

Morphological variation within the diatom taxon *Cyclotella comensis* and its importance for quantitative temperature reconstructions

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SUMMARY

1. The morphologically complex taxon *Cyclotella comensis* Grunow had no clear relationship with environmental parameters in a study using sediment surface samples from the Swiss Alps. The morphological heterogeneity of the taxon was investigated by applying a principal component analysis (PCA) to 9000 presence/absence descriptions of valves from surface samples of six lakes from different altitudes (15 characteristics, 100 valves each lake). The PCA allowed the classification of six morphs, which differed mainly in size and length of striae. Photographs of the morphs are shown in this paper.
2. Sixty-eight sediment surface samples were analysed using these newly defined six morphs. Summer temperature explained a major part of the variance between the morphs as assessed by a redundancy analysis (RDA). Summer temperature optima and tolerances were estimated using weighted averaging.
3. The influence of the revised *C. comensis* taxonomy on the diatom inferred summer temperature of a high alpine lake is discussed in a multiproxy context for the past 800 years.

Keywords: Alps, climate, diatoms, morphometry, multivariate analyses, training set

Introduction

Diatoms are increasingly used for biomonitoring and to infer past environmental conditions. Besides studies on water quality and surface water acidification, diatoms have also been used as qualitative indicators for past climate change (e.g. Bradbury, 1988; Smol, 1988). Recently, quantitative inference models for diatoms in relation to temperature based on strong relationships of diatom assemblages to altitude or latitude have been elaborated for different geographical regions such as the Alps (Wunsam, Schmidt & Klee, 1995; Lotter *et al.*, 1997, Lotter, Pienitz & Schmidt, 1999), Fennoscandia (Weckström, Korhola & Blom, 1997), the North American arctic (Pienitz,

Smol & Birks, 1995) and Papua New Guinea (Vyverman & Sabbe, 1995). However, the relationship between the distribution of diatoms and temperature is not fully understood and there are still reservations amongst diatomists whether transfer functions may be used for reliable climate reconstructions (e.g. Anderson 2001).

Despite the many modern diatom–temperature training sets that exist, there have been only a few applications to infer past temperature (e.g. Schmidt *et al.*, 1998). Another way to quantitatively reconstruct past climate is using diatoms via inferring changes in past lake-water salinity and conductivity (e.g. Fritz, 1990), or via changes in lake-water pH (e.g. Psenner & Schmidt, 1992). However, besides the reconstruction of past climates, modern training sets also provide valuable autecological information on different diatom taxa. Nevertheless, taxonomic precision and consistency, not only for the modern training set but

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also for the down-core samples, are major issues in such studies (Birks, 1994). This might seem trivial, but it is not, especially when taxonomic groups as complex as *Cyclotella comensis* Grunow are involved. Originally described in the last century from Lago di Como in northern Italy by Grunow (in Van Heurck, 1885), this taxon is present in a variety of lakes under different trophic and climatic conditions. As it shows broad morphological variability and as there are many transitional forms, *C. comensis* is often difficult to separate from other, small *Cyclotella* species (see Krammer & Lange-Bertalot, 1991a). Multivariate methods have been used in diatom taxonomy by Haworth & Hurley (1986) and Teubner (1995) to separate different *Cyclotella* species and by Theriot (1987) to separate *Stephanodiscus* species on the basis of morphological features visible by light microscopy.

In our modern diatom training set from the Alps, several morphologically similar taxa were originally attributed to *C. comensis* (Lotter *et al.*, 1997). Visual inspection of the frequency distribution of this taxon along an environmental gradient (altitude) showed, however, a trimodal distribution, suggesting that several ecologically distinct taxa may be involved. The question arises whether differences in the physical environment would also be reflected in its valve morphology of this taxon.

The aim of the present study was threefold: (i) to separate and define the different morphs originally summarized as *C. comensis* in the modern training set by Lotter *et al.* (1997) based on morphometric methods, (ii) to assess and compare the temperature optima and tolerances of these morphs with the results of similar studies, and (iii) to reconstruct summer temperatures taking into account the newly defined ecomorphs for an Alpine lake for the past 800 years.

Methods

Field and laboratory methods

Surface sediments were taken from the deepest part of 68 small hard-water lakes in Switzerland. These lakes are distributed along an altitudinal gradient from 334 to 2339 m a.s.l. Temperature and elevation explains the major part of the variance in the diatom data and quantitative inference models for diatoms in relation to temperature were established (Lotter *et al.*, 1997).

All temperature data in this paper refer to mean summer air temperature (i.e. the mean of June, July and August) which ranges from 4.7 to 21.8 °C. Summer surface water temperatures are highly correlated with air temperatures (Livingstone & Lotter, 1998; Livingstone, Lotter & Walker, 1999).

A sediment core from the Bachsee, located at 2265 m a.s.l. in the Swiss Alps, was retrieved from the deepest part of the lake in 1996 with a modified Livingstone piston corer (Merkt & Streif, 1970).

Sediment samples for diatom analyses were treated with hot 30% H₂O₂ and 10% HCl. The cleaned and rinsed samples were mounted in Naphrax (Northern Biological Supplies, Ipswich, U.K.) on glass slides. A total of 500 valves for modern and 300 valves for subfossil samples were identified at 1000× magnification using oil immersion and phase contrast. The diatom taxonomy follows Krammer & Lange-Bertalot (1986, 1988, 1991a, b).

Zonation of the diatom stratigraphic data was carried out on percentage data using the optimal sum of squares partitioning (Birks & Gordon, 1985), as implemented in the program ZONE (see Lotter & Juggins, 1991). The significant number of diatom assemblage zones (DAZ) was assessed by a broken-stick model (Bennett, 1996).

Numerical analyses

Classification

Taxa should only be used for the purpose of bio-indication if they are morphologically and ecologically distinct. For example, Hürlimann & Straub (1991) described ammonium-sensitive morphs of the *Fragilaria capucina* complex and *sensu* Lange-Bertalot (1980) and Theriot & Stoermer (1984) described a relationship between nutrients and areola density in *S. niagarae*. We used a morphometric approach to define morphs and evaluated the ecological significance of this classification by their distribution in 68 lakes in Switzerland.

Cyclotella comensis morph classification

Following Cox (1997) the term morph is used to express morphological differences below the species level. Six lakes of the modern training set (Lotter *et al.*, 1997) with abundant *C. comensis* distributed along an altitudinal gradient were selected for the classification of *C. comensis* morphs (Table 1). For each lake surface

sediment sample, 100 valves were encoded using 15 presence/absence morphological characteristics visible under the light microscope (Table 2, column a). The resulting 9000 presence/absence data of the encoded 600 valves were analysed by two sequential principal component analyses (PCA) using the software SYSTAT (version 8.0). Many redundant characters masked the distinctiveness of potential clusters and in a subsequent PCA only the characteristics with the best separating properties (the highest component loadings) were used. An arbitrary cut-off level for the component loading was set at $|0.5|$. Consequently, only five of the original 15 characteristics were used for the classification of morphs (Table 2, bold). A lack of overlap of the 95% confidence ellipsoids was considered as a significant separation of the morphs. In addition, the diameters of all morphs in all modern training-set samples were measured to evaluate a potential temperature dependent size distribution.

Morph–environment relationship

To study whether these morphological variations result from ecological differentiation, the 68 surface sediment samples were recounted, taking the newly defined *C. comensis* morphs into account. The labels of the surface sediment slides were covered to avoid bias during counting. To estimate the explanatory power of the individual environmental parameters for the morphs, a redundancy analysis (RDA) was chosen, because of the short gradient length in the data (1.7 standard deviation units), as assessed by a detrended correspondence analysis (DCA). Additionally, an unrestricted Monte-Carlo permutation test (500 simulations) was applied to assess the significance of each individual environmental variable. These ordinations and permutation tests were assessed using CANOCO (version 4.0).

Optima and tolerances were assessed by weighted averaging with classical deshrinking using leave-

Table 1 Selected Swiss lakes for characterization of *C. comensis* morphs

Lakes	Elevation (m)	Maximum depth (m)	Summer air temperature (°C)	Alkalinity (mg L ⁻¹)	TP (µg L ⁻¹)
Hagelseewli	2339	18.5	6.6	1.61	19
Obersee	1734	14.5	9.9	2.83	22
Seealpsee	1141	15.0	12.9	1.87	17
Lag Grond	1016	5.0	13.9	2.71	20
Seelisbergsee	738	37.5	15.3	2.34	28
Le Loclat	432	9.2	17.3	5.37	63

Table 2 Two sequential principal component analyses (PCA) of 9000 presence-/absence-data of the 600 valves from six lakes to assess clusters of *Cyclotella comensis*. (a) Examples of characteristics in Fig. 2, (b) PCA component loadings including all characteristics, (c) PCA component loadings including only characteristics with component loadings $> |0.5|$ (bold)

	a	b		c	
		Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues (λ)		4.141	2.187	2.420	0.983
Star shaped contour	b	0.378	0.161		
Strongly radially undulated	d	0.587	-0.619	0.663	0.519
Delicately radially structured	i	-0.315	0.497		
Flat central area	f	-0.192	0.793		
Rough central area	e	0.074	-0.008		
Strutted process	h	0.203	0.069		
Conspicuous strutted process	e	0.609	-0.233	0.769	0.142
Broad marginal zone	d	0.848	0.083	-0.784	0.342
Irregular marginal zone	a	0.774	-0.391	0.631	-0.670
Bifurcated striae	h	0.293	0.344		
Shadow lines	d	-0.060	0.074		
One striae prolonged	c	0.289	0.071		
Rimoportulae	i	-0.523	0.550	-0.631	-0.356
Diameter c. 10 µm	b	0.179	0.226		
Diameter c. 5 µm	h	-0.302	0.233		
Total variance explained (%)		24.358	12.863	48.395	19.655

one-out cross validation, implemented in the program CALIBRATE (S. Juggins, unpublished data). The morphs were tested for the significance of their response to mean summer temperature by means of a hierarchical series of response models fitted by generalized linear modelling (Huisman, Olf & Fresco, 1993) using the program HOF (J. Oksanen, unpublished data).

Quantitative reconstruction of diatom inferred temperature

An inference model for summer air temperature using weighted averaging partial least squares regression and calibration (WA-PLS; ter Braak & Juggins 1993) was established and applied to fossil diatom assemblages from a Bachsee sediment core. A comparison of diatom-inferred summer air temperature based on the original training set using the *C. comensis* complex and the six newly defined *C. comensis* morphs was assessed.

Results

Cyclotella comensis morph classification

According to their component loading, the characteristics of the rim (Table 2, bold) appeared to discriminate better between groups than characteristics of the central area (Table 2). After removing these redundant variables the variance explained by the first two PCA axis increased from 37.2 to 63% and the species scores revealed four significantly distinct clusters (Fig. 1), with their 95% confidence ellipsoids not overlapping. Each cluster was characterized by a specific feature of the marginal zone.

The COMS had a marginal zone with striae of unequal length. As a result, the outline of the central area appeared star-shaped. The diameter of this morph varied between 5 and 12 μm (Fig. 2a–c).

In contrast, three closely related morphs (CBZ, CBSF, CBF), which had striae (c. 3 μm) of equal length (Fig. 2d–h) were separated by differences in diameter. Morph CBZ (Fig. 2d–f) had a diameter of 10 μm or more, whereas morph CBSF (Fig. 2g) was between 5 and 10 μm , and morph CBF (Fig. 2h) was 5 μm or less.

Morph CGG (Fig. 2i) had 5–6 conspicuous light dots (rimoportulae) visible on the rim. The central area was weakly radially undulated and the diameter varied between 5 and 9 μm .

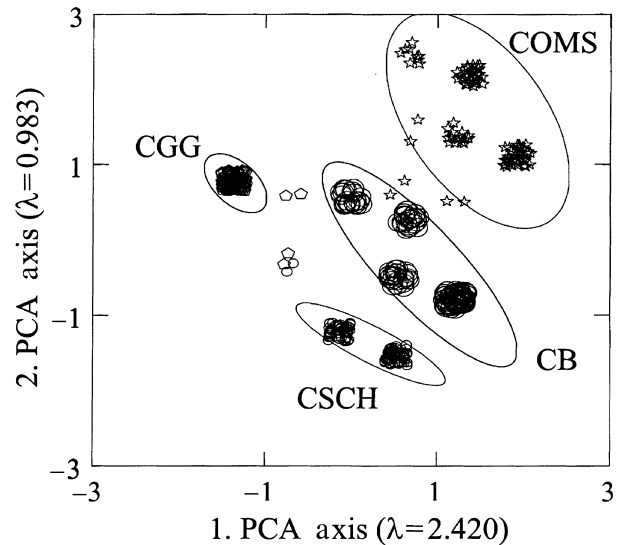


Fig. 1 First two axis of a principal component analysis (PCA) of 600 valves, from six lakes, encoded with 15 presence/absence characteristics, with 95% confidence ellipsoids around clusters formed by valves with the same marginal zone. Stars: COMS (striae of unequal length); large circles: CB (striae of equal length, broad marginal zone); small circles: CSCH (narrow marginal zone, without dots) and pentagons: CGG (marginal zone with obvious dots).

Morph CSCH (Fig. 2j–l) had an extremely narrow marginal zone, but without the bright features (light dots) of the rim of CGG (Fig. 2i). The striae were up to 1 μm long. The central area was strongly radially undulated and appeared slightly elevated. This heavily silicified morph ranged between 3 and 5 μm in diameter.

Morph–environment relationships

The RDA of the recounted 68 training set samples revealed that the first two RDA axes explain 97.5% of the morph–environment relationship. Summer temperature was highly correlated with the first RDA axis and provided the strongest environmental gradient, explaining 87.6% of the total variance (Fig. 3). As assessed by an unrestricted Monte-Carlo permutation test, the six morphs were significantly related to summer air temperature ($P = 0.0006$) whereas alkalinity ($P = 0.86$) and total phosphorus (TP) ($P = 0.82$) were not statistically significant. Thus the morphology of the marginal zone, which defined the morphs, was highly correlated with altitude but not with phosphorus or alkalinity. In the RDA

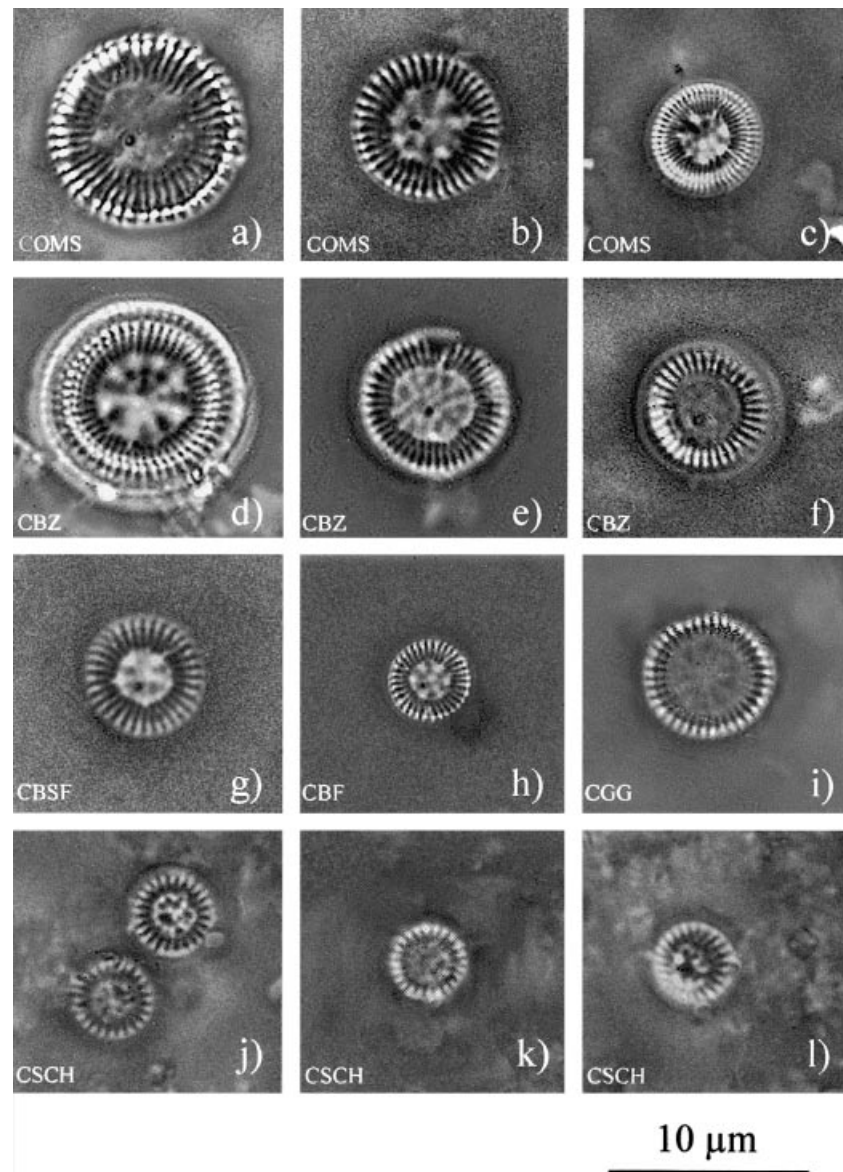


Fig. 2 *Cyclotella comensis* ecomorphs: (a–c) COMS (striae of unequal length); (d–h) CB (striae of equal length, broad marginal zone); (d–f) CBZ (diameter around 10 µm); (g) CBSF (diameter c. 7 µm); (h) CBF (diameter c. 5 µm); (i) CGG (marginal zone with conspicuous dots); (j–l) CSCH (narrow marginal zone, without dots).

(Fig. 3) the centroids of morphs CBZ, COMS, CBSF, CGG, CBF and CSCH showed a progression from warm to cold.

The original *C. comensis* complex and the morph CBF did not show a unimodal relationship to summer air temperature as tested by a generalized linear model (Fig. 4). In contrast, morphs COMS, CBZ, CBSF, CGG and CSCH had significant responses to summer temperature. For CSCH the model suggested a negatively sigmoidal, and for CBZ a positively sigmoidal relationship with summer temperature.

Optima and tolerances of the Cyclotella comensis morphs

The *C. comensis* morphs had specific temperature optima and tolerances as assessed by cross-validated WA (Table 3). The original *C. comensis* complex had a cross-validated optimum of 13.0 °C and a cross-validated temperature tolerance of 3.8 °C. The COMS had an optimum of 14.9 °C and the narrowest tolerance of 2.0 °C and CBZ had an estimated temperature optimum of 15.1 °C with a tolerance of 2.5 °C. Therefore, the morphs COMS and CBZ are considered

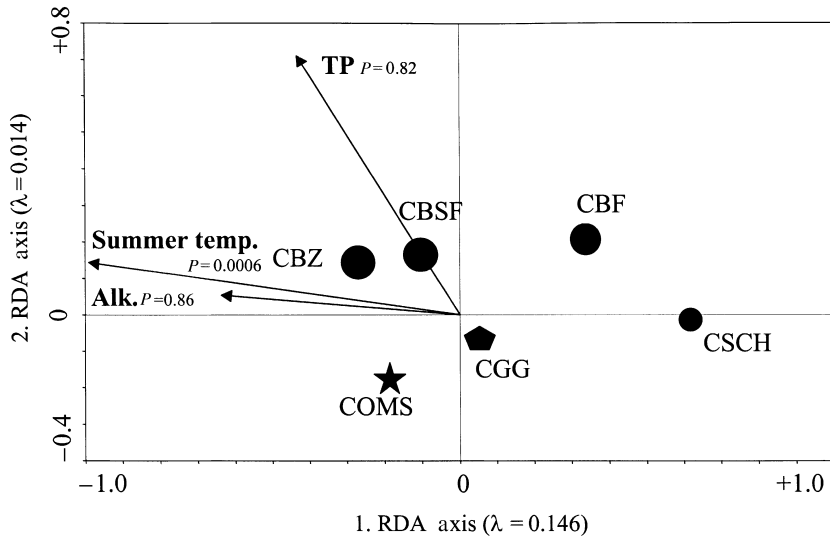


Fig. 3 First two axes of a redundancy analysis (RDA) to demonstrate the relationship among the *Cyclotella comensis* morphs, derived from 68 training set lakes, in relation to summer air temperature, overturn alkalinity (Alk) and total phosphorus (TP).

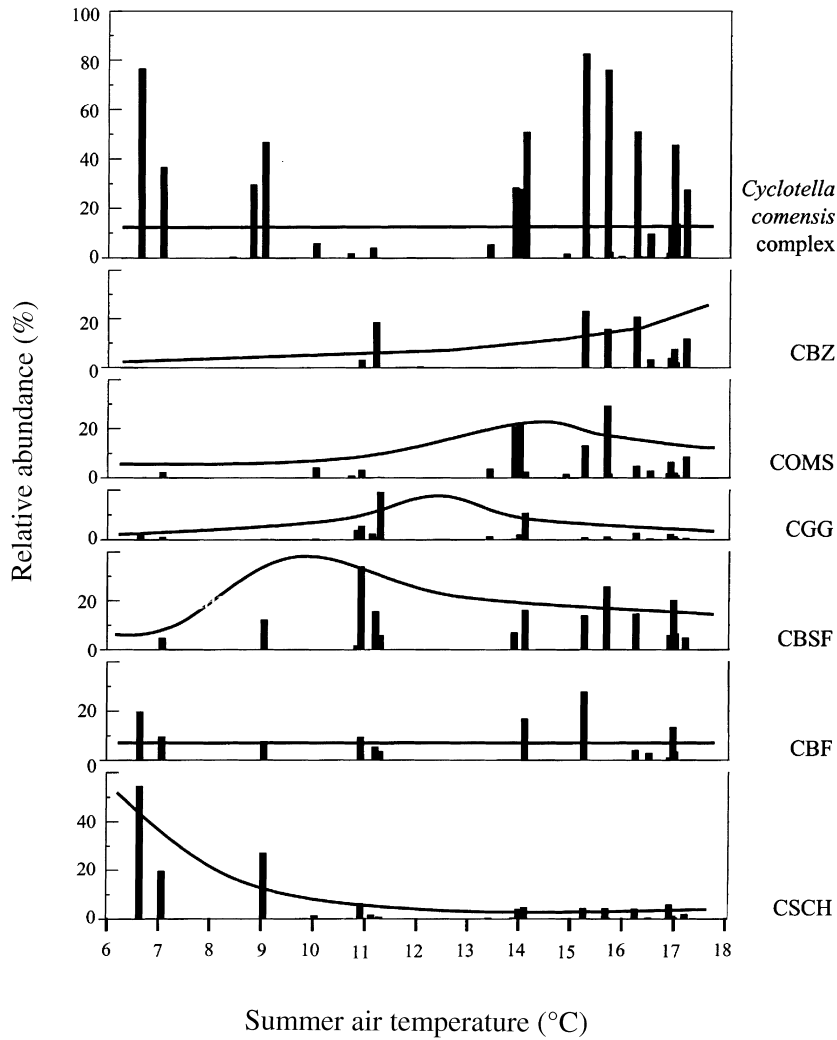


Fig. 4 Relative abundance of *C. comensis* ecomorphs along the summer temperature gradient. The significant relationships with summer temperature were tested by a Huisman–Olf–Fresco model (solid lines) (Huisman *et al.*, 1993).

Table 3 Cross-validated weighted averaging summer air temperature optima and tolerances for *C. comensis* ecomorphs

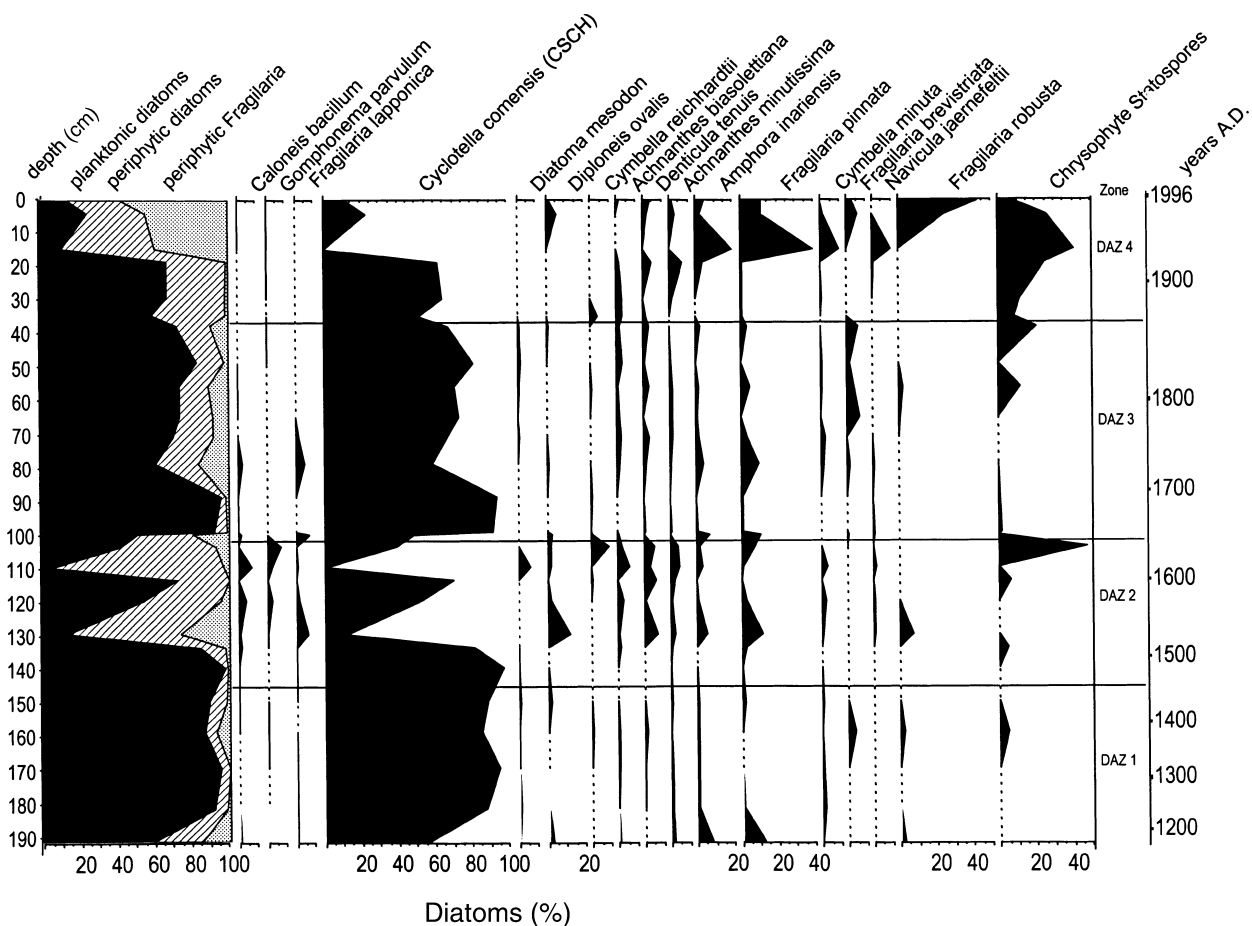
	Optimum (°C)	Tolerance (°C)
<i>C. comensis</i> complex	13.0	3.8
CBZ	15.1	2.5
COMS	14.9	2.0
CBSF	13.7	3.0
CBF	12.5	4.2
CGG	12.4	2.7
CSCH	8.9	4.0

as good, warm temperature indicators, whereas the morph CSCH, which had a lower optimum (6.2 °C) than that of CBZ, is considered a good cool temperature indicator. The inferred values for CSCH are probably still too high, because it had a sigmoidal negative response, not unimodal as assumed by weighted averaging.

Using the morphs, the cross-validated root mean squared error of prediction (RMSEP; ter Braak & Juggins, 1993) of the cross-validated WA-PLS model (an error estimate rather than a confidence interval) was only slightly improved from 2.30 to 2.27 °C. Consistent with the results from the RDA (Fig. 3), phosphorus showed no significant relationship to the morphs. The range of TP optima of the morphs [21–39 (g TP L⁻¹)], was very narrow compared with the TP-gradient of the training set [6–520 (g TP L⁻¹)].

Bachsee biostratigraphy

The low temperature ecomorph CSCH dominated large parts of the biostratigraphy of Bachsee (Fig. 5) a lake in the Swiss Alps (2265 m a.s.l.). The top 2 m contained four DAZ. The DAZ 1 (200–145 cm) and DAZ 3 (100–35 cm) were dominated by 80% CSCH and DAZ 2 (145–105 cm) showed a decrease in this

**Fig. 5** Diatom biostratigraphy of the Bachsee (2265 m a.s.l.), showing selected taxa only.

morph and an increase in periphytic diatoms such as *F. pinnata* Ehrenberg and *Diatoma mesodon* Ehrenberg, together with *Caloneis bacillum* Grunow and *Amphora inariensis* Krammer. In the uppermost DAZ 4 (30–0 cm), CSCH was replaced by *F. pinnata* and *F. brevistriata* Grunow.

Temperature reconstruction of the Bachsee

Splitting *C. comensis* into different ecomorphs modified the summer temperature reconstruction (Fig. 6), because the high optimum of the original undivided *C. comensis* complex biased the temperature reconstruction. The diatom-inferred summer air temperature estimated using the optimum of the original *C. comensis* complex varied between 12 and 15 °C for DAZ 1 and 3, whereas summer temperatures inferred from DAZ 2 were between 8 and 11.5 °C. The temperature values inferred from DAZ 1 declined continuously from 14.5 to 6.5 °C.

In contrast, the reconstruction based on the cold-indicating ecomorph CSCH suggests a much more

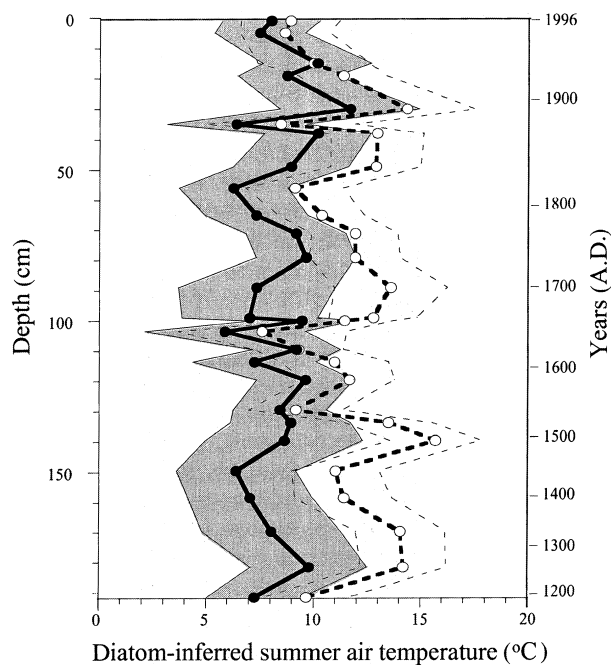


Fig. 6 Diatom-inferred summer air temperature for the Bachsee using a weighted averaging partial least squares two-component model. Solid line: inference using the newly defined *C. comensis* (CSCH) morph; dashed line with circles: inference using original *C. comensis* complex as published by Lotter *et al.* (1997). Shaded band, dashed lines: sample-specific error estimates.

constant climate at the Bachsee over the past 800 years. The diatom-inferred summer temperatures were between 6 and 10 °C over the whole period.

Discussion

The approach of quantitative environmental reconstruction is based on the assumption of a unimodal distribution of species along an environmental gradient, which may not reflect reality. On the basis of our results, we advocate the use of detailed morphological description to separate complex taxa such as *C. comensis*, in order to satisfy the statistical requirements of unimodal inference models.

Diatom inferred temperature reconstruction for the Bachsee

Reconstructions using the revised *C. comensis* taxonomy indicate that the temperature remained between 5 and 10 °C over the past 800 years at the Bachsee. These low temperatures are in agreement with an analysis of plant macrofossils, which showed that the timberline was below the Bachsee during the major part of the Holocene (L. Wick, unpublished data). The Alpine tree-line ecotone is regarded as strongly thermally controlled and is located around the 10 °C July isotherm (e.g. Kupfer & Cairns, 1996). In contrast, the diatom-inferred summer air temperature of the Bachsee based on the original *C. comensis* complex was significantly higher than using the newly defined *C. comensis* ecomorphs. Because the optima of the remaining diatom taxa are much lower than that of the original *C. comensis* complex, the high abundance of the *C. comensis* complex determines the magnitude of the inferred temperature curve.

The alternation of CSCH with *F. pinnata* (Fig. 5) also occurred in the Hagelseewli (2339 m a.s.l.), which is located in the same area. There *C. comensis* grew during the ice-free period in summer while *F. pinnata* occurred as a littoral diatom when the lake was only partly ice free. Hence, the changes in these two taxa could be used to infer the length of the ice-cover (Lotter & Bigler 2000). The dominance of *F. pinnata* from 130 to 110 cm (c. AD 1600) is synchronous with a dominance of *Procladius* (Skuse) in Bachsee (I. Walker, unpublished data), a cold-indicating chironomid (Lotter *et al.*, 1997). This suggests a period of cooler

climate at the Bachsee around AD 1600, which is in accordance with documentary data for Switzerland (Pfister, 1992) and the northern hemisphere (Jones *et al.*, 1998).

Cyclotella comensis ecomorphs

For reconstruction purposes it is very important to use the highest possible taxonomic resolution in order to identify taxa with contrasting temperature optima (Birks, 1994). The independent morphological and ecological approaches led to a successful classification of *C. comensis* ecomorphs. For temperature reconstructions it is, according to our study, most important to distinguish COMS and CBZ as warm-indicators and CSCH as a cold-indicator.

The *C. comensis* ecomorphs described in this paper are partly recognized in the literature. However, our discrimination system is new, because it focuses on the marginal zone and ignores the central area. The morphs, with the exception of CGG, occur in different abundances in the type material of *C. comensis* Grunow from Lago di Como (198 m a.s.l., slide 2862 a, under the curation of the Naturhistorisches Museum in Vienna). The COMS strongly resembles Grunow's drawing in Van Heurck's Atlas (Figs 16 and 17, Van Heurck, 1885). Straub (1987) reinvestigated material from Lago di Como. His 'Form A' seems to be identical with COMS while the CB (*Comensis* with broad trim) complex (CBZ, CBSF and CBF) seems to correspond with 'Form B'. Teubner (1995) analysed *Cyclotella* frustules of four lakes using a morphometric approach. She found valves similar to the CB complex and COMS and suggested that CB might be a heterovalvar sister valve of COMS, which resembles '*C. comensis* (4)' as defined by Wunsam *et al.* (1995). Both morphs occur at the warm end of the temperature gradient. The cold-preferring morph CSCH was probably the taxon described by Kling & Håkansson (1988, Fig. 33) from Char lake, which seems to be comparable with lakes at the cold end of the Swiss temperature gradient. The morph CGG was described by Kling & Håkansson (1988) as *C. gordonensis*, and by Wunsam *et al.* (1995) as '*Cyclotella* sp. aff. *C. gordonensis* (2)'.

There was a distinct decrease in cell diameter with increasing altitude. Jewson (1992) found the greatest decrease in cell diameter of *S. neoastraea* during nutrient stress in summer and low light conditions

in late autumn, whereas Drebes (1966) described the necessity of a minimal temperature for sexual reproduction of *S. palmeriana* (Grev.) Grunow. Pienitz & Smol (1993) found a comparable reduction in size with increasing latitude in Canadian subarctic lakes. It would, however, require culture studies to determine whether small cell diameters in high elevation lakes are related to disadvantageous conditions for sexual reproduction for *C. comensis*, and to assess their temperature optima.

This paper demonstrates the value of increased taxonomic resolution for environmental bioindication, if the additional effort is justified by greater ecological information.

Acknowledgments

We are grateful to François Straub, Joachim Hürtilman, Wolfram Scheffler for inspiring taxonomical, and to John Birks for stimulating statistical discussions. Thanks to the participants of the European Diatom Database Initiative (EDDI) meeting organized by John Anderson in January 1999 in Copenhagen, as well as to two anonymous reviewers for useful comments. Special thanks to Toni Menninger and Platt Bradbury for critical reading of the manuscript and discussion of the concept. This study would not exist without the multivariate statistics lecture of Prof. Riedwyl, University of Bern. The study was supported by the Priority Programme Environment grant 5001-44600 and the EU 'Environment and Climate Program' Project CHILL 10.000 under contract ENV4-CT97-0642 and is CHILL-10,000 contribution 15.

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(Manuscript accepted 4 January 2001)