

Quantifying human-induced eutrophication in Swiss mountain lakes since AD 1800 using diatoms

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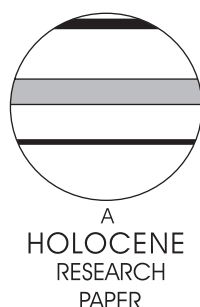
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Received 23 November 2006; revised manuscript accepted 10 June 2007



Abstract: Sedimentary diatom assemblages from three lakes in the southeastern Swiss Alps were analysed at high temporal resolution since AD 1800. Altered land-use patterns, increasing population and exploitation through tourism are clearly reflected in annually laminated sediments of Lej da San Murezzan (Lake St Moritz) and Lej da Silvaplana (Lake Silvaplana). Diatom assemblages originally dominated by *Cyclotella* taxa are replaced by taxa indicating higher total phosphorus (TP) concentrations, such as *Asterionella formosa*, *Fragilaria crotonensis* and *Stephanodiscus parvus*. In Lej da la Tscheppa, located well above the treeline in a catchment that was hardly exposed to human impact, *Cyclotella comensis* prevails throughout the entire sediment sequence. Quantitative estimates of past TP concentrations were inferred using a newly developed regional diatom-TP inference model based on 119 modern samples. In Lej da la Tscheppa diatoms imply stable, low TP concentrations (~10 µg/l), which can be considered as natural background concentration. Elevated TP levels are inferred for Lej da San Murezzan (max. 60 µg/l) since AD 1910 and for Lej da Silvaplana (max. 40 µg/l) since AD 1950, corroborated by changes in sedimentary biogenic silica concentration and organic carbon content. Since ~AD 1970 improved waste water management led to a considerable reduction in TP loading in Lej da Silvaplana and Lej da San Murezzan.

Key words: Eutrophication, diatoms, Switzerland, annual laminations, varved sediments, land use, waste water management, human impact, Alpine lakes.

Introduction

Aquatic ecosystems in regions with intensive agricultural land use and urban development are often exposed to increased nutrient input (Hall *et al.*, 1999), a process that is also referred to as anthropogenic eutrophication. This is leading to increased pro-

duction, having a strong influence on the role and function of aquatic ecosystems, with serious effects on water quality, food-chain, fishery and recreation. In contrast to lowland sites, where nutrient concentrations can increase dramatically (Lotter, 1998; Kauppila *et al.*, 2002; Bradshaw *et al.*, 2006), mountainous areas with low human impact are in general less exposed to eutrophication. However, even remote sites can be affected to a certain degree, for example through atmospheric nutrient deposition (Wolfe *et al.*, 2001) or intensive animal husbandry (Hausmann *et al.*, 2002).

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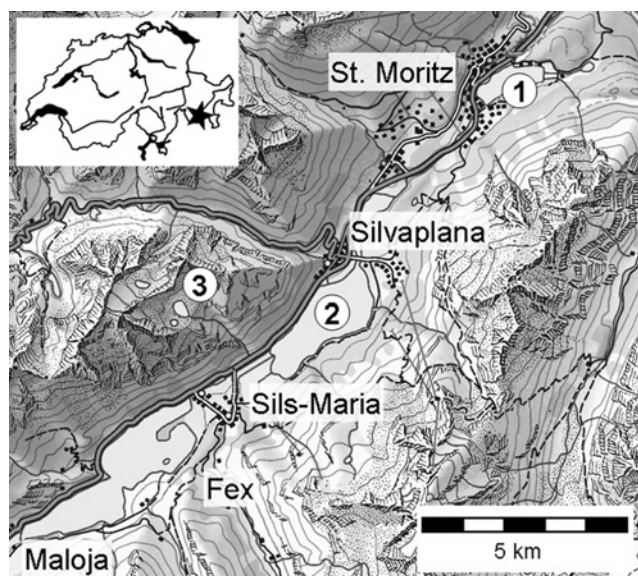


Figure 1 Location of the study sites in the Upper Engadine in south-eastern Switzerland: 1, Lej da San Murezzan; 2, Lej da Silvaplana; 3, Lej da la Tscheppa. Reproduced by permission of swisstopo (BA068145)

The restoration of aquatic ecosystems affected by eutrophication is challenging and cost-intensive (Anderson and Rippey, 1994). In addition, the definition of restoration targets is often hampered by the lack of relevant observational data from the pre-eutrophication period. To achieve a 'good status' of water bodies as required by the European Water Framework Directive (WFD; European Council, 2000), quantitative reference conditions need to be determined (Bennion, 1994; Lotter, 2001a; Lotter and Psenner, 2004; Bennion *et al.*, 2004; Räsänen *et al.*, 2006). In the absence of long-term monitoring data the most adequate approach to define site-specific natural background conditions for lakes involves palaeoecological methods and the analysis of sedimentary archives (eg, Finsinger *et al.*, 2006; Guhrén *et al.*, 2007). In particular, the diatom record has been shown to be a very valuable tool to estimate quantitatively past nutrient concentrations, ie, total phosphorus (TP) (eg, Hall and Smol, 1992; Wunsam and Schmidt, 1995; Lotter *et al.*, 1998). Historical estimates of TP based on sedimentary diatoms were also successfully validated with observational data (eg, Bennion *et al.*, 1995; Lotter, 1998; Hausmann and Kienast, 2006).

The Upper Engadine valley in southeastern Switzerland underwent a strong tourism-induced exploitation during the past century, increasing the pressure on terrestrial and aquatic ecosystems. Our three study lakes are hydrologically connected in the order Lej da la Tscheppa, Lej da Silvaplana and Lej da San Murezzan (Figure 1). While human impact in the catchment of the high-altitude site Lej da la Tscheppa has been minor (von Gunten *et al.*, 2008), the two other sites on the valley bottom have been exposed considerably to human activity such as agriculture and urban development (Züllig, 1982a; Ariztegui and Dobson, 1996). Already at the beginning of the twentieth century, a strong impact on lake sediment properties was reported and ascribed to increased loadings of domestic sewage to Lej da San Murezzan (Schmassmann, 1924). By analysing the fossil pigment record, the eutrophication history of Lej da San Murezzan was assessed qualitatively (Züllig, 1982a, b). Increased nutrient concentrations stimulating primary production also altered the silica biogeochemistry (Schelske *et al.*, 1987) and the amount of total organic carbon (TOC) and sulphur (Ariztegui and Dobson, 1996). Moreover, traces of human activity were recorded in Lej da Silvaplana, altering the silica concentra-

tion (Blass *et al.*, 2007a) even though the visible effects of human activity in the sediment seem less pronounced than in Lej da San Murezzan. All these investigations suggest increased human impact particularly during the past century, even though human activity was recorded already during the Bronze Age by palynological studies (Gobet *et al.*, 2003).

Despite extensive sedimentary evidence of eutrophication in the Upper Engadine, quantitative estimates of past nutrient concentrations such as TP are still missing. The main aims of this study are to analyse the dynamics, interannual to subdecadal variability and diversity in diatom assemblage composition in several lakes in the Upper Engadine region that are affected to a different degree by human impact. Furthermore, we infer quantitatively diatom-based TP concentrations since AD 1800 by applying a newly developed TP inference model based on a combination of three existing regional diatom calibration sets.

Sites

The lakes studied are located in the Upper Engadine, a valley located in southeastern Switzerland at an altitude of about 1800 m a.s.l. surrounded by mountain peaks exceeding 4000 m a.s.l. (Figure 1). The climate in the Upper Engadine is continental, with large diurnal temperature variations and relatively dry conditions. The town of Sils-Maria (1802 m a.s.l.), which is located close to the investigated lakes (Figure 1), has a mean annual temperature of 1.4°C (January -7.8°C , July 10.8°C) and a mean annual precipitation of 978 mm/yr (Climate normals 1961–1990). Air masses from the south (ie, the Mediterranean Sea) as well as from the north (ie, the North Atlantic Ocean) influence the regional climate (Urfer *et al.*, 1979). The bedrock in the Upper Engadine consists predominantly of granite and gneiss, with locally outcropping carbonates (Ohlendorf, 1998). The dominant trees in the Upper Engadine are Swiss stone pine (*Pinus cembra*) and larch (*Larix decidua*), which form the treeline at c. 2200 m a.s.l., but also spruce (*Picea abies*) and green alder (*Alnus viridis*) are present (Gobet *et al.*, 2003).

Lej da San Murezzan (also referred to as Lake St Moritz) at 1768 m a.s.l. has a maximum depth of 44 m, an area of 0.8 km² and a water residence time of <1 yr (Züllig, 1982a; Schelske *et al.*, 1987). The lake is ice-covered from January to May (ice-break up dates have been recorded since AD 1832; Livingstone, 1997), followed by a stable summer stratification from June through November (Bosli-Pavoni, 1971) causing hypolimnetic anoxia. The TP concentration (depth-weighted average value for the entire water column) in Lej da San Murezzan is 15 µg/l and indicates mesotrophic nutrient conditions, the lake-water pH is 6.8 (both measured 27 August 2002; Bigler *et al.*, 2006).

Lej da Silvaplana (also referred to as Lake Silvaplana), which is located upstream of Lej da San Murezzan (Figure 1) at 1791 m a.s.l., has a maximum depth of 77 m and an area of 2.7 km² (Bosli-Pavoni, 1971). It is a dimictic lake that is ice-covered from January to May, with a water residence time of <1 yr (LIMNEX, 1994). The lake does not become anoxic during summer stratification (Blass *et al.*, 2007a). The TP concentration (depth-weighted average value for the entire water column) is 8 µg/l and indicates oligotrophic conditions, the lake-water pH is slightly alkaline (pH = 7.8) (both measured 11 September 2002; Bigler *et al.*, 2006). The glacial meltwater supply is large during the summer months, as the lake catchment includes c. 5% (6 km², status 1998) glaciated areas (Blass *et al.*, 2007b).

In contrast, Lej da la Tscheppa is located well above the modern treeline at 2616 m a.s.l. It has a maximum depth of 32 m, a surface area of 0.08 km² (Margreth, 2006; von Gunten *et al.*, 2008) and drains into Lej da Silvaplana. The lake is ice-covered from December to

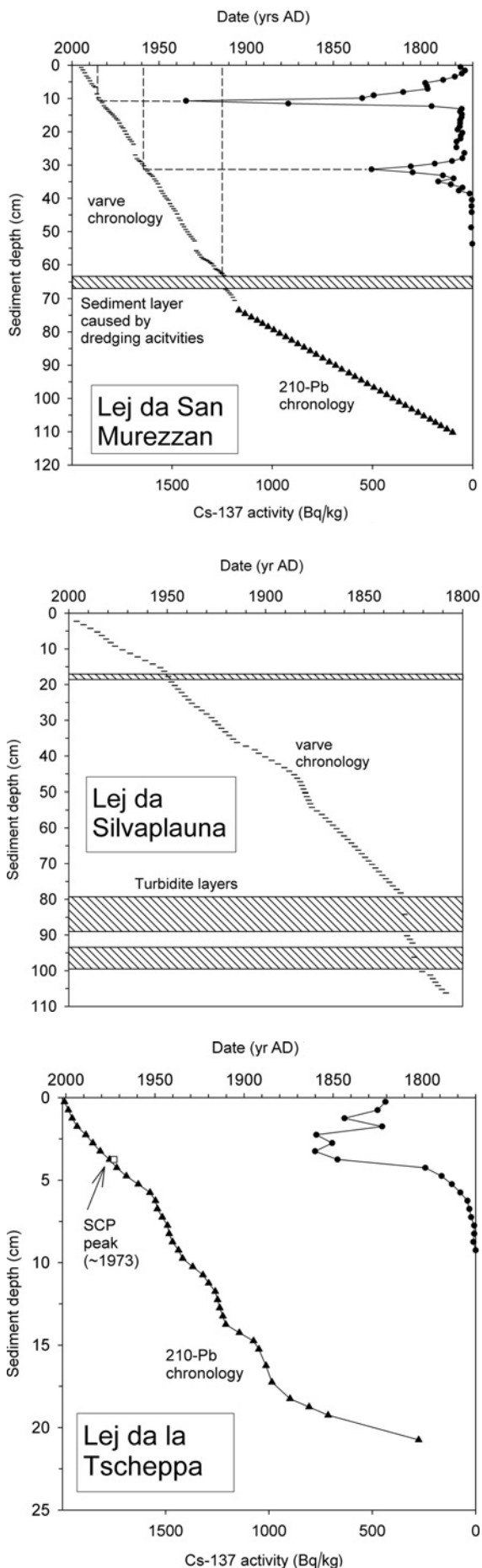


Figure 2 Chronologies for the three study lakes Lej da San Murezzan, Lej da Silvaplauna and Lej da la Tscheppa

June and has an anoxic hypolimnion. The TP concentration (depth-weighted average value for the entire water column) is 10 $\mu\text{g/l}$ and the pH 6.9 (both measured 08 August 2002; Bigler *et al.*, 2006).

Material and methods

Coring and chronology

In Lej da San Murezzan, a sediment core was collected in 1997 in the deepest part of the lake using a freeze-corer (Lotter *et al.*, 1997a). A varve chronology was established based on the counting of annual sediment layers on petrographic thin-sections, and successfully validated with measurements of the ^{137}Cs activity, showing distinct peaks in connection with the Chernobyl fall-out in AD 1986 (varve-dated to AD 1986) and the nuclear bomb testing peak in AD 1963 (varve-dated to AD 1959) at sediment depths of 11.0 and 31.5 cm, respectively (Figure 2). The chronology was additionally confirmed by several well-dated marker beds. As dredging operations were carried out on the northwestern shore of the lake between AD 1911 and 1914, including subsequent deposition of dredged material in the deepest part of the lake (Borner, 1922), a distinct clay-rich layer can be identified in our core at 63–67 cm depth. Distinct silt/clay layers are also identified resulting from increased erosion as a consequence of forest clearing preceding the construction of ski slopes in the early 1970s and from a major flood event (AD 1987). As the varves are not properly distinguishable prior to AD 1908, the oldest part of the chronology is based on ^{210}Pb dating (Figure 2).

Lej da Silvaplauna reveals a very characteristic varve pattern (Ohlendorf, 1998). A core from Lej da Silvaplauna was collected in 2002 using a gravity corer. The chronology of Lej da Silvaplauna (Figure 2) was established through visual correlation to a well-dated parallel core. The dating of this core is based on varve counting on digital photographic close-ups and thin-sections, validated by a combination of ^{137}Cs , ^{210}Pb and turbidite deposits originating from historically known flood events (Blass *et al.*, 2007a, b). Owing to the characteristic varve pattern, the visual correlation did not cause any additional dating uncertainty.

In Lej da la Tscheppa, a sediment core was collected in 2002 using a gravity corer. In contrast to the other two lakes, the sediments of Lej da la Tscheppa are not annually laminated. The depth–age model used in this study (Figure 2) is based on a ^{210}Pb chronology, which was validated with ^{137}Cs measurements and the record of spheroidal carbonaceous particles (von Gunten *et al.*, 2008). However, an unpublished chronology of a recently collected Holocene sequence of Lej da la Tscheppa based on ^{14}C dates (M. Sturm, unpublished data, 2006) suggests that the dates in the lower part of our core could be considerably older.

Sediment analysis: diatoms and organic carbon

All sediment cores were sampled at fixed depth intervals. In Lej da San Murezzan, samples were analysed contiguously at 1 cm intervals. In Lej da Silvaplauna and Lej da la Tscheppa, the sediment cores were sampled at 0.5 cm intervals, and every second sample was analysed for diatoms (except for Lej da la Tscheppa prior to AD 1880). Standard techniques involving hot H_2O_2 (30%) and HCl (10%) treatment were applied for diatom preparation (Battarbee, 1986; Renberg, 1990) and samples were permanently mounted on slides using Naphrax®. Identification and enumeration of diatoms was done under a light microscope with phase-contrast optics at 1000 \times magnification. Diatom taxonomy followed largely the European freshwater diatom flora (Krammer and Lange-Bertalot, 1986–1991). In addition, the taxonomy was adapted to the diatom calibration set applied within this study. A minimum of 400 valves was identified and enumerated in each sample. However, in some turbidite layers this sum could not be reached.

Total carbon in Lej da San Murezzan and Lej da la Tscheppa was determined by gas chromatography (HEKAtech, Euro EA Element analyser) using freeze-dried and homogenized sediment samples. Inorganic carbon content was measured with a Coulometer (Coulometric Inc., 5011 CO₂-Coulometer), and the percentage organic carbon content (C_{org}) was calculated by subtracting inorganic from total carbon.

Numerical analyses

Stratigraphical diatom data are displayed as relative abundances (Figures 3–5), using the programs TILIA 2.0.b.4, TILIA*Graph 2.0.b.4, and TGView 2.0.2 (Grimm, 1992–2004). The numerical zonation of the diatom assemblages is based on the optimal partitioning approach (Birks and Gordon, 1985) using the program ZONE (Lotter and Juggins, 1991), with the number of statistically significant zones determined using the ‘broken stick’ model (Bennett, 1996). Diversity and variability changes within the diatom stratigraphical data were assessed by rarefaction analysis using the program RAREPOLL (Birks and Line, 1992), and rate-of-change analysis (with chord distance between adjacent samples as dissimilarity measure) using the program RATEPOL (J.M. Line and H.J.B. Birks, unpublished program, 1994), respectively.

Detrended correspondence analysis (DCA; Hill and Gauch, 1980) was performed to assess the direction and magnitude of floristic change within each diatom stratigraphy in relation to the calibration set samples (Figure 6). For this purpose, the fossil data from Lej da San Murezzan, Lej da Silvaplauna and Lej da la Tscheppa were added as passive samples in the DCA of the calibration set samples, resulting in time trajectories for each lake (smoothed by a running average; $n=9$). The DCA was implemented using CANOCO version 4.5 (ter Braak and Smilauer, 2002), using default settings (detrending by segments, no downweighting of rare species).

Calibration set and TP inference model

A diatom-TP inference model (Figure 7) was developed using the original Swiss diatom calibration set consisting of 68 surface samples and nine well-dated fossil samples (Lotter *et al.*, 1997b, 1998), as well as two more recently assembled extensions including 21 surface samples and seven well-dated fossil samples (Hausmann and Kienast, 2006) and 30 surface samples (Bigler *et al.*, 2006). Diatom taxonomy was harmonized to the highest possible common taxonomic level. Some subspecies of taxonomically ambiguous groups were merged, such as for example the groups around *Achnanthes minutissima* and *Fragilaria capucina*. All diatom percentage data were square-root transformed prior to inference model development. TP estimates for each sample were based on monitoring data, mostly reflecting overturn TP, and a depth-weighted mean was calculated in case several TP measurements from the water column were available. To achieve a homogeneous distribution along the TP gradient, all TP data were log-transformed. The inference model was developed using weighted-averaging partial least square (WA-PLS) regression (ter Braak and Juggins, 1993), implemented by the program C2 (Juggins, 2003).

Modern diatom responses (ie, optima and tolerance) were modelled using Gaussian logit regression (GLR), which is a form of a generalized linear model that fits a Gaussian-like species response curve to the data (Birks, 1995). We used the GLR program (version 1.1, S. Juggins, unpublished program, 1994) to estimate the optima and tolerances of each taxon and to test the statistical significance of the diatom-TP relationship within the calibration set. The significance of each optimum was also tested using a maximum-likelihood model with Poisson error distribution (Huisman *et al.*, 1993) performed by the Huisman-Olff-Fresco (HOF) pro-

gram (version 2.2, J. Oksanen, unpublished program, 1996). Methods based on HOF and GLR can provide better estimated optima than WA-based methods, because they can assess statistical significance of the optima (Birks, 1995). Optima and tolerances were only reported if both methods exhibited significant fits (see Appendix 1).

Results

Stratigraphical data

Prior to AD 1905 (STMO-D1), the assemblages in Lej da San Murezzan are dominated by diatoms indicating oligotrophic conditions, such as *Cyclotella cyclopuncta* and *Cyclotella comensis* (Figure 3). *Achnanthes minutissima*, a very common diatom with rather unspecific ecological requirements, is also abundant. After AD 1905, a distinct increase of *Asterionella formosa* and the arrival of *Stephanodiscus parvus* indicates a first nutrient enrichment (STMO-D2). The diatom assemblage recorded in the subsequent zone STMO-D3 is closely associated with the sediment layer originating from dredging operations in AD 1911–1914 (Borner, 1922; Ariztegui and Dobson, 1996). This layer is dominated by *Denticula tenuis*, a periphytic diatom occurring mainly in littoral habitats (eg, Lotter and Bigler, 2000), and other periphytic diatoms, such as *Cymbella delicatula*, *Denticula kuetzingii* and *Fragilaria construens* var. *venter*. After AD 1917, the diatom assemblages are dominated by planktonic species that are indicative of nutrient-rich conditions, such as *Asterionella formosa*, *Fragilaria crotonensis*, *Stephanodiscus parvus* and *Tabellaria flocculosa* (STMO-D4, STMO-D5). The most characteristic feature in the youngest part of the stratigraphy (STMO-D6) is the appearance of *Aulacoseira granulata*, a diatom that was basically absent in the sediment record prior to AD 1980. Moreover, prevailing diatoms during the most recent 15 years indicate to some extent a reversal of the assemblage, as the abundance of *Cyclotella* species slightly increased, whereas *Stephanodiscus parvus* decreased. Overall, the rate of change within the diatom assemblage is low prior to AD 1905, indicating stable conditions in Lej da San Murezzan (Figure 8). After AD 1905, the rates of change increase distinctly, with peak values within minerogenic layers originating from episodic events (eg, AD 1911–1914, 1931, 1960s). The diatom diversity shows the opposite pattern, with generally high values prior to AD 1910 and lower values afterwards (Figure 8). C_{org} in Lej da San Murezzan reveals stable and low values (~2%) during the nineteenth century. After AD 1905, the organic carbon content is considerably higher (average of ~4%), and also shows larger fluctuations (Figure 8).

The diatom stratigraphy of Lej da Silvaplauna prior to AD 1840 (SVP-D1, SVP-D2) is dominated by diatoms indicative of low nutrient concentrations, such as *Cyclotella comensis* and *C. cyclopuncta*, but also *Achnanthes minutissima* (Figure 4). At the transition from SVP-D1 to SVP-D2, a turbidite (93.0–99.5 cm) was recorded containing too few diatoms to allow a relative abundance display (Figure 4). Also major parts within the zone SVP-D2 are originating from a mass-flow layer (79.0–89.5 cm sediment depth) with low diatom concentrations containing several typically periphytic diatom genera (eg, *Amphora*, *Cymbella* and *Diploneis*). However, diatom concentrations in this second turbidite are considerably higher than in the first one. Around AD 1840 (SVP-D3), several diatom taxa previously not present in Lej da Silvaplauna are recorded, such as *Stephanodiscus parvus*, *S. hantzschii*, *Fragilaria crotonensis* and *Tabellaria flocculosa*. Moreover, the relative abundance of *Asterionella formosa* increases. This diatom assemblage indicative of increased nutrient availability persists for more than 40 years. After AD 1880, the *Stephanodiscus* species, but also *Fragilaria crotonensis* and *Tabellaria flocculosa* exhibit a decline, whereas the

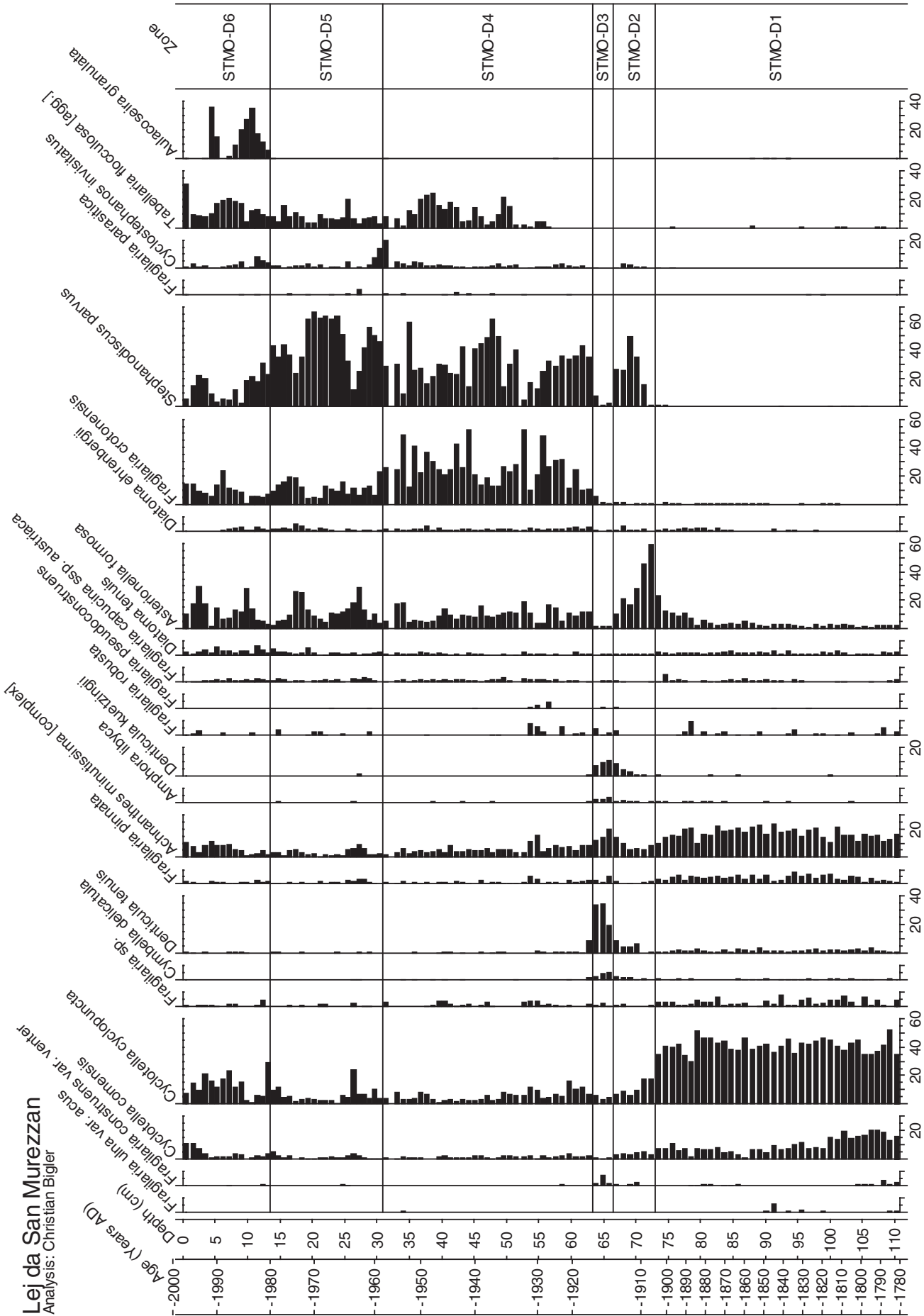


Figure 3 Abundant diatom taxa recorded in the sediment core of Lej da San Murezzan. Only taxa occurring at least in five samples with a minimal abundance of 3% in one sample are displayed

Lej da la Tscheppa
 Analysis: Lucien von Gunten

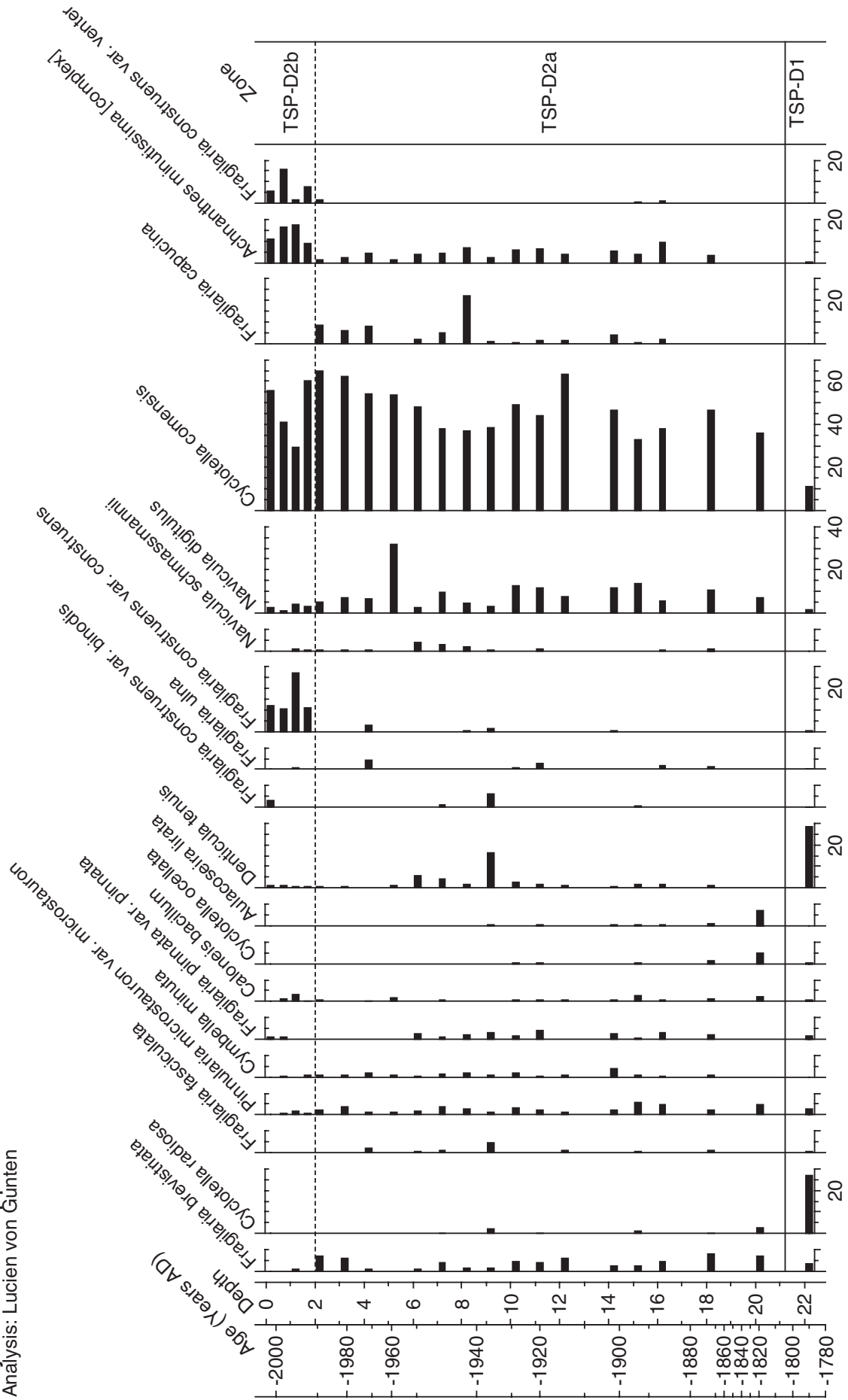


Figure 5 Abundant diatom taxa recorded in the sediment core of Lej da la Tscheppa. Only taxa occurring at least in three samples with a minimal abundance of 3% in one sample are displayed

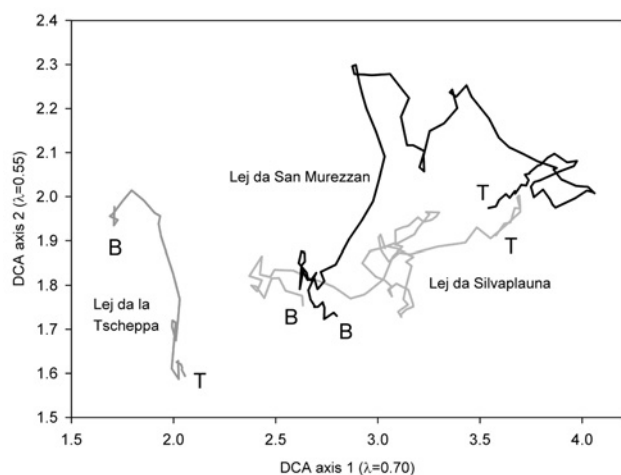


Figure 6 Comparison of diatom assemblage developments in all three study lakes by means of DCA. The trajectories (running mean, $n = 9$) from the bottom (B) to the top (T) of each sediment sequence are projected as passive samples onto the biplot of the calibration set data (not shown)

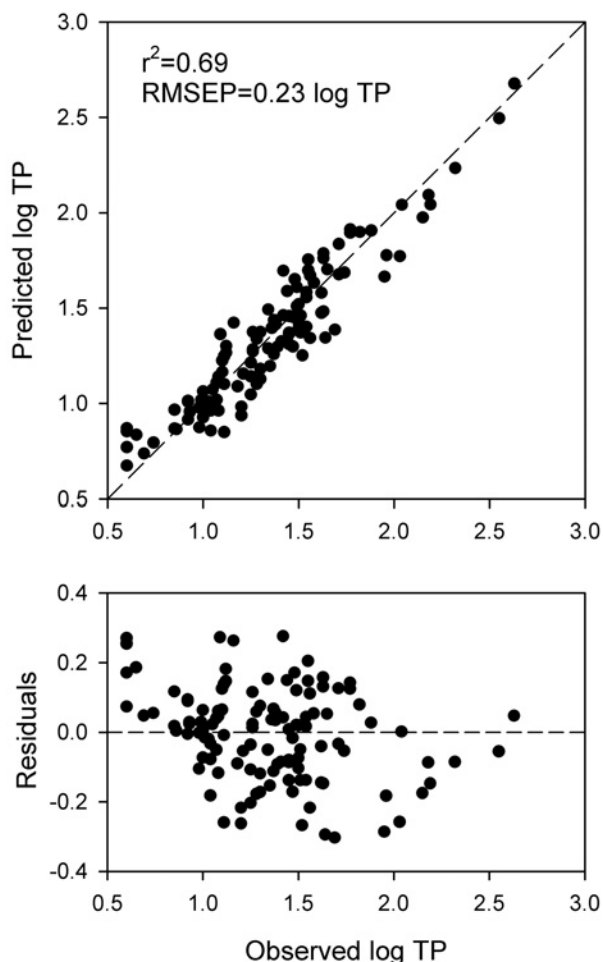


Figure 7 Plot of observed against predicted log TP values (upper panel) and residuals (lower panel) of the combined Swiss diatom calibration set ($n = 119$) using a two-component WA-PLS model

abundance of *Cyclotella* species increases (SVP-D4). The subsequent zone (SVP-D5) shows similar diatom assemblages, but a tendency to larger sample-to-sample variability. In some samples, *Cyclotella cyclopuncta* dominates, whereas others show a relatively high abundance of *Asterionella formosa*. During AD 1965–1980 (SVP-D6), *Stephanodiscus parvus* shows distinctly increasing relative abundances and reaches values higher than 40% in some sam-

ples, a magnitude that was never recorded before. After AD 1980 (SVP-D7), the relative abundance of this diatom decreases abruptly to values below 10% and it is partly replaced by *Cyclotella cyclopuncta*, the most common diatom in Lej da Silvaplana throughout the past two centuries. Rates of change fluctuate throughout the past two centuries, hardly showing consistent patterns or trends as recorded in Lej da San Murezzan (Figure 8). Similarly, diatom diversity is variable, with lowest values recorded prior to AD 1860 and after AD 1950.

The diatom stratigraphy of Lej da la Tscheppa has been analysed at lower temporal resolution than Lej da San Murezzan and Lej da Silvaplana, which is a consequence of a comparably low sedimentation rate (von Gunten *et al.*, 2008). The oldest sample, forming its own local diatom assemblage zone (TSP-D1), is dominated by *Cyclotella radiosa*, *C. comensis* and *Denticula tenuis*. During the major part of the stratigraphy (TSP-D2), *Cyclotella comensis* prevails with a relative abundance exceeding 60% in some samples. Periphytic taxa such as *Achnanthes minutissima* and *Navicula digitulus* are also relatively abundant (Figure 5). Since AD 1990 (TSP-D2b), small *Fragilaria* species (*F. construens* var. *venter*, *F. construens* var. *construens*) increase considerably. Even though the assemblage shift from TSP-D2a to TSP-D2b seems eye-catching, the zonation approach did not identify this boundary as statistically significant. Additional details on the diatom stratigraphy is presented by von Gunten *et al.* (2008). Highest rates of change are observed since AD 1990 (TSP-2b). Overall, the diatom diversity shows a decreasing trend throughout the past centuries (Figure 8). Interestingly, the C_{org} content in Lej da la Tscheppa reveals low values (~2%) during major parts of the twentieth century (AD 1940–1995), and higher values (~6%) before and after this period (Figure 8).

Lake development as assessed by correspondence analysis

Both Lej da San Murezzan and Lej da Silvaplana show overall a similar pattern of floristic changes as assessed by DCA (Figure 6), indicating that the two lakes underwent a comparable development. The trajectories are very similar at the bottom (B) and the top (T) of the two cores, but deviate to a certain extent in between. Lej da San Murezzan shows larger excursions in the DCA trajectory, indicating larger variability in diatom assemblages. Interestingly, the most recent parts of the trajectories are directed towards initial diatom community compositions, confirming the beginning of a recovery recorded in the stratigraphical data (Figures 3 and 4). In contrast to Lej da San Murezzan and Lej da Silvaplana, the time trajectory of Lej da la Tscheppa differs fundamentally and shows mainly changes along the second DCA axis, whereas the scores on the first axis remain relatively constant (Figure 6).

TP inference model and quantitative reconstructions

Weighted-averaging partial least square (WA-PLS) regression including two PLS components showed highest prediction ability, similar to the original Swiss inference model (Lotter *et al.*, 1998). The final transfer function yielded a bootstrapped coefficient of determination (r^2) of 0.69 and a root mean square error of prediction (RMSEP) of 0.23 log-transformed TP. Outliers (prediction residual > 0.4) were iteratively ($n = 6$) identified and excluded from the calibration set, and in the final transfer function 119 out of the total 135 samples were incorporated. We display observed against predicted log-TP values including the residuals of the 119 samples used for calibration and reconstruction (Figure 7). Optima and tolerances for each diatom taxon occurring in at least 10% of the calibration set samples are listed in Appendix 1. The fossil

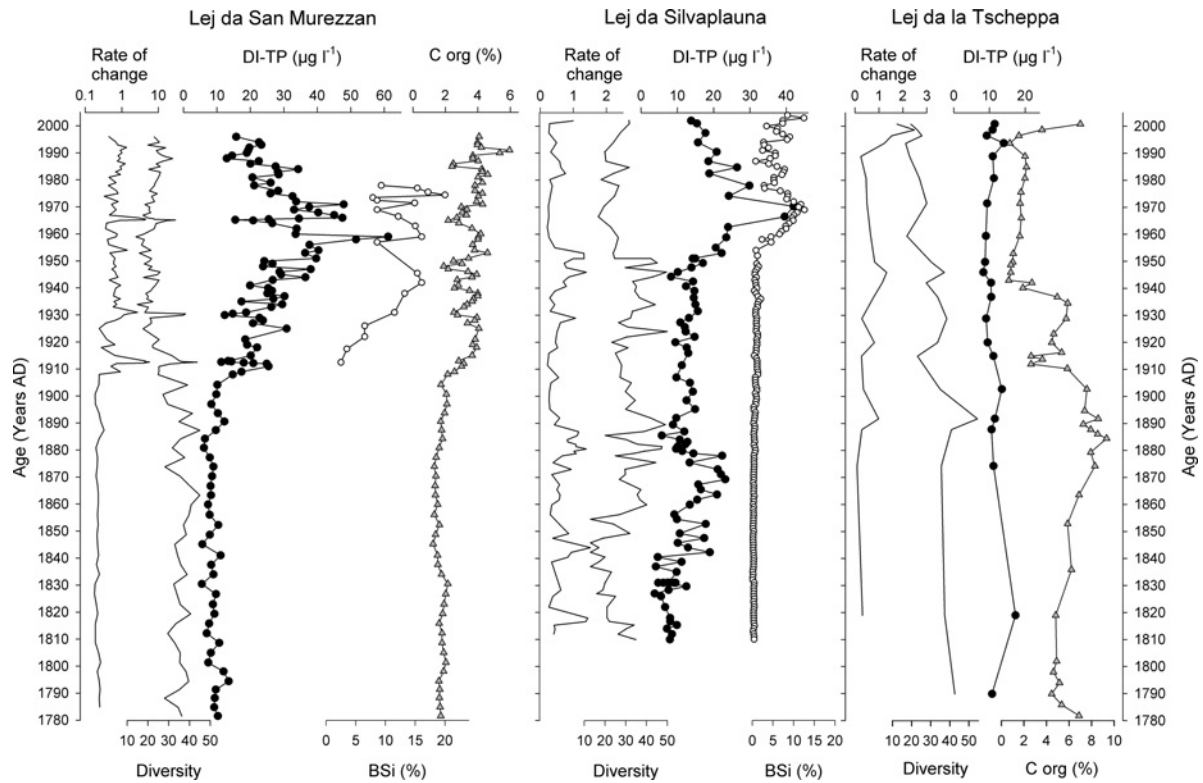


Figure 8 Diatom-inferred total phosphorus (DI-TP), rate of change and diversity for Lej da San Murezzan, Lej da Silvaplauna and Lej da la Tscheppa. For comparison, independent geochemical proxies (C_{org} and BSi) are displayed, i.e., for Lej da San Murezzan C_{org} (own data, same core as diatoms) and BSi (redrawn from Schelske *et al.*, 1987, parallel core), for Lej da Silvaplauna BSi (redrawn from Blass *et al.*, 2007a, parallel core) and for Lej da la Tscheppa C_{org} (own data, same core as diatoms)

diatom taxa recorded in our three study lakes were in general well represented in the calibration set. For Lej da San Murezzan, on average 99% (minimum 95%) of the fossil assemblage is present in the calibration set, whereas it is 88% (64%) for Lej da Silvaplauna and 90% (69%) for Lej da la Tscheppa.

Diatom-inferred TP (DI-TP) estimates of Lej da San Murezzan suggest concentrations of $\sim 10 \mu\text{g/l}$ until the beginning of the twentieth century. Concomitant with distinct changes in sediment colour, diatom assemblages point to progressively increasing TP levels (Figure 8) that are culminating towards the early 1960s ($>50 \mu\text{g/l}$). DI-TP during this period corresponds well with observational data, as a TP concentration of $43 \mu\text{g/l}$ is reported at the end of the 1960s (Bosli-Pavoni, 1971). At the present-day, diatoms suggest TP levels that are in good agreement with observational data ($\sim 20 \mu\text{g/l}$). However, the current TP concentrations in Lej da San Murezzan exceed the natural background conditions of $\sim 10 \mu\text{g/l}$. Similar to Lej da San Murezzan, diatom-based TP estimates in Lej da Silvaplauna suggest a TP concentration of $\sim 10 \mu\text{g/l}$ at the beginning of the nineteenth century (Figure 8). Slightly higher TP values ($10\text{--}20 \mu\text{g/l}$) are inferred between AD 1840 and 1880, a time-period that shows no signs of elevated nutrient concentrations in Lej da San Murezzan. Subsequently, the diatom record suggests again a lower TP concentration ($<15 \mu\text{g/l}$) until AD 1950. From AD 1950 onwards, the TP concentration increases steadily, culminating at the end of the 1970s ($>30 \mu\text{g/l}$). However, observational data from the end of the 1960s showed lower TP concentrations (Bosli-Pavoni, 1971) than inferred from diatoms. Since AD 1980, progressively decreasing TP-values are inferred. In the surface sample of the sediment core (AD 2002), the diatom record suggests a TP concentration of $14 \mu\text{g/l}$, a value that is slightly overestimating the observational data ($8 \mu\text{g/l}$). Diatom-based estimates of TP in Lej da

la Tscheppa do not reveal any major changes during the past centuries (Figure 8). The lake has always been oligotrophic and diatoms suggest stable TP concentrations of $\sim 10 \mu\text{g/l}$, which are identical to observational data (Bigler *et al.*, 2006).

Discussion

Diatom-inferred eutrophication patterns are supported by independent evidence

Diatom records have been successfully used in many parts of the world as proxy indicators to quantitatively estimate past TP concentrations (eg. Hall and Smol, 1999). However, an increased nutrient input affects not only the diatom assemblages, but also many other aspects of lake properties (eg. Wetzel, 2001). For our study lakes, there is independent evidence of eutrophication-induced effects on the biological, physical and chemical properties of the lake and its sedimentary record. For instance, the pronounced productivity increase associated with the diatom assemblage shifts in Lej da San Murezzan is also reflected in the accumulation rates of algal pigments. Pronounced increases of carotenoids, Fucoxanthin, Peridinin, Neoxanthin, Diadinoxanthin, Zeaxanthin and Lutein were recorded by Züllig (1982a). Moreover, planktonic Cladocera assemblages show a marked compositional shift associated with eutrophication in Lej da San Murezzan. *Bosmina longispina* dominates the cladoceran assemblage prior to eutrophication, whereas the more recent sediments reveal high relative abundances of *Daphnia longispina* (group) and *Bosmina longirostris*, both considered as indicators of nutrient-enriched situations (Züllig, 1982a; Boucherle and Züllig, 1983).

The increased production and the diatom assemblage shift resulting from phosphorus enrichment is also associated with

increased concentration of biogenic silica (BSi) and organic carbon (C_{org}). The BSi concentrations in the sediments of Lej da San Murezzan increased distinctly between AD 1910 and 1930, representing a four-fold increase of silica deposition with peak concentrations in the 1960s and 1980s (Figure 8, data redrawn from Schelske *et al.*, 1987). Similarly, also the C_{org} record reflects nutrient changes; and high diatom-inferred nutrient levels are in general associated with elevated C_{org} values, even though the magnitude of nutrient enrichment seems hardly reflected in the C_{org} record (Figure 8). BSi concentrations are also in good agreement with diatom-inferred eutrophication patterns in Lej da Silvaplana (Figure 8; Blass *et al.*, 2007a). In high-altitude Lej da la Tscheppa, periods with low DI-TP seem to be associated with low C_{org} values, even though the pattern is less pronounced than in Lej da San Murezzan, presumably owing to the relatively stable DI-TP concentrations.

Variability and recovery of diatom assemblages in relation to TP changes and improved waste water management

In Lej da San Murezzan, the interannual variability of diatom assemblages is closely related to DI-TP changes. The recorded diatom assemblage variability and diversity during the nineteenth century can be considered as natural. The first known sewer that discharged into Lej da San Murezzan was established AD 1885 (Kasper, 1964). Subsequently, the diatom record shows some initial though small shifts, with increasing rates of change and increasing DI-TP concentrations (Figure 8). Nutrient levels in Lej da San Murezzan first increased with the exploitation of St Moritz as a tourist resort at the beginning of the twentieth century, which was facilitated by the construction of a railway (operated since AD 1903) that made St Moritz easily accessible by mass transport. As a consequence, the rates of change within the diatom community increase considerably, whereas diatom diversity at the same time decreases (Figure 8), highlighting that human-induced nutrient enrichment affects ecosystem stability in a negative way. A decreasing diatom diversity as caused by nutrient enrichment is also observed in lakes with differing catchment properties (eg, Lotter, 1998, 2001b; Rusak *et al.*, 2004) and experimental studies (Proulx *et al.*, 1996). Since AD 1960, sewage input to the lake was systematically reduced, for example by directing wastewater from the town of St Moritz to the River Inn downstream of Lej da San Murezzan in AD 1969, and the establishment of regional sewage treatment plants at the beginning of the 1970s (Bosli-Pavoni, 1971; Züllig, 1982a). These wastewater management measures led to a substantial reduction of TP concentrations, with positive effects on diatom diversity. However, rates of change were not affected by the TP reduction and remain at levels above the pre-enrichment period. Interestingly, the post-AD 1970 reduction of TP has also led to the expansion of *Aulacoseira granulata*, a diatom previously not recorded in Lej da San Murezzan. This illustrates that the restoration does not necessarily involve a re-establishment of taxa previously prevailing in a lake, a phenomenon that has also been observed in other lakes restored from nutrient enrichment (Lotter, 1998; Hausmann *et al.*, 2002).

In Lej da Silvaplana, the relation between TP, rates of change and diatom diversity is not as clear as in Lej da San Murezzan. High rates of change are mostly recorded within mass flow layers that contain a higher proportion of benthic diatom taxa (eg, *Amphora* spp., *Cymbella* spp., *Denticula tenuis*), which are typically not found in the pelagial zone. A first diatom diversity increase is recorded during the period with slightly enriched nutrient concentrations (AD 1840–1880) in Lej da Silvaplana. However, this nutrient increase is not reflected in the BSi record, suggesting that a different process than human-induced eutrophication might be responsible for the TP increase. During this time period, the glaciers

in the Upper Engadine started to retreat from the ‘Little Ice Age’ (LIA) maximum, which had an effect on sedimentation patterns in Lej da Silvaplana (Ohlendorf *et al.*, 1997). It is likely that the extensive glacier and snow melting led to increased run-off, erosion and TP export from the catchment (eg, Hodson *et al.*, 2004), which was immediately used by the algal community in Lej da Silvaplana, having a positive effect on diatom diversity. In support of this hypothesis recent seasonal measurements of the TP concentrations in a main tributary to Lej da Silvaplana indicate high TP concentrations during the summer melting period (LIMNEX, 1994). The pronounced human-induced TP increase starting AD 1950 in Lej da Silvaplana had similar effects on diatom diversity as in Lej da San Murezzan, where periods with highest TP concentrations show lowest diatom diversity. As in Lej da San Murezzan, the DI-TP reconstruction in Lej da Silvaplana reflects in general the wastewater management in the lake catchment. In Sils-Maria, discharge of waste water into the lake started in AD 1960, and a sewage treatment plant was established in AD 1972 (modernized in AD 1987). Additional establishment of sewage treatment plants in the lake’s catchment took place in Maloja (AD 1975) and in Fex (AD 1999) (Reich, 2002; Blass *et al.*, 2007a).

The diatom assemblage shifts recorded in Lej da San Murezzan and Lej da Silvaplana as a consequence of human-induced eutrophication are typical for nutrient-enriched lakes, both in the Alps and in lowland regions (Lotter, 2001b). In Seebergsee, a small lake (0.06 km²) located at the present-day treeline in the Swiss Alps, *Cyclotella*-dominated diatom assemblages were replaced by *Stephanodiscus parvus* within less than a decade as a consequence of drastic nutrient enrichment caused by summer farming including animal husbandry (Hausmann *et al.*, 2002). In Baldeggsee, a relatively large lake (5.2 km²) affected by agriculture, a similar diatom assemblage shift took place within several decades (Lotter, 1998), whereas in Lago Maggiore, a large prealpine lake (213 km²) south of the Alps, the diatom assemblages were replaced within a few years (Marchetto *et al.*, 2004). These diatom assemblage shifts in response to nutrient enrichment are also typical for lowland lakes in a wider geographical range including for example Scotland (Bennion *et al.*, 2004), Ireland (Taylor *et al.*, 2006) or Canada (Hall *et al.*, 1997), illustrating that the same processes are controlling diatom assemblage shifts in both lowland and high-altitude lakes in response to man-made nutrient enrichment.

Calibration set and performance of TP inference model

The original calibration set for the Alpine region (Lotter *et al.*, 1997b, 1998) does not include lakes from southeastern Switzerland, and is restricted to hardwater lakes with generally alkaline water chemistry. Moreover, the number of high-altitude sites with low TP values is relatively small in the original calibration set. To increase the number of high-altitude sites and to cover larger environmental gradients (eg, water chemistry, bedrock) with biogeographical relevance to our study sites in the Upper Engadine two additional modern calibration sets were added (Hausmann and Kienast, 2006; Bigler *et al.*, 2006). However, the combination of these three calibration sets does not improve the prediction ability of the inference model, as the coefficient of determination slightly decreases (from 0.79 to 0.69) and RMSEP slightly increases (from 0.19 to 0.23). This is due to the taxonomical harmonization of diatom data, where some information is lost as diatom data from three analysts were combined, and also due to the enlargement of the environmental gradients, which has a negative effect on the prediction ability of inference models (Hausmann and Kienast, 2006). However, our newly developed model compares well with similar inference models from elsewhere in Europe or North America (Kauppila *et al.*, 2002: table 3). According to the residuals between observed and predicted TP values, our inference

model seems to overestimate TP values at the lower end of the TP gradient (Figure 6).

Reference conditions in alpine lakes

As many lakes today are affected to a certain degree by human impact (eg, nutrient enrichment, acidification, pollution), the identification of minimally impacted lakes that represent ecological and chemical reference conditions is difficult (Bennion *et al.*, 2004). Palaeolimnological approaches have a strong potential to facilitate the determination of reasonable management goals for lakes, supporting also the implementation of the European WFD. However, lakes have complex, locally specific and long histories of nutrient enrichment, and identifying a general temporal window for reference conditions is often difficult (Taylor *et al.*, 2006). It is therefore important to assess reference conditions on a regional scale, as has been done for example in Ireland (Leira *et al.*, 2006), Scotland (Bennion *et al.*, 2004) or Finland (Miettinen *et al.*, 2005) and also in marine environments as, for example, in Denmark (Andersen *et al.*, 2004). From our study, nutrient reference conditions can be derived for the Upper Engadine Valley and adjacent regions, as diatom-inferred pre-enrichment TP values are consistently around 10 µg/l in the three studied lakes. This value is corroborated by pre-enrichment DI-TP values of the same magnitude in geographically comparable lakes, such as Lago Maggiore (Marchetto *et al.*, 2004) or Mondsee (Bennion *et al.*, 1995). In smaller Alpine lakes, the reference TP concentration may be somewhat higher, as illustrated in

Seeburgsee, where the TP background level was estimated to around 25 µg/l (Hausmann *et al.*, 2002).

Conclusions

Our study clearly shows a site-specific response of lake ecosystems to nutrient enrichment. While Lej da la Tscheppa, located well above the tree-line, according to the diatom record is not affected by increasing nutrient levels, Lej da Silvaplauna and Lej da San Murezzan show an obvious, yet temporally different eutrophication pattern. In Lej da Silvaplauna two phases with elevated nutrient levels occurred: a first natural enrichment phase with moderately increased DI-TP levels between AD 1840 and 1880, and a second human-induced phase with a more pronounced eutrophication since AD 1950. In Lej da San Murezzan a man-made TP increase is recorded after AD 1910. The nutrient enrichment led to a succession of diatom taxa, and *Cyclotella* spp.-dominated assemblages characteristic of oligotrophic conditions are gradually replaced by assemblages consisting of *Asterionella formosa*, *Tabellaria* spp., *Fragilaria crotonensis* and *Stephanodiscus* spp. The human-induced nutrient enrichment decreases diatom assemblage stability (as evidenced by increasing rates of change) and diatom diversity, and affects the geochemical lake properties substantially (eg, BSi, organic carbon). Both lakes show clear signs of recovery since AD 1970 as a consequence of improved waste water management that

Appendix 1

Taxon	No. of occ.	TP optima	Tolerance interval	
<i>Achnanthes biasolettiana</i> Grunow var. <i>biasolettiana</i>	50	19	7	52
<i>Achnanthes conspicua</i> Mayer	22	67	28	161
<i>Achnanthes curtissima</i> Carter	13	7	5	10
<i>Achnanthes laevis</i> Oestrup var. <i>laevis</i> Oestrup	15	–		
<i>Achnanthes lanceolata</i> (Breb.) Grunow	43	45	18	112
<i>Achnanthes levanderi</i> Hustedt	14	4	<4	9
<i>Achnanthes marginulata</i> Grunow in Cleve et Grunow	10	6	<4	11
<i>Achnanthes minutissima</i> Kutzing (complex)	114	<4		
<i>Achnanthes pusilla</i> (Grunow) De Toni	11	<4		
<i>Achnanthes subatomoides</i> (Hustedt) Lange-Bertalot et Archibald	12	13	8	20
<i>Achnanthes zieglerei</i> Lange-Bertalot	14	<4		
<i>Amphora fogediana</i> Krammer	12	15	4	54
<i>Amphora inariensis</i> Krammer complex (incl. <i>A. pediculus</i>)	75	<4		
<i>Amphora libyca</i> Ehrenberg	46	13	8	21
<i>Amphora ovalis</i> Kutzing	21	18	12	25
<i>Amphipleura pellucida</i> Kutzing	14	25	17	36
<i>Asterionella formosa</i> Hassall	75	67	30	151
<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen	32	71	38	135
<i>Brachysira (Anomoeoneis) vitrea</i> (Grunow) Ross	36	8	<4	18
<i>Caloneis bacillum</i> (Grunow) Cleve	31	<4		
<i>Caloneis silicula</i> (Ehrenberg) Cleve	20	13	6	28
<i>Cyclotella bodanica</i> complex (incl. <i>C. praetermissa</i> , <i>C. quadrijuncta</i>)	37	58	32	104
<i>Cyclotella comensis</i> Grunow in Van Heurck	66	–		
<i>Cyclotella cyclopuncta</i> Hakansson et Carter	18	9	6	15
<i>Cyclotella distinguenda</i> Hustedt complex	62	30	18	51
<i>Cyclotella krammeri</i> Hakansson	33	98	29	333
<i>Cyclotella meneghiniana</i> Kutzing	11	327	65	>427
<i>Cyclotella ocellata</i> Pantocsek	51	57	35	93
<i>Cyclotella pseudostelligera</i> Hustedt (incl. <i>C. stelligera</i>)	71	35	17	74
<i>Cyclotella radiosa</i> (Grunow) Lemmermann	69	32	15	70
<i>Cyclotella rossii</i> Håkansson	25	43	24	77
<i>Cymbella affinis</i> Kutzing	26	12	5	31
<i>Cymbella cesatii</i> (Rabenhorst) Grunow	16	<4		
<i>Cymbella delicatula</i> Kutzing	14	11	7	18
<i>Cymbella gracilis</i> (Ehrenberg) Kutzing	11	15	9	24
<i>Cymbella helvetica</i> Kutzing	10	–		

(Continued)

Appendix 1 (continued)

Taxon	No. of occ.	TP optima	Tolerance interval	
<i>Cymbella microcephala</i> Grunow	75	15	4	54
<i>Cymbella minuta</i> f. <i>semicircularis</i>	25	7	<4	16
<i>Cymbella minuta</i> Hilse ex Rabenhorst	59	11	<4	34
<i>Cymbella silesiaca</i> Bleisch in Rabenhorst	42	<4		
<i>Cymbella sinuata</i> Gregory	12	–		
<i>Cocconeis placentula</i> Ehrenberg complex	49	–		
<i>Cyclostephanos dubius</i> (Fricke) Round	18	75	42	137
<i>Cyclostephanos invisitatus</i> (Hohn et Hellerman) Theriot et al.	31	141	75	265
<i>Denticula tenuis</i> Kutzing	63	8	<4	19
<i>Diploneis elliptica</i> (Kutzing) Cleve	17	<4		
<i>Diploneis oblongella</i> (Naegeli) Cleve-Euler	12	12	9	17
<i>Diploneis oculata</i> (Brebisson) Cleve	25	11	6	18
<i>Diploneis ovalis</i> (Hilse) Cleve	29	13	9	20
<i>Diatoma mesodon</i> (Ehrenberg) Kutzing	15	19	12	29
<i>Diatoma tenuis</i> Agardh	25	>427		
<i>Fragilaria arcus</i> (Ehrenberg) Cleve	15	17	11	29
<i>Fragilaria (Pseudostaurosira) brevistriata</i> Grunow	75	–		
<i>Fragilaria capucina</i> Desmazieres complex	62	–		
<i>Fragilaria construens</i> (Ehr.) Grunow f. <i>binodis</i> (Ehr.) Grunow	22	9	4	20
<i>Fragilaria (Staurosira) construens</i> (Ehr.) Grunow f. <i>construens</i>	37	19	9	37
<i>Fragilaria construens</i> (Ehr.) Grunow f. <i>venter</i> (Ehr.) Hustedt	73	11	5	23
<i>Fragilaria crotonensis</i> Kitton	50	>427		
<i>Fragilaria (Staurosira) elliptica</i> Schumann	13	9	4	19
<i>Fragilaria nanana</i> Lange-Bertalot	45	23	9	55
<i>Fragilaria parasitica</i> (Smith) Grunow	25	<4		
<i>Fragilaria (Staurosirella) pinnata</i> Ehrenberg complex	83	7	<4	14
<i>Fragilaria (Pseudostaurosira) pseudoconstruens</i> Marciniak	20	<4		
<i>Fragilaria robusta</i> (Fusey) Manguin	19	6	<4	13
<i>Fragilaria ulna</i> (Nitzsch.) Lange-Bertalot var. <i>acus</i>	78	45	17	117
<i>Fragilaria ulna</i> (Nitzsch.) Lange-Bertalot var. <i>ulna</i>	62	60	20	179
<i>Gomphonema angustum</i> Agardh	13	–		
<i>Gomphonema parvulum</i> Kutzing	24	–		
<i>Gomphonema pumilum</i> (Grunow) Reichardt et Lange-Bertalot	11	17	10	31
<i>Gyrosigma acuminatum</i> (Kutzing) Rabenhorst	35	20	10	40
<i>Meridion circulare</i> (Greville) Agardh var. <i>circulare</i>	35	33	13	88
<i>Melosira</i> sp.	12	48	27	85
<i>Navicula cryptocephala</i> Kutzing	36	22	15	35
<i>Navicula cryptotenella</i> Lange-Bertalot	69	<4		
<i>Navicula laevissima</i> Kutzing	11	11	6	19
<i>Navicula lanceolata</i> (Agardh) Ehrenberg	33	29	16	51
<i>Navicula menisculus</i> Schumann	61	15	7	32
<i>Navicula minima</i> Grunow	14	17	7	42
<i>Navicula pupula</i> Kutzing	60	13	6	30
<i>Navicula radiosa</i> Kutzing	14	4	<4	11
<i>Navicula rhynchocephala</i> Kutzing	33	<4		
<i>Navicula schoenfeldii</i> Hustedt	14	6	<4	14
<i>Navicula seminulum</i> Grunow	18	–		
<i>Navicula seminulum</i> var. <i>intermedia</i> Hustedt	16	<4		
<i>Navicula trivialis</i> Lange-Bertalot var. <i>trivialis</i>	13	17	10	30
<i>Navicula utermoehlii</i> Hustedt	16	31	18	54
<i>Navicula wildii</i> Lange-Bertalot	12	14	10	21
<i>Navicula vitabunda</i> Hustedt	12	15	10	23
<i>Nitzschia alpina</i> Hustedt	10	12	7	22
<i>Nitzschia angustata</i> Grunow	13	15	7	30
<i>Nitzschia dissipata</i> (Kutzing) Grunow var. <i>dissipata</i>	60	–		
<i>Nitzschia dissipata</i> (Kutzing) Grunow var. <i>media</i> (Hantzsch) Grunow	10	–		
<i>Nitzschia fonticola</i> Grunow	47	<4		
<i>Nitzschia frustulum</i> (Kutzing) Grunow var. <i>frustulum</i>	13	31	12	78
<i>Nitzschia graciliformis</i> Lange-Bertalot et Simonsen	10	23	9	59
<i>Nitzschia gracilis</i> Hantzsch	33	<4		
<i>Nitzschia lacuum</i> Lange-Bertalot	28	23	11	49
<i>Nitzschia palea</i> (Kutzing) Smith	12	7	4	12
<i>Nitzschia paleacea</i> Grunow in Van Heurck	14	91	46	180
<i>Nitzschia perminuta</i> (Grunow) Peragallo	33	<4		
<i>Nitzschia pura</i> Hustedt	11	–		
<i>Nitzschia recta</i> Hantzsch ex Rabenhorst	11	–		
<i>Pinnularia interrupta</i> Smith	10	17	8	37
<i>Pinnularia microstauron</i> (Ehrenberg) Cleve	30	9	5	14

(Continued)

Appendix 1 (continued)

<i>Stephanodiscus alpinus</i> Hustedt in Huber-Pestalozzi	30	–		
<i>Stephanodiscus hantzschii</i> Grunow in Cleve-Euler et Grunow	32	109	46	256
<i>Stephanodiscus minutulus</i> (Kutzing) Cleve et Moller	18	>427		
<i>Stephanodiscus parvus</i> Stoermer et Håkansson	71	>427		
<i>Stauroneis anceps</i> Ehrenberg fo. <i>gracilis</i> Rabenhorst	13	8	5	13
<i>Surirella linearis</i> Smith	13	7	<4	20
<i>Tabellaria flocculosa</i> (Roth) Kutzing	15	9	6	13
<i>Thalassiosira pseudonana</i> Hasle et Heimdal	36	–		

affects biological (ie, diatoms) and chemical (ie, TP) properties of the lakes.

Acknowledgements

We thank O. Heiri, I. Holderegger, P. Inauen, G. Lemcke, V. Matta, F. Oberli, C. Stengel and A. Zwyssig for support in the field and laboratory. B. Ammann and E. Gobet are kindly acknowledged for many stimulating discussions about environmental history and human impact in the Upper Engadine. C. Bigler and A. Blass were supported by the NCCR Climate program of the Swiss National Science Foundation (SNF). Some of the data were acquired within the EU-research program ENVIRONMENT, project: 'BIOMASS Biodiversity of micro-organisms in aquatic systems' (BBW-No. 95.0395–2), and the SNF-project ENLARGE (SNF-no. 200021–10).

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