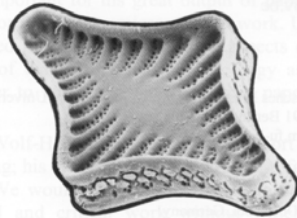


LANGE-BERTALOT-FESTSCHRIFT



Studies on Diatoms

Dedicated to
Prof. Dr. Dr. h.c. Horst Lange-Bertalot
On the Occasion of his 65th Birthday



Edited by
Regine Jahn, John P. Kociolek
Andrzej Witkowski & Pierre Compère



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STUDIES ON DIATOMS

The effect of eutrophication on diatom diversity: examples from six Swiss lakes

André F. Lotter¹

Dedicated to Prof. Dr. Dr. h.c. Horst Lange-Bertalot on the occasion of his 65th birthday

Abstract

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Diatom assemblages in sediment cores from six Swiss lakes give evidence of anthropogenic eutrophication. The lakes react individually with respect to the onset and dynamics of eutrophication. There is, however, a common pattern of succession of planktonic diatom assemblages that is driven by resource competition and can be described by five distinct successional phases. Phase *A*, characterized by several *Cyclotella* species, represents baseline nutrient conditions. During phase *B*, *Fragilaria crotonensis*, *Tabellaria*, and *Asterionella formosa* become more important, whereas small *Stephanodiscus* species become dominant during phase *C*. Phase *D* represents the peak of eutrophication, often also evidenced by instrumental water chemistry measurements. Assemblages dominated by *S. parvus* and higher occurrences of *Aulacoseira granulata* characterize this phase. Phases *B* to *D* indicate increasing nutrient loading often also confirmed by sedimentological features such as increases in the organic and carbonate content of the deposits. Due to water protection measures (e.g., legislation, sewage treatment, and lake restoration programs), nutrient input in these lakes was drastically reduced in the last decades. Many lakes showed a recovery that is often evidenced in the diatom assemblages of successional phase *E*, with increased occurrences of *Cyclotella radiosa*. This trajectory of diatom assemblage change is, however, not reversible along the total phosphorus gradient.

The diversity of both modern as well as downcore diatom assemblages decreases with increasing concentrations of total phosphorus, following a negative logarithmic function, and thus gives evidence that nutrient enrichment leads to a loss in diatom diversity in these lakes.

Introduction

During the last century eutrophication of freshwater systems has become one of the major man-made problems. Nutrient enrichment in lakes and rivers through wastewater and intensive agriculture is not only a threat to drinking water but also to aquatic ecosystems. Biodiversity is generally considered as an indicator of environmental quality and sustainability. However, biological diversity tends to decrease with increasing nutrient levels (e.g. Williams 1964, Tilman 1982, Kilham 1982, Kilham & Kilham 1984). This may even be observed on short time-scales such as in the seasonal cycle of a lake (Moss 1973).

¹ Universiteit Utrecht, Botanische Palaeo-Ecologie, Budapestlaan 4, NL-3584 CD Utrecht, Netherlands
e-mail: a.lotter@bio.uu.nl

Increasing nutrient levels do not only influence the productivity of primary producers in aquatic ecosystems but have also a major impact on the specific composition of algal communities. As a consequence, competition amongst groups of algae (e.g. Kilham & Hecky 1988, Kilham et al. 1986, Sommer 1989) as well as changes in the entire aquatic food web is the result.

During the history of a lake, natural nutrient enrichment usually takes place on time-scales of centuries to millennia, whereas anthropogenic eutrophication happens in years to decades and the effect of eutrophication is often only apparent after a certain threshold is passed. In many cases there are no long time-series of biological observations or instrumental measurements of water chemistry to assess the timing and dynamics of eutrophication and its biological response. Therefore, baseline values for water quality standards can often only be assessed by means of palaeolimnological methods (Anderson 1995a, b), i.e., the study of the sedimentary record. Here, diatoms with their fossilizable valves play a major role.

Recently, several quantitative inference models were developed that relate the occurrence of diatoms to nutrient concentrations in the water column such as total phosphorus (TP, e.g., Anderson & Rippey 1994, Bennion 1994, Hofmann 1994, Wunsam & Schmidt 1995, Bennion et al. 1996, Lotter et al. 1998) or total nitrogen (e.g. Christie & Smol 1993) in the water column. Application of these "transfer functions" to sedimentary diatom assemblages showed that these models are able to infer past nutrient concentrations (e.g. Bennion et al. 1995, Anderson 1997, Schönfelder 1997, Lotter 1998) and are, therefore, valuable tools in assessing baseline nutrient levels.

The aim of the present study was to investigate the timing and dynamics of eutrophication in six selected Swiss lakes, to assess successional patterns in diatom assemblages related to eutrophication and to study the impact of nutrient enrichment on the diversity of diatom assemblages. This contribution is dedicated to Horst Lange-Bertalot in recognition of his many distinguished contributions to our understanding of diatom ecology and taxonomy.

Sites and methods

Six Swiss lakes, all having annually laminated sediments, were sampled at the deepest part of their basins in 1996 using freeze cores (Lotter et al. 1997a) and short gravity cores. The lakes are situated on the Swiss Plateau (Greifensee, Baldeggersee), at the border to the Alps (Vitznauer Becken of Vierwaldstättersee), in the northern (Seerbergsee) and eastern Swiss Alps (Lej da San Murezzan), as well as in the foreland of the southern Swiss Alps (Ponte Tresa Basin of Lago di Lugano, see Fig. 1). Characteristic morphometric and limnological data for these lakes are presented in Table I.

The sediment chronologies are based on varve counts that were carried out on petrographic thin-sections of epoxy-impregnated sediment (Lotter & Lemcke 1999). The amount of organic matter was determined by combusting ca. 1 g of dry sediment at 550 °C for 4 hours, whereas combustion at 950 °C for 2 hours was used to estimate the carbonate content (Heiri et al. 2001).

For diatom analyses, contiguous samples including a known number of years were taken. Between 200 and 500 mg of freeze-dried sediment was treated with 10 % HCl and 30 % H₂O₂ before mounting on slides using Naphrax. Between 300 and 500 valves were counted in each sample. Diatom-inferred TP values were

estimated using a two-component weighted-averaging partial least squares regression and calibration model specifically elaborated for the Alps (Lotter et al. 1998). Diatom diversity was estimated by calculating Hill's (1973) N₂ values, which represent the effective number of occurrences.

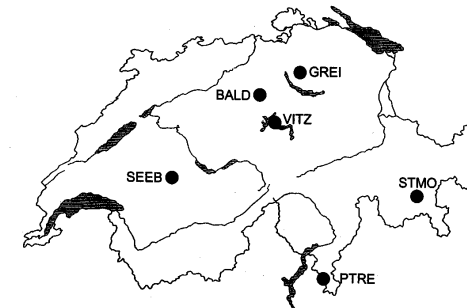


Fig. 1. Map of Switzerland with the location of the six studied lakes.

GREI: Greifensee; BALD: Baldeggersee; VITZ: Vierwaldstättersee, Vitznauer Becken; SEEB: Seerbergsee; STMO: Lej da San Murezzan; PTRE: Lago di Lugano, Ponte Tresa Basin.

Table I. Characteristic data for the six lakes investigated in this study.

	Greifen- see	Baldegger- see	Vitznauer Becken	Seerberg- see	Lej da San Murezzan	Ponte Tresa Basin
Latitude (N)	47°21'	47°12'	47°01'	46°34'	46°29'	45°58'
Longitude (E)	8°41'	8°16'	8°26'	7°26'	9°51'	8°52'
Elevation [m asl]	435	463	434	1831	1768	271
Max. depth [m]	32.5	66.0	151.0	15.5	44.0	62.0
Mean depth [m]	17.8	33.4	95.0	6.6	25.0	33.0
Surface area [km ²]	8.49	5.22	24.95	0.06	0.78	1.10
Catchment area [km ²]	147.80	68.40	22.10	0.23	21.50	5.00
Volume [km ³]	0.151	0.174	2.300	0.004	0.020	0.030
Water renewal time [yrs]	1.1	4.3	0.9	n.a.	0.1	0.7
Mean pH	7.8	7.7	8.1	8.3	7.6	7.7
Conductivity [μS cm ⁻¹ at 20 °C]	450	360	220	180	140	190
Total phosphorus [μg l ⁻¹]	90	150	7	15	40	180
Total nitrogen [mg l ⁻¹]	2.4	1.6	0.8	0.4	0.3	0.8
Si [mg l ⁻¹]	1.3	1.5	0.9	1.0	0.6	3.0

Phases of anthropogenic eutrophication

Parameters such as the amount of organic matter or the carbonate content of the sediment are in general good proxies for detecting past changes in the trophic state of lakes. Furthermore, Niessen & Sturm (1987) and Lotter et al. (1997b) showed that the increase in calcite crystal size may be used as a good indicator for past eutrophication in hardwater lakes.

GREIFENSEE

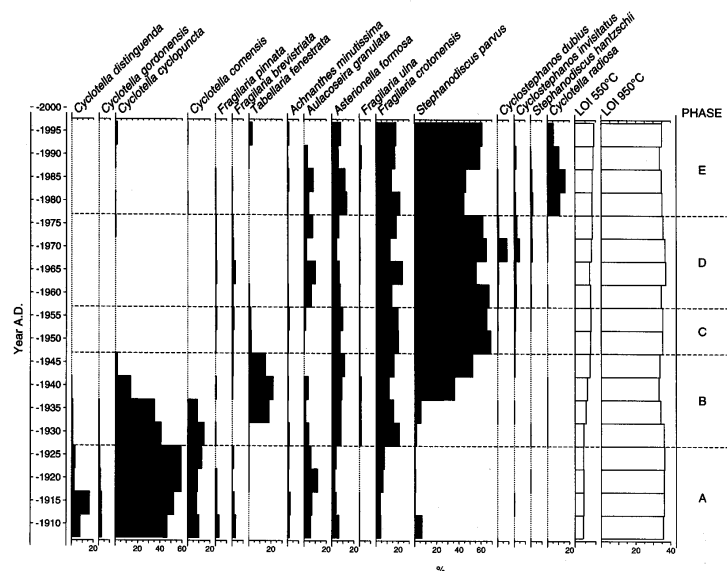


Fig. 2. Diatom assemblages and loss-on-ignition values (LOI) for a sediment core from Greifensee. Only selected taxa are shown.

The amount of organic matter (as represented by the loss-on-ignition at 550 °C) in the sediments started to increase in Greifensee (Fig. 2) in the 1930s, in Baldeggersee (Fig. 3) in the 1960s, in Vitznauer Becken (Fig. 4) in the late 1950s, in Lej da San Murezzan (Fig. 5) in the early 1910s, and in Ponte Tresa Basin (Fig. 6) in the mid-1970s.

BALDEGGERSEE

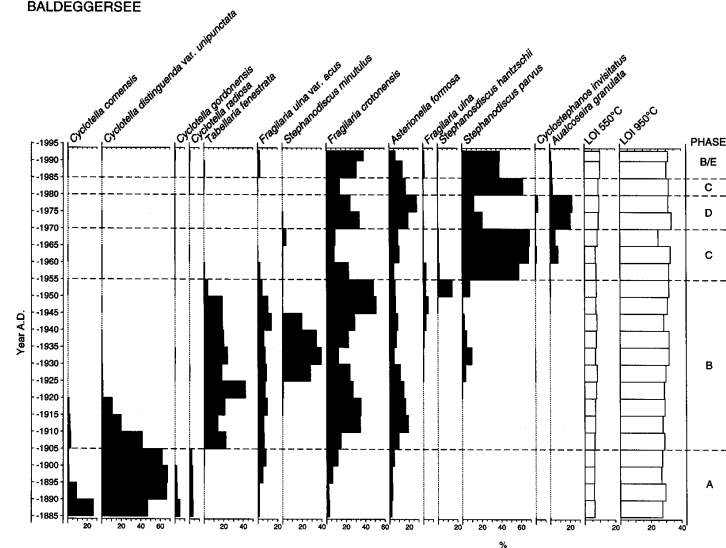


Fig. 3. Diatom assemblages and loss-on-ignition values (LOI) for a sediment core from Baldeggersee. Only selected taxa are shown.

The general increase towards the top of the cores is due to ongoing and incomplete mineralization and decomposition of organic matter.

The carbonate content (as represented by the loss-on-ignition at 950 °C) goes commonly parallel with the increase in organic matter with the exception of Greifensee (Fig. 2) and Baldeggersee (Fig. 3), where the sediments were already very rich in carbonates.

The diatom stratigraphies from all six lakes exhibit a characteristic succession of assemblages that are related to increasing nutrient concentrations. For description purposes these successional stages were simplified into the following five phases of trophic change:

Phase A

Small and medium-sized centric diatoms of the genus *Cyclotella* characterize this phase. Typical taxa are *C. comensis* Grunow, *C. ocellata* Pantocsek, *C. distinguenda* var. *unipunctata* (Hustedt) Håkansson et J.R. Carter, *C. gordonensis* H.J. Kling et Håkansson, *C. cyclopuncta* Håkansson et J.R. Carter. These taxa are commonly regarded as having

oligo- to mainly mesotrophic affinities (e.g. De Wolf 1982) and are today found in lakes of low to medium nutrient status (Wunsam et al. 1995, Lotter et al. 1998). They have been shown to dominate the diatom assemblages over several millennia in hardwater lakes (e.g. Lotter 1988, 2001) and may, therefore, be considered as the diatom assemblages representing the background nutrient conditions in hardwater lakes.

VIERWALDSTÄTTERSEE: VITZNAUER BECKEN

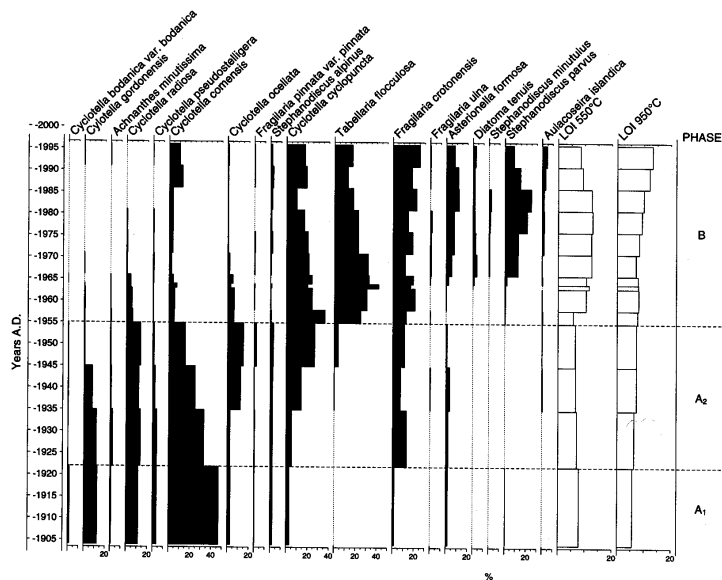


Fig. 4. Diatom assemblages and loss-on-ignition values (LOI) for a sediment core from Vitznauer Becken of Vierwaldstättersee. Only selected taxa are shown.

Phase B

The relative amounts of *Cyclotella* species decrease during this phase, whereas other planktonic diatoms such as *Fragilaria crotonensis* Kitton, *F. ulna* (Nitzsch) Lange-Bertalot, *Tabellaria fenestrata* (Lyngbye) Kützing, and *Asterionella formosa* Hassall become more important. Small *Stephanodiscus* species such as *S. parvus* Stoermer et Håkansson also start to increase during this phase. This change in diatom assemblages is indicative of a first step in nutrient enrichment.

LEJ DA SAN MUREZZAN

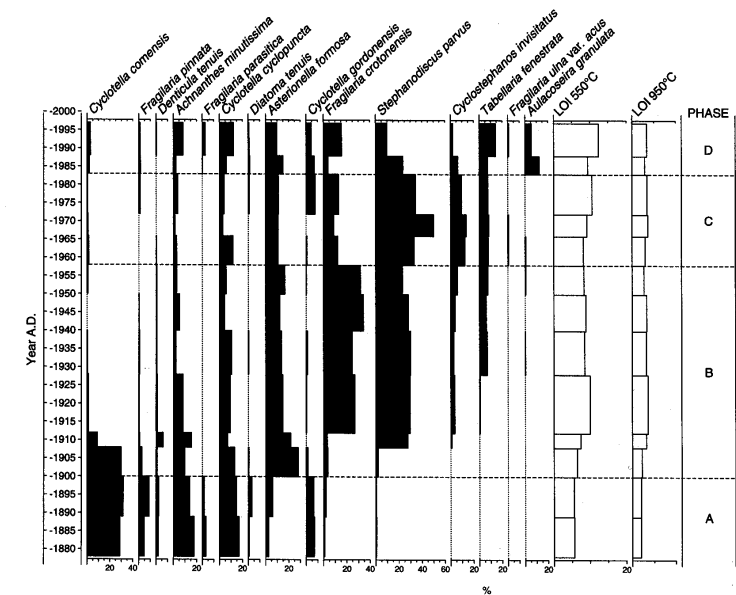


Fig. 5. Diatom assemblages and loss-on-ignition values (LOI) for a sediment core from Lej da San Murrezzan. Only selected taxa are shown.

Phase C

During this phase, *S. parvus* usually becomes the dominant planktonic diatom and represents eutrophic to hypertrophic conditions. As a consequence of the increased phosphorus loading the Si:P ratio declines, thus favouring small *Stephanodiscus* species.

Phase D

In addition to *S. parvus*, other planktonic taxa such as *Aulacoseira granulata* (Ehrenberg) Simonsen become important during the peak of eutrophication. Often *Cyclostephanos* species (*C. dubius* (Fricke) Round, *C. invisitatus* (M.H. Hohn et Helleman) E.C. Theriot, Stoermer et Håkansson) also increase during this phase.

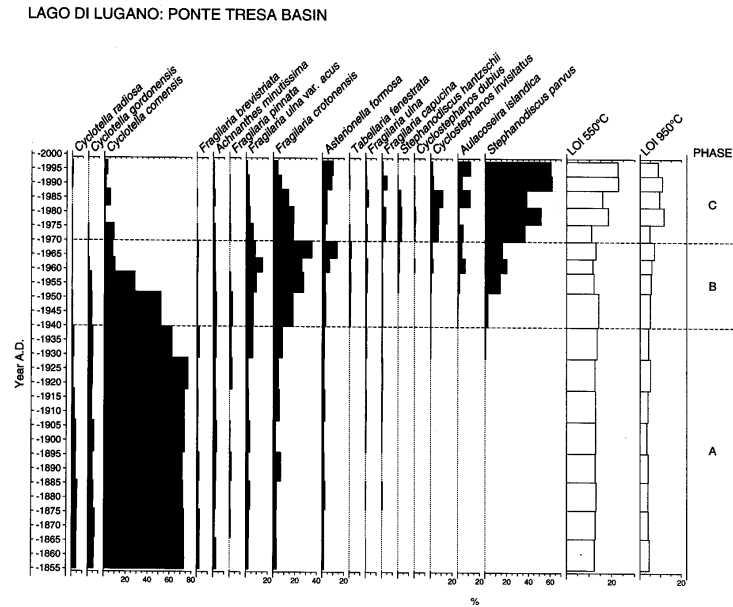


Fig. 6. Diatom assemblages and loss-on-ignition values (LOI) for a sediment core from Ponte Tresia Basin of Lago di Lugano. Only selected taxa are shown.

Phase E

This phase is characterized by decreasing amounts of *S. parvus* and increasing numbers of diatoms characteristic of phase B. Often an expansion of *Cyclotella radiosa* (Grunow) Lemmermann is observed. It represents the decrease in nutrient input that nowadays mainly results from sewage treatment, lake restoration programmes, and phosphate elimination in detergents.

It is interesting to note that the diatom assemblages do not change back to the ones characteristic of phase B despite the decrease in nutrient loading.

These successional phases are closely comparable with published diatom stratigraphies from eutrophic lakes (e.g. Bradbury 1975, Fritz 1989, Lotter 1989, 1998, Kümmerlin 1991, Alefs & Müller 1999, Hürlimann et al. 1999).

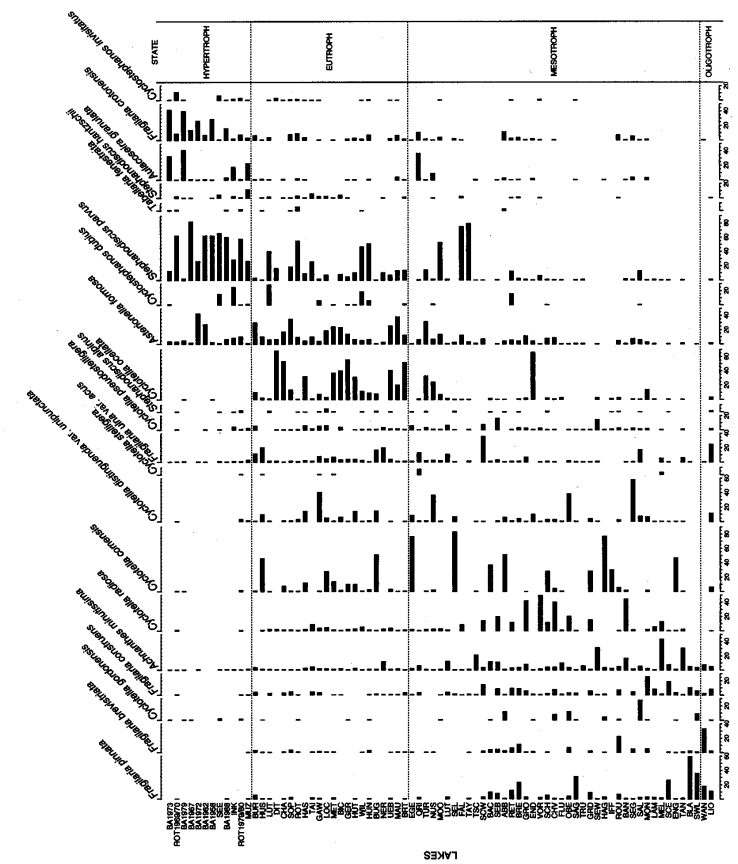


Fig. 7. Diatom assemblages in surficial sediments from the deepest part of 77 small Swiss lakes. The lakes are ordered along a total phosphorus gradient (for details see Lotter et al. 1998). Only selected taxa are shown.

Diatoms and total phosphorus

Analyses of surficial sediment samples in more than 70 small Swiss lakes (Fig. 7) show that the diatom assemblages change with increasing nutrient content in the water column (Lotter et al. 1998), especially with increasing concentrations of total phosphorus (TP). Oligotrophic and mesotrophic lakes as defined by OCDE (1982, i.e., TP concentrations during mixing $< 35 \mu\text{g l}^{-1}$) are mainly characterized by higher numbers of *Cyclotella* species as well as periphytic *Fragilaria* species, whereas eutrophic (TP concentrations between 35 and $100 \mu\text{g l}^{-1}$) lakes are characterized by generally higher amounts of *S. parvus* and *A. formosa*. Diatom assemblages in hypertrophic (TP $> 100 \mu\text{g l}^{-1}$) Swiss lakes, however, are today dominated by *S. parvus* and *F. crotonensis*. Moreover, in most cases they lack *Cyclotella* and periphytic *Fragilaria* species. A zonation along a TP gradient, similar to the phases distinguished in the six sediment cores, can also be distinguished in the modern diatom assemblages. However, the five successional stages detected in the diatom stratigraphies are more detailed than the trophic classification according to Vollenweider (OCDE 1982) and, therefore, follow the trophic gradient in much finer resolution.

Diatom-inferred TP reconstructions were carried out for all six lakes. Comparison of the inferred TP concentrations with TP measurements in the water column over the last 30–50 years (e.g. Liechti 1994) shows, in general, good agreement with the major development of TP concentrations (see, e.g. Lotter 1998). As mesotrophic lakes dominate the modern diatom training set (Fig. 7 and Lotter et al. 1998), the peak values of eutrophication are underestimated by the diatom-inferred TP reconstruction (Greifensee, Baldeggersee), whereas the TP concentrations at the lower end of the gradient (Vitznauer Basin, Lej da San Murezzan) are overestimated. Nevertheless, the diatom assemblages as well as the sediment properties give evidence for the different timing of eutrophication of the six lakes. The earliest evidence for a first step in eutrophication (transition $A \rightarrow B$) are found after the turn of the last century in Lej da San Murezzan (Fig. 5) and Baldeggersee (Fig. 3), followed by Vitznauer Becken (here $A_1 \rightarrow A_2$, Fig. 4) and Greifensee (Fig. 2) in the 1920s, and Ponte Tresa Basin (Fig. 6) in the 1940s. The timing of the peak of eutrophication (phase D), however, is more comparable between the lakes and is also often evidenced by regular water chemistry measurements (Liechti 1994). Generally, the TP levels start to increase steeply after the 2nd World War. In Greifensee the measured TP concentrations were below $100 \mu\text{g l}^{-1}$ in the early 1950s, increased to about $400 \mu\text{g l}^{-1}$ in the mid-1960s, before they eventually peaked with over $500 \mu\text{g l}^{-1}$ in the 1970s and then decreased to less than $100 \mu\text{g l}^{-1}$ today. In Baldeggersee the TP concentrations increased from below $100 \mu\text{g l}^{-1}$ in the early 1950s to peak values of over $500 \mu\text{g l}^{-1}$ in the mid-1970s and then decreased to below $100 \mu\text{g l}^{-1}$ today. In Vierwaldstättersee TP concentrations were around $10 \mu\text{g l}^{-1}$ in the mid-1950s and increased to over $30 \mu\text{g l}^{-1}$ in the late 1970s before decreasing again to modern values of below $10 \mu\text{g l}^{-1}$. According to sporadic measurements in Lej da San Murezzan, its hypolimnion was already anoxic in the early 20th century (Züllig 1982) and TP values were around $40 \mu\text{g l}^{-1}$ in the early

1990s (Züllig 1995). Limnological observations in Lago di Lugano go only back to the early 1980s when TP concentrations were already about $150 \mu\text{g l}^{-1}$.

In the context of anthropogenic eutrophication, Seebergsee is a special case. The diatom assemblages of this small, subalpine lake (Fig. 8) give evidence of a strong, early eutrophication in the 16th and 17th century (Hausmann et al. 1997) which is attributed to land-use changes. There is, however, a very dynamic process of reoligotrophication that takes place within few decades due to a decrease in land-use intensity during the Little Ice Age (i.e. cold period between the mid-16th and the mid-19th century). This long-term trophic development is very much in contrast with the general history of lowland lakes in Switzerland and underlines the importance of palaeolimnological results for the understanding the present-day trophic status and susceptibility of lakes.

SEEBERGSEE

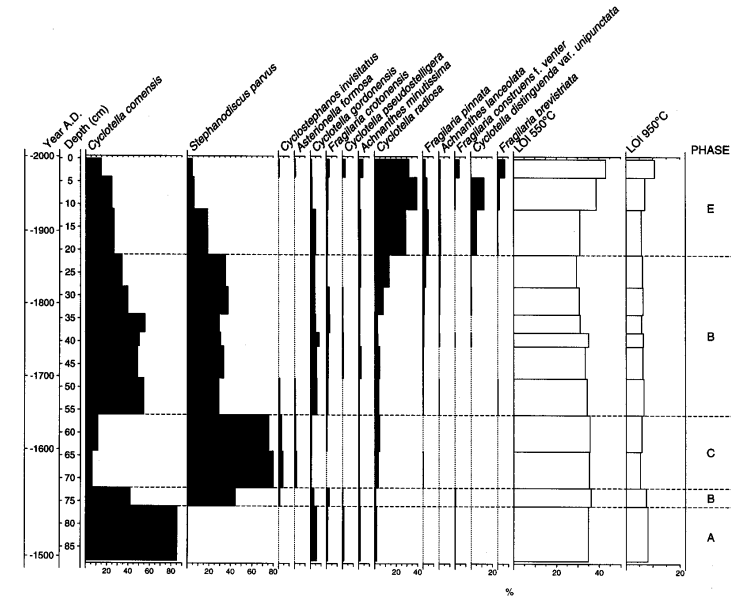


Fig. 8. Diatom assemblages and loss-on-ignition values (LOI) for a sediment core from Seebergsee. Only selected taxa are shown.

Eutrophication and diatom diversity

The assessment of past ecological diversity as deduced from the sedimentary record has been widely discussed (e.g. Brown & Caseldine 1999). Besides processes such as taxonomical resolution, taphonomy, and the ability of an organism to fossilize, one of the major issues in assessing past diversity is the choice of a sound measure that takes account of richness and equitability. Several numerical methods are used in ecology (see e.g. Magurran 1988). In palaeoecology and palaeolimnology the application of most of these indices may be problematic as the richness heavily depends on count size and accumulation rates (see e.g. Smol 1981). Numerical solutions to estimate past organismal richness are rarefaction analyses (Birks & Line 1992, Odgaard 1999) or the calculation of Hill's (1973) N_2 values, i.e. the effective number of occurrences. The latter measure was used as a proxy for the diversity in the modern surface diatom assemblages as well as in the downcore assemblages.

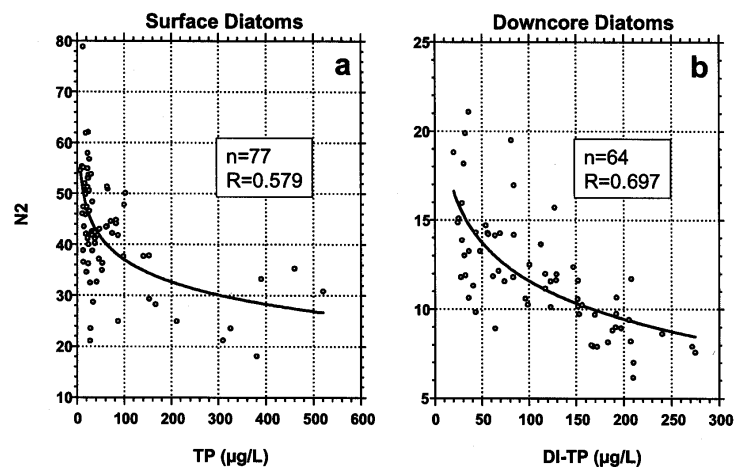


Fig. 9. The relationship between the total phosphorus concentration (TP) and the diatom diversity as estimated using Hill's (1973) N_2 .

a. Measured epilimnetic TP versus N_2 of modern surface sediment diatom assemblages from 77 small Swiss lakes.

b. Diatom-inferred TP values versus N_2 of downcore diatom assemblages from Greifensee, Baldeggersee, Vitznauer Becken, Lej da San Murezzan, and Ponte Tresa Basin.

Fig. 9 shows the relationship between the TP concentration during the mixing period and the N_2 values. Both modern and downcore diversity data follow a negative logarithmic model with highest N_2 values at the lower end of the TP gradient. The regression using the modern surface sediment assemblages explains 33 % of the variance, whereas the downcore model explains 49 % of the variance. According to these results, the beta diversity (sensu Whittaker 1977) decreases along the TP gradient in both the modern and subfossil assemblages. Out of theoretical considerations, low diversities would also be expected at the lowest end of the gradient, where hardly any TP is present and thus only a few very specialized diatoms could thrive (Tilman 1982). The large part of unexplained variance in the regression models, however, shows that factors other than TP also have an influence on the diversity. In contrast to in vitro experiments, nature does not keep all factors constant except the one variable of interest. Covarying factors such as the Si:P ratio (Kilham 1986, Sommer 1989), mixing regimes (Sommer 1988), zooplankton predation, and other physical, chemical and biological factors may also affect this relationship in nature. Moreover, sampling at the deepest part of the basins gives emphasis to the planktonic diatom communities which are, of course, already less diverse as the periphytic diatom communities occupying various benthic and littoral habitats. Diversity of thanatocoenoses such as diatom assemblages in surficial and downcore sediments is, of course, affected by taphonomical processes and, therefore, only a fraction of the overall diversity of a lake as a whole with its diverse habitats is represented in the sedimentary record. Furthermore, diversity is also a concept strongly linked with taxonomical resolution and, depending on the species classification, it will vary (e.g. Mann & Droop 1996). In sedimentary diatom assemblages, diatom diversity is hardly comparable with the one encountered in taxonomical studies where samples from a maximum of different ecological niches are collected and analysed (e.g., Lange-Bertalot 1993). Nevertheless, it is unclear to what extent such "modern" studies are compromised by inclusion of dead or transported frustules in the estimation of diversity. For diversity to have any useful biological meaning it must apply to coeval living populations. In contrast to present-day studies that represent snapshots of diversity in time, sedimentary studies allow estimation of rates of diversity change through time. They thus reflect changes in the availability of habitats and ecological niches.

Acknowledgements

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