, the diatom-inferred values are still well within the annual TP range (Figure 5). Moreover, not all diatoms bloom during spring (e.g. Alefs *et al.*, 1996). Taxa blooming in summer and autumn (e.g. *Fragilaria crotonensis*) generally encounter lower TP concentrations during this season. In addition to TP, intra- and interannual variability in climate (e.g. Kilham *et al.*, 1996; Livingstone and Lotter, 1997), nutrient ratios (e.g. Sommer, 1989), grazing pressure (e.g. Bürgi *et al.*, 1985), light availability, and

BA93-C Diatom-inferred TP   Grain-size
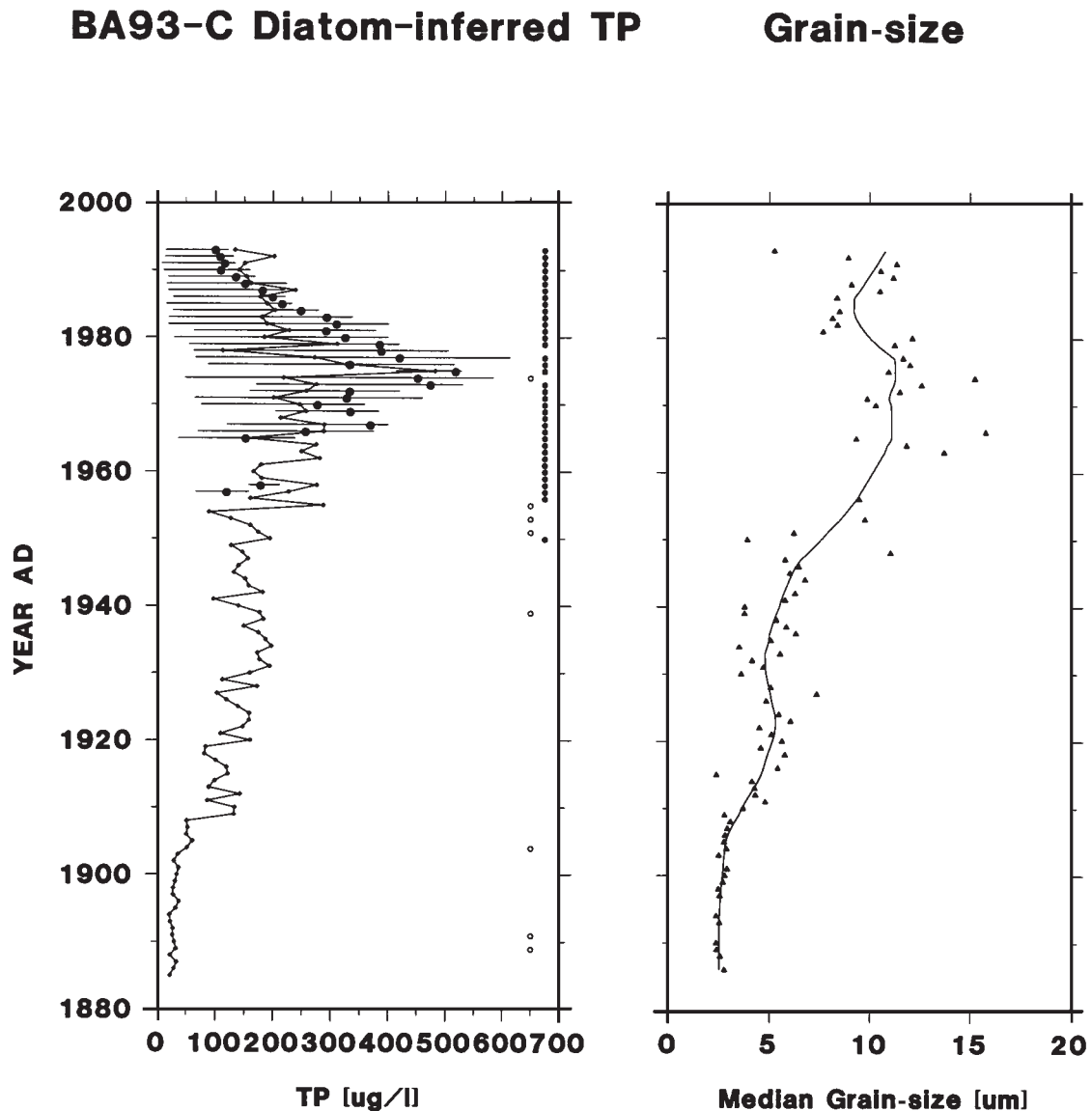
Figure 5 Measured total phosphorus (TP) during spring circulation compared to diatom-inferred TP values and median grain-size distribution in the Baldeggersee annual layers (see Lotter *et al.*, 1997c). The large filled circles show the measured spring circulation TP values for the uppermost 15 m, whereas the horizontal lines represent the annual TP range in the uppermost 15 m of the water column. The dots on the right side of the graph represent samples with close (filled dots; 2nd percentile) and good modern analogues (open dots; 5th percentile).

competition between algal groups (e.g. Tilman, 1977) may, among others, all be important factors that control the qualitative and quantitative composition of diatom assemblage.

Comparison of the Baldeggersee samples with the modern surface-sediment samples in the calibration data-set (see Lotter *et al.*, 1998) was made to find the closest modern analogues and to assess the reliability of the diatom-inferred TP reconstruction. Close and good analogues were defined as core samples having a squared chord distance of less than 0.586 and 0.688, respectively, which represent the second and fifth percentile of the distribution of the dissimilarities among the 77 samples in the modern calibration set (Birks *et al.*, 1990; Bartlein and Whitlock, 1993). According to this procedure the samples representing the years between 1993 and 1950 have close analogues, whereas there are few good analogues for the older samples (years 1939, 1904, 1891, 1889; Figure 5). This mainly reflects the lack of assemblages with high amounts of *Tabellaria fenestrata* and *Fragilaria crotonensis* in the modern calibration data set, whereas modern *Stephanodiscus parvus* assemblages are more common (Lotter *et al.*, 1998).

The reconstructed epilimnetic TP concentrations show an increasing trend until 1977 with a subsequent decrease. Two inde-

pendent lines of stratigraphical evidence may be used to support the TP reconstructions in Baldeggersee. First, results of Boucherle and Züllig (1983) show a complete change in cladocera assemblages from *Bosmina longispina* to *B. longirostris* occurring around 1910 in the sediment of Baldeggersee. *B. longirostris*, commonly regarded as an indicator of eutrophic conditions (Hofmann, 1987) subsequently reached up to 20 times higher accumulation rates than *B. longispina*. Increasing diatom and carotenoid accumulation rates around 1910 (Züllig, 1982) are also indicative of a very dynamic step in nutrient enrichment.

Second, Niessen and Sturm (1987) suggested a relationship between PO_4 concentrations in Baldeggersee and the size of calcite crystals. New results (Lotter *et al.*, 1997c) support this hypothesis. Growth of calcite crystals is inhibited when PO_4 is present in the lake water (Kunz and Stumm, 1984; Dove and Hochella, 1993). As PO_4 concentration is greatest in spring and as it inhibits carbonate precipitation, this leads to supersaturation of carbonate in the water column. The first algal bloom reduces nutrients in the water column substantially, which then permits fast precipitation of large calcites. During summer, when PO_4 concentrations decrease, precipitation of much smaller, microcrystalline calcites takes place (Kunz and Stumm, 1984). Grain-size

analyses in annual layers of core BA93-C (Figure 5) show increases in calcite size that parallel the increased diatom-inferred TP concentrations beginning in 1909, continuing in the mid-1950s and mid-1960s, and decreases in calcite size coincident with the decrease in TP in the late 1970s.

Diversity

Rarefaction analysis was used to estimate the biostratigraphical diversity of the diatom flora in Baldeggersee. As the sampling in sediment depth as well as in time was contiguous, the counting sums were kept lower than in traditional palaeolimnological investigations (e.g. Battarbee, 1986). Because of the relatively low sums and the dominance of a few planktonic taxa (*Cyclotella distinguenda* var. *unipunctata*, *Tabellaria fenestrata*, *Fragilaria ulna* var. *acus*, *F. crotonensis*, *Stephanodiscus minutulus*, *S. parvus*, *Asterionella formosa*, *Aulacoseira granulata*), the number of taxa inferred by rarefaction is low. Nevertheless, the results of the rarefaction analysis (Figure 4) show distinct trends through time. Around 1900 the diversity decreases rapidly and reaches a first minimum in 1910. After a sharp increase, the diversity values oscillate until, in the late 1940s, they show a decreasing trend again. Minimum values are reached in the late 1960s before diversity increases again with some fluctuations. The diatom diversity closely mirrors the different phases of nutrient enrichment in Baldeggersee, with decreasing numbers of taxa during the eutrophication phases. After each eutrophication pulse the number of taxa initially decreases, but the assemblage diversity recovers, at least partially, following each pulse. These results compare well with experimental evidence of algal species richness in relation to nutrient enrichment (e.g. Proulx *et al.*, 1996).

Conclusions

The high-resolution diatom stratigraphy of Baldeggersee highlights the potential of palaeolimnological methods in reconstructing past environments. The use of annually laminated sediments allows a direct and precise comparison with time-series of measured chemical and physical environmental data that are of importance for aquatic ecosystems. This 'modern' palaeolimnological case study covering the last 110 years allows several conclusions to be drawn.

1) Disentangling the effects of nutrients and climate on the composition and relative abundance of diatom assemblages is important in all discussions about past diatom changes. For Baldeggersee the influence of TP concentrations and the lake restoration programme were more important for the changes in the diatom assemblages than climatic variables such as spring temperature.
2) A quantitative WA-PLS inference model compiled for central Europe that relates diatom assemblages to epilimnetic TP concentrations may be reliably applied to subfossil diatom assemblages in Baldeggersee. Comparison of measured and hindcasted TP concentrations are, within the errors of the model, in good agreement.
3) Qualitative changes in the diatom assemblages as well as diatom-inferred TP concentrations point to three major steps in anthropogenic eutrophication during the last 110 years and one decrease in trophic status after the installation of the lake restoration programme in 1982 in Baldeggersee. Synchronous increases and a recent decrease in calcite grain-size present independent stratigraphical evidence for the changes in trophic status and support the timing and direction of eutrophication.
4) Interannual variability in the taxonomic diatom composition is rather low. The various significant changes in assemblage composition took place within time spans of a single year. This suggests that these changes have been triggered because certain threshold values with regard to phosphorus and/or silica concentrations have been reached.
5) The pulses of eutrophication led to decreased diatom diversity. After initial phases of low diversity the diatom diversity slowly recovered but did generally not reach the original diversity level again. The strong oscillations observed in diversity seem to mirror the disturbance regime controlled by nutrient enrichment and could indicate that not only the diatom coenoses but also the whole aquatic food web has been in disequilibrium.

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References

Adam, F. and **Birrer, A.** 1943: Biologisch-chemische Studie am Baldeggersee. *Mitteilungen Naturforschende Gesellschaft Luzern* 14, 21–98.

Alefs, J., Müller, J. and **Lenhart, B.** 1996: Die jährliche Änderung der Diatomeenvergesellschaftung seit 1958 in einem warvendatierten Sedimentkern aus dem Ammersee (Oberbayern). *Limnologica* 26, 39–48.

Anderson, N.J. 1990: The biostratigraphy and taxonomy of small *Stephanodiscus* and *Cyclostephanos* species (Bacilllariophyceae) in a eutrophic lake, and their ecological implications. *British Phycological Journal* 25, 217–35.

—— 1995: Naturally eutrophic lakes: reality, myth or myopia? *Trends in Ecology and Evolution* 10, 137–38.

Anderson, N.J. and **Battarbee**, R.W. 1994: Aquatic community persistence and variability: a palaeolimnological perspective. In Giller, P.S., Hildrew, A.G. and Raffaelli, D., editors, *Aquatic ecology: scale, patterns and processes*, Oxford: Blackwell Scientific Publications, 233–59.

Anderson, N.J. and **Rippey, B.** 1994: Moniitoring lake recovery from point-source eutrophication: the use of diatom-inferred epilimnetic total phosphorus and sediment chemistry. *Freshwater Biology* 32, 625–39.

Anderson, N.J., Odgaard, B.V., Segerström, U. and **Renberg, I.** 1996: Climate-lake interactions recorded in varved sediments from a Swedish boreal forest lake. *Global Change Biology* 2, 399–405.

Bachofen, R. 1960: *Stoffhaushalt und Sedimentation im Baldegger- und Hallwilersee*. PhD Dissertation, Universität Zürich, 118 pp.

Bartlein, P.J. and **Whitlock, C.** 1993: Paleoclimatic interpretation of the Elk Lake pollen record. *Geological Society of America Special Paper* 276, 275–93.

Battarbee, R.W. 1986: Diatom analysis. In Berglund, B.E., editor, *Handbook of Holocene palaeoecology and palaeohydrology*, Chichester: J. Wiley, 527–70.

Bennett, K.D. 1996: Determination of the number of zones in a biostratigraphical sequence. *New Phytologist* 132, 155–70.

Bennion, H., Wunsam, S. and **Schmidt, R.** 1995: The validation of diatom-phosphorus transfer functions: an example from Mondsee, Austria. *Freshwater Biology* 34, 271–83.

Birks, H.J.B. 1986: Numerical zonation, comparison and correlation of Quaternary pollen-stratigraphical data. In Berglund, B.E., editor, *Handbook of Holocene palaeoecology and palaeohydrology*, Chichester: J. Wiley, 743–74.

—— 1995: Quantitative palaeoenvironmental reconstructions. In Maddy,

D. and Brew, J.S., editors, *Statistical modelling of Quaternary science data*, Cambridge: Quaternary Research Association, 161–254.

Birks, H.J.B. and **Gordon, A.D.** 1985: *Numerical methods in Quaternary pollen analysis*. London: Academic Press, 317 pp.

Birks, H.J.B. and **Line, J.M.** 1992: The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. *The Holocene* 2, 1–10.

Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C. and **ter Braak, C.J.F.** 1990: Diatoms and pH reconstruction. *Philosophical Transactions Royal Society London* B327, 263–78.

Boucherle, M.M. and **Züllig, H.** 1983: Cladoceran remains as evidence of change in trophic state in three Swiss lakes. *Hydrobiologia* 103, 141–46.

Bürgi, H.R. 1994: Seenplankton und Seensanierung in der Schweiz. *Limnologische Berichte Donau 1994* 2, 71–100.

Bürgi, H.R., Weber, P. and **Bachmann, H.** 1985: Seasonal variations in the trophic structure of phyto- and zooplankton communities in lakes in different trophic states. *Schweizerische Zeitschrift für Hydrologie* 47, 197–224.

Dove, P.M. and **Hochella, M.F.** 1993: Calcite precipitation mechanisms and inhibition by orthophosphate: in situ observations by scanning force microscopy. *Geochimica Cosmochimica Acta* 57, 705–14.

Gächter, R. 1987: Lake restoration. Why oxygenation and artificial mixing cannot substitute for a decrease in the external phosphorus loading. *Schweizerische Zeitschrift für Hydrologie* 49, 170–85.

Gächter, R. and **Imboden, D.M.** 1985: Lake restoration. In Stumm, W., editor, *Chemical processes in lakes*, New York: J. Wiley, 365–88.

Gibson, C.E., Foy, R.H. and **Bailey-Watts, A.E.** 1996: An analysis of the total phosphorus cycle in some temperate lakes: the response to enrichment. *Freshwater Biology* 35, 525–32.

Heck, K.L., van Belle, G. and **Simberloff, D.S.** 1975: Explicit calculation of the rarefaction diversity mesaurement and the determination of sufficient sample size. *Ecology* 56, 1459–61.

Hofmann, W. 1987: Cladocera in space and time: analysis of lake sediments. *Hydrobiologia* 145, 315–21.

Jacobson, G.L. and **Grimm, E.C.** 1986: A numerical analysis of Holocene forest and prairie vegetation in central Minnesota. *Ecology* 67, 958–66.

Kilham, P., Kilham, S.S. and **Hecky, R.E.** 1986: Hypothesized resource relationship among African planktonic diatoms. *Limnology and Oceanography* 31, 1169–81.

Kilham, S.S. 1986: Dynamics of Lake Michigan natural phytoplankton communities in continuous cultures along a Si:P loading gradient. *Canadian Journal of Fisheries and Aquatic Science* 43, 351–60.

Kilham, S.S. and **Kilham, P.** 1975. *Melosira granulata* (Ehr.) Ralfs: morphology and ecology of a cosmopolitan freshwater diatom. *Verhandlungen Internationale Vereinigung für Limnologie* 19, 2716–21.

Kilham, S.S., Theriot, E.C. and **Fritz, S.C.** 1996: Linking planktonic diatoms and climate in the large lakes of the Yellowstone ecosystem using resource theory. *Limnology and Oceanography* 41, 1052–62.

Klee, R. and **Schmidt, R.** 1987: Eutrophication of Mondsee (upper Austria) as indicated by the diatom stratigraphy of a sediment core. *Diatom Research* 2, 55–76.

Krammer, K. and **Lange-Bertalot, H.** 1986–1991. Bacillariophyceae. 1.–4. Teil. *Süsswasserflora von Mitteleuropa* 2/1–2/4. Stuttgart: G. Fischer Verlag.

Kunz, B. and **Stumm, W.** 1984. Kinetik der Bildung und des Wachstums von Calciumcarbonat. *Vom Wasser* 62, 279–93.

Leavitt, P.R., Sanford, P.R., Carpenter, S.R., Kitchell, J.F. and **Benkowski, D.** 1993: Annual fossil records of food-web manipulation. In Carpenter, S.R. and Kitchell, J.F., editors, *The trophic cascade in lakes*, Cambridge: Cambridge University Press, 278–309.

Livingstone, D.M. and **Lotter, A.F.** 1998: The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. *Journal of Paleolimnology*, in press.

Livingstone, D.M. and **Schanz, F.** 1994: The effects of deep-water siphoning on a small, shallow lake: a long-term case study. *Archiv für Hydrobiologie* 132, 15–44.

Lotter, A.F. 1989a: Evidence of annual layering in Holocene sediments of Soppensee, Switzerland. *Aquatic Sciences* 51, 19–30.

—— 1989b: Subfossil and modern diatom plankton and the paleolimnology of Rotsee (Switzerland) since 1850. *Aquatic Sciences* 51, 338–50.

Lotter, A.F. and **Birks, H.J.B.** 1997: The separation of the influence of nutrients and climate on the varve time-series of Baldeggersee, Switzerland. *Aquatic Sciences* 59, 362–75.

Lotter, A.F. and **Juggins, S.** 1991: POLPROF, TRAN and ZONE: programs for plotting, editing and zoning pollen and diatom data. *INQUA-Subcommission for the study of the Holocene, Working Group on Data-Handling Methods, Newsletter* 6, 4–6.

Lotter, A.F., Ammann, B. and **Sturm, M.** 1992: Rates of change and chronological problems during the late-glacial period. *Climate Dynamics* 6, 233–39.

Lotter, A.F., Birks, H.J.B., Hofmann, W. and **Marchetto, A.** 1997a: Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *Journal of Paleolimnology* 18, 395–420.

—— 1998: Modern Diatom, Cladocera, Chironomid, and Chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. *Journal of Paleolimnology*, in press.

Lotter, A.F., Renberg, I., Hansen, H., Stöckli, R. and **Sturm, M.** 1997b: A remote controlled freeze corer for sampling unconsolidated surface sediments. *Aquatic Sciences* 59, 295–303.

Lotter, A.F., Sturm, M., Teranes, J.L. and **Wehrli, B.** 1997c: Varve formation since 1885 and high-resolution varve analyses in hypertrophic Baldeggersee (Switzerland). *Aquatic Sciences* 59, 304–25.

Lund, J.W.G. 1971: An artificial alteration of the seasonal cycle of *Melosira italica* subsp. *subarctica* in an English lake. *Journal of Ecology* 59, 521–33.

Maberly, S.C., Hurley, M.A., Butterwick, C., Corry, J.E., Heaney, S.I., Irish, A.E., Jaworski, G.H.M., Lund, J.W.G., Reynolds, C.S. and **Roscoe, J.V.** 1994: The rise and fall of *Asterionella formosa* in the south basin of Windermere: analysis of a 45-year series of data. *Freshwater Biology* 31, 19–34.

Marchetto, A. and **Bettinetti, R.** 1995: Reconstruction of the phosphorus history of two deep, subalpine Italian lakes from sedimentary diatoms, compared with long-term chemical measurements. *Memorie Istituto Italiano di Idrobiologia* 53, 27–38.

McQuoid, M.R. and **Hobson, L.A.** 1996: A 91-year record of seasonal and interannual variability of diatoms from laminated sediments in Saanich Inlet, British Columbia. *Journal of Plankton Research* 19, 173–94.

Niessen, F. and **Sturm, M.** 1987. Die Sedimente des Baldeggersees (Schweiz) – Ablagerungsraum und Eutrophierungsentwicklung während der letzten 100 Jahre. *Archiv für Hydrobiologie* 108, 365–83.

Nipkow, F. 1927: Über das Verhalten der Skelette planktischer Kieselalgen im geschichteten Tiefenschlamm des Zürich- und Baldeggersees. Neue Beiträge zur Biologie der Planktondiatomeen und zur Biomorphose der subalpinen Seen. PhD Dissertation ETH Zürich, Nr. 455, 50 pp.

OCDE, 1982: *Eutrophisation des eaux. Méthodes de surveillance, d'évaluation et de lutte*. Paris: OCDE.

Overpeck, J.T., Webb, T. and **Prentice, I.C.** 1985: Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. *Quaternary Research* 23, 87–108.

Pienitz, R., Smol, J.P. and **Birks, H.J.B.** 1995: Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. *Journal of Paleolimnology* 13, 21–49.

Proulx, M., Pick, F.R., Mazumder, A., Hamilton, P.B. and **Lean, D.R.S.** 1996: Experimental evidence for interactive impacts of human activities on lake algal species richness. *Oikos* 76, 191–95.

Rosen, G. 1981: Phytoplankton indicators and their relations to certain chemical and physical factors. *Limnologica* 13, 263–90.

Schaller, T.L. 1996: *Redox-sensitive metals in recent lake sediments. Proxy-indicators of deep-water oxygen and climate conditions*. PhD dissertation ETH Zürich, No. 11901, 115 pp.

Schindler, D.W. 1985: The coupling of elemental cycles by organisms: evidence from whole-lake chemical perturbations. In Stumm, W., editor, *Chemical processes in lakes*, New York: J. Wiley, 225–50.

Simola, H., Hanski, I. and **Liukkonen, M.** 1990: Stratigraphy, species richness and seasonal dynamics of plankton diatoms during 418 years in Lake Lovojärvi, South Finland. *Annales Botanici Fennici* 27, 241–59.

Sommer, U. 1989: The role of competition for resources in phytoplankton succession. In Sommer, U., editor, *Plankton ecology: succession in plankton communities*, Berlin: Springer, 57–106.

Stadelmann, P. 1984: Die Zustandsentwicklung des Baldeggersees (1900 bis 1980) und die Auswirkung von see-internen Massnahmen. *Wasser, Energie, Luft* 76, 85–95.

ter Braak, C.J.F. 1987–1992: *CANOCO – a FORTRAN program for canonical community ordination*. Ithaca, New York: Microcomputer Power, 95 pp.

ter Braak, C.J.F. and **Juggins, S.** 1993: Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. *Hydrobiologia* 269/270, 485–502.

ter Braak, C.J.F. and **Prentice, I.C.** 1988: A theory of gradient analysis. *Advances in Ecological Research* 18, 271–317.

ter Braak, C.J.F., Juggins, S., Birks, H.J.B. and **van der Voet, H.** 1993: Weighted averaging partial least squares regression (WA-PLS): definition and comparison with other methods for species-environment calibration. In Patil, G.P. and Rao, C.R., editors, *Multivariate Environmental Statistics*, Elsevier, 525–60.

Tilman, D. 1977: Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* 58, 338–48.

Tilman, D., Kilham, S.S. and **Kilham, P.** 1982: Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecol Syst* 13, 349–72.

van Donk, E. and **Kilham, S.S.** 1990: Temperature effects on silicon- and phosphorus limited growth and competitive interactions among three diatoms. *Journal of Phycology* 26, 40–50.

Wehrli, B. and **Wüest, A.** 1996: Zehn Jahre Seenbelüftung: Erfahrungen und Optionen. *Schriftenreihe der EAWAG* 9, 1–128.

Wehrli, B., Lotter, A.F., Schaller, T. and **Sturm, M.** 1997: High-resolution varve studies in Baldeggersee (Switzerland): project overview and limnological background data. *Aquatic Sciences* 59, 285–94.

Willén, E. 1991: Planktonic diatoms – an ecological review. *Algological Studies* 62, 69–106.

Wunsam, S., Schmidt, R. and **Klee, R.** 1995: *Cyclotella*-taxa (Bacillariophyceae) in lakes of the Alpine region and their relationship to environmental variables. *Aquatic Sciences* 57, 360–86.

Züllig, H. 1982: Untersuchungen über die Stratigraphie von Carotinoiden im geschichteten Sediment von 10 Schweizer Seen zur Erkundung früherer Phytoplankton-Entfaltungen. *Schweizerische Zeitschrift für Hydrologie* 44, 1–98.