

Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate

André F. Lotter¹, H. John B. Birks², Wolfgang Hofmann³ & Aldo Marchetto⁴

¹*Geobotanical Institute, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland, and Swiss Federal Institute of Environmental Science and Technology (EAWAG), CH-8600 Dübendorf, Switzerland (e-mail: lotter@sgi.unibe.ch)*

²*Botanical Institute, University of Bergen, Allégaten 41, N-5007 Bergen, Norway, and Environmental Change Research Centre, University College London, 26 Bedford Way, London, WC1H 0AP, UK (e-mail: john.birks@bot.uib.no)*

³*Max-Planck-Institut für Limnologie, August-Thienemann-Strasse 2, D-24302 Plön, Germany (e-mail: hofmann@mpil-ploen.mpg.d400.de)*

⁴*Consiglio Nazionale delle Ricerche, Istituto Italiano di Idrobiologia, Largo Vittorio Tonolli, 50-52, I-28048 Verbania Pallanza, Italy (e-mail: marchett@iii.to.cnr.it)*

Received 11 October 1996; accepted 15 March 1997

Key words: transfer functions, weighted-averaging partial-least-squares, summer temperatures, surface sediments, modern training-sets, Switzerland

Abstract

Diatom, chrysophyte cyst, benthic cladocera, planktonic cladocera, and chironomid assemblages were studied in the surface sediments of 68 small lakes along an altitudinal gradient from 300 to 2350 m in Switzerland. In addition, 43 environmental variables relating to the physical limnology, geography, catchment characteristics, climate, and water chemistry were recorded or measured for each lake. The explanatory power of each of these predictor variables for the different biological data-sets was estimated by a series of canonical correspondence analyses (CCA) and the statistical significance of each model was assessed by Monte Carlo permutation tests. A minimal set of environmental variables was found for each biological data-set by a forward-selection procedure within CCA. The unique, independent explanatory power of each set of environmental variables was estimated by a series of CCAs and partial CCAs. Inference models or transfer functions for mean summer (June, July, August) air temperature were developed for each biological data-set using weighted-averaging partial least squares or partial least squares. The final transfer functions, after data screening, have root mean squared errors of prediction, as assessed by leave-one-out cross-validation, of 1.37 °C (chironomids), 1.60 °C (benthic cladocera), 1.62 °C (diatoms), 1.77 °C (planktonic cladocera), and 2.23 °C (chrysophyte cysts).

Introduction

Sediments are among the few continuous proxy archives that provide information about past environments over time periods of single years to millennia. Palaeoecological and palaeolimnological studies of lacustrine deposits can provide the long time-series that are needed not only to reconstruct past environmental conditions but also to assess the natural variability of

biotic and abiotic systems. Moreover, they can yield information about the reaction of these systems to different perturbations and, given a good time-control, it is possible to estimate phases and amplitudes of disturbances. Despite this potential, palaeoecological studies have often been descriptive and narrative (Birks, 1992, 1993). Processes driving observed patterns in the proxy records have to be inferred. Changes in past environmental conditions are often only described in

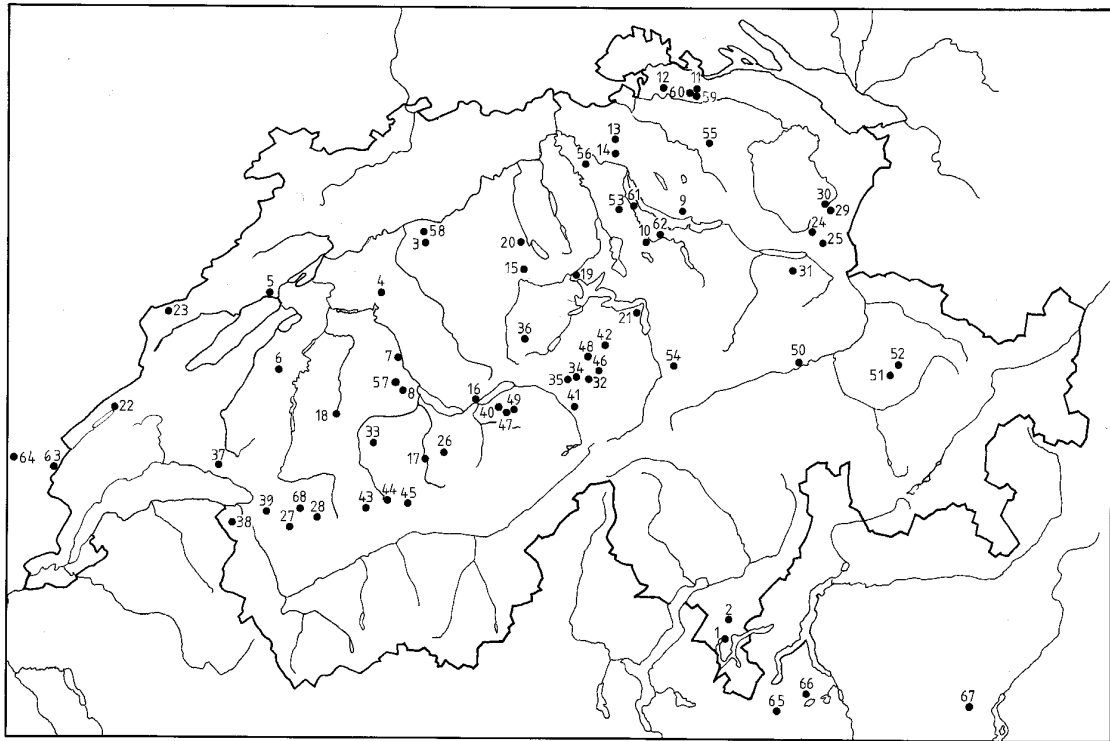


Figure 1. Map of Switzerland showing the location of the 68 sampled lakes. Numbers refer to lakes in Table 1.

a qualitative way. To test hypotheses concerning past environmental changes and also to evaluate biological and climate models, it is necessary to quantify palaeoecological proxy data (Birks, 1995).

Early attempts to quantify climatic variables such as temperature from palaeoecological data were carried out by Iversen (1944). However, it was only in the 1970s that mathematical methods began to be applied to the reconstruction of palaeoenvironments in a rigorous and quantitative way (e.g. Imbrie & Kipp, 1971). Diatoms have played an important role in the development of quantitative methods for environmental reconstruction: early work concentrated on the relationship between diatom assemblages and lake-water pH using linear regression techniques (e.g. Renberg & Hellberg, 1982). In the late 1980s much effort was put into the development of numerically robust and ecologically realistic mathematical methods for environmental reconstruction as well as for reliable error estimation (e.g. ter Braak & Barendregt, 1986; ter Braak, 1987; ter Braak & Looman, 1986, 1987; ter Braak & van Dam, 1989; Birks et al., 1990). Most of the required protocols, inferential techniques, and

quality control guidelines were developed in connection with lake acidification studies (e.g. Munro et al., 1990; Charles, 1990; Birks et al., 1990; Birks, 1995) and can now be directly transferred to other studies of past environmental change. In recent years, several studies have used aquatic organisms to estimate palaeo-temperatures (e.g. Walker et al., 1991a, 1997; Levesque et al., 1993, 1994; Cwynar & Levesque, 1995).

High-latitude and high-altitude sites have recently become a focal point for research with respect to the expected future warming of the earth's climate. A better understanding of the reaction of these ecosystems to environmental change in the past (e.g. Fritz, 1996) will greatly enhance the ability to predict future environmental change. In mountainous regions, however, such as the Alps of central Europe with their complex topography and climate, quantitative reconstructions, especially climatic reconstructions, need a much more refined scale of investigation than is currently available at a broad continental scale (e.g. Huntley & Prentice, 1988, 1993).

This study was undertaken to assess the potential of using different aquatic organisms, such as diatoms, cladocera, chironomids, and chrysophytes, as environmental indicators for quantitative palaeoenvironmental reconstructions in Late-Glacial and Holocene time-series in the geographical region of Central Europe with particular reference to the Alps. In this paper, we focus on the different modern training-sets, and their quantitative relationship to present-day climate in the Alps. In addition, we outline the statistical bases for the numerical regression and calibration methods used. In a second, separate contribution we concentrate on the relationship of these data-sets to trophic state (Lotter et al., in press).

Sites, environmental variables and microfossils studied

We sampled the surficial sediments of 68 small lakes (Figure 1) of similar size between 1993 and 1994. These lakes are situated along an altitudinal gradient from 300 to 2350 m above sea level (a.s.l.), which is also a major climatic gradient (Table 1). To minimize the effects of low pH that might override effects of other important environmental variables on the aquatic organisms, only lakes in calcareous bedrock regions were chosen.

At each lake several echo-sounding tracks were carried out to locate the deepest part of the basin and water chemistry was determined (Table 1 and Müller et al., in press). Four short sediment cores were taken with a modified Kajak corer (6.2 cm diameter) in the deepest part of each lake. The top 5 cm of two of the cores were extruded in 1-cm increments in the field, the third core was cut open longitudinally in the lab, photographed, and checked for stratigraphical consistency of the uppermost sediment, and the remaining core has been archived in a cold room. For this study the topmost one centimetre was used for analysis.

Geographical lake and catchment data are given in Table 1. Lakes and catchments were digitized from 1:25 000 topographic maps. On the basis of different GIS maps of Switzerland with a spatial resolution of 100 × 100 m the area covered by glaciers, loose rocks, carbonaceous, siliceous, and mixed bedrock was estimated for each catchment. Land-use for each catchment was subdivided into areas covered by agricultural land, urban areas, wooded areas, unwooded green areas, and bare ground. Climatic variables estimated for each lake were the number of growing degree

days (>5 °C), mean annual as well as mean monthly values for temperature and precipitation. Mean seasonal temperatures (winter: December, January, February; spring: March, April, May; summer: June, July, August; autumn: September, October, November) as well as winter and summer precipitation were also calculated (Table 2).

All organisms have been analysed by one analyst only, thus providing data sets with a consistent taxonomy and nomenclature (Birks, 1995).

Samples for diatom and chrysophyte cyst analysis comprised ca 0.5 cm³ and were treated with hot 30% H₂O₂ and 10% HCl before mounting on slides with Naphrax. For each slide, a minimum of 500 diatom valves was counted at a magnification of 1250 ×, using a Leitz DM microscope with phase contrast. For diatom identification, the floras of Krammer & Lange-Bertalot (1986–1991) were used. The taxonomy of the centric diatoms, especially the *Cyclotella* species, largely follows Wunsam et al. (1995).

The chrysophyte cyst to diatom ratio (C/D) was determined by counting the number of cysts occurring together with the first 1000 diatom valves. Samples having a C/D ratio higher than 0.02 were further examined. A minimum of 125 cysts or at least 1000 fields of view, whichever came first, were analysed. Cyst taxonomy follows Duff et al. (1995).

Sample sizes for zoological microfossil analysis ranged from 0.6 to 27.2 g dry weight (mean = 6.8 g). The sediment was treated with 10% KOH on a magnetic stirrer. For cladoceran analysis, the remains of Bosminidae and Chydoridae were examined in the separate fractions >100 μm and 55–100 μm. Subsamples equivalent to 0.009–3.4 g dry weight (mean = 0.3 g) were counted under a microscope at 100 × magnification. As different fragments of the animals such as shells, head shields, and post-abdomens are generally well-preserved, only the most abundant component, which in most cases is the shell, is taken into account (Frey, 1986). Densities were calculated as numbers per gram dry weight. If chydorid numbers per sample were <100, additional non-quantitative samples were counted. For identification, the keys by Frey (1958, 1959), Flössner (1972), and Lieder (1983) were used. Nomenclature follows Flössner (1972). Identification of *Bosmina* (*Eubosmina*) remained unclear in several cases. *Bosmina* (*Eubosmina*) morphs with a very long mucro and a very short mucro are called *Bosmina* sp. A and *Bosmina* sp. B, respectively. In the chydorids, a quantitative separation of the small *Alona* species is difficult. As identification is mainly based on the pores

Table 1. Major variables characterizing the climate, limnology, and catchment of the investigated lakes. The water chemistry refers to spring circulation concentrations

Lakes Number Name	Geography		Catchment			Climate			Land-use			Geology			Biology																
	Abbr- vation	Eleva- tion [m asll [N]	Longi- tude [E]	Maximum depth [m]	Open water area [km ²]	Inflowing water area [km ²]	Annual Catchment area [km ²]	Winter tempera- ture [°C]	Spring tempera- ture [°C]	Summer tempera- ture [°C]	Autumn tempera- ture [°C]	Degree- days	Annual precipi- tation [mm]	Bare Agri- land [%]	Urban wood- land [%]	Green unwooded [%]	Chert's rock [%]	Loose rock [%]	Carbonate bedrock [%]	Siliceous bedrock [%]	Mixed bedrock [%]	Clado- phyte taxa	Chro- ceru taxa	Chiro- nomid taxa							
1	Lago di Muzzano	MUZ	337 45° 59' 53" N	8° 55' 42" E	3.2	0.22	0	11.3	2.9	10.7	20.0	11.8	22948	1785	0.0	29.1	50.5	16.5	3.9	0	24	5	66	5	48	15	12	16			
2	Lago d'Oniglo	ORI	416 46° 03' 07" N	8° 56' 38" E	6.0	0.07	1	1.19	11.1	2.8	10.4	19.6	11.4	22041	1817	1.0	5.1	14.3	78.6	1.0	0	17	0	83	0	48	18	10	8		
3	Bunglähisee	BUR	465 47° 10' 10" N	7° 40' 09" E	31.0	0.19	2	4.29	8.9	0.7	8.3	17.1	9.3	16721	1049	1.0	61.3	9.6	25.6	2.5	0	96	4	0	0	40	18	20	25		
4	Moosee	MOO	521 47° 01' 25" N	7° 38' 42" E	21.0	0.31	1	10.41	8.7	0.4	8.2	17.0	9.1	16410	1048	1.5	66.3	9.0	21.9	1.3	0	60	40	0	0	45	11	18	12		
5	Le Luchat	LOC	432 47° 01' 13" N	6° 59' 52" E	9.2	0.05	0	0.88	9.1	1.0	8.5	17.3	9.5	17226	892	0.0	60.8	2.9	33.3	2.9	0	29	71	0	0	34	14	13	27		
6	Lac de Steodorf	SEE	609 46° 47' 14" N	7° 02' 29" E	7.5	0.10	3	7.38	8.2	0.0	7.8	16.4	8.6	15160	1031	0.3	77.1	7.0	14.6	1.0	0	95	5	0	0	24	n.a.	6	17		
7	Gerzensee	GER	603 46° 49' 55" N	7° 32' 53" E	10.0	0.27	2	2.70	8.3	0.1	7.8	16.6	8.8	15578	1044	0.0	78.2	14.9	5.0	2.0	0	32	n.a.	0	0	32	n.a.	17	26		
8	Uebeschsee	UEB	641 46° 44' 07" N	7° 34' 00" E	14.5	0.15	2	2.16	8.2	0.0	7.7	16.3	8.6	15139	1187	6.3	80.0	5.3	6.1	2.3	0	97	3	0	0	37	18	21	22		
9	Lütelsee	LUT	500 47° 15' 38" N	8° 46' 22" E	6.0	0.13	4	6.02	8.4	0.2	7.9	16.6	8.9	15721	1352	7.1	67.0	7.1	10.2	8.6	0	25	40	35	0	41	n.a.	19	8		
10	Wilensee	WIL	730 47° 10' 20" N	8° 37' 13" E	21.0	0.03	1	0.50	7.3	-0.7	6.6	15.4	7.9	13274	1612	5.1	89.8	1.0	4.1	0.0	0	100	0	0	0	35	n.a.	16	24		
11	Hütwellsee	HUT	434 47° 36' 39" N	8° 50' 42" E	15.0	0.35	2	3.71	8.6	0.3	8.3	17.0	8.9	16351	922	3.1	68.2	3.1	25.4	0.3	0	96	4	0	0	35	14	20	18		
12	Husenensee	HUS	409 47° 37' 22" N	8° 02' 20" E	14.0	0.08	1	1.33	8.7	0.4	8.4	17.0	8.9	16537	903	5.1	32.7	4.1	54.1	4.1	0	100	0	0	0	36	16	19	16		
13	Mettemhölsler See	MET	418 47° 28' 31" N	8° 29' 35" E	12.5	0.03	0	0.50	8.8	0.6	8.5	17.1	9.1	16684	1043	4.0	44.6	25.7	19.8	5.9	0	72	28	0	0	46	n.a.	17	26		
14	Unterer Chutzensee	CHA	439 47° 25' 58" N	8° 29' 26" E	7.8	0.19	1	1.29	8.8	0.6	8.4	17.0	9.1	16495	1037	12.0	25.0	10.0	45.0	8.0	0	100	0	0	0	51	n.a.	22	31		
15	Soppensee	SOP	596 47° 05' 31" N	8° 04' 56" E	26.5	0.23	0	1.59	8.2	0.1	7.5	16.3	8.7	15172	1266	2.0	80.8	5.1	12.1	0.0	0	94	6	0	0	40	11	22	9		
16	Burgsee	BUR	613 46° 41' 55" N	7° 53' 11" E	19.0	0.09	1	1.18	8.3	0.2	7.9	16.3	8.9	15431	1193	4.1	31.6	8.2	51.0	5.1	0	25	75	0	0	28	30	15	22		
17	Blausee	BLA	887 46 32' 01" N	7° 39' 55" E	10.0	0.01	0	0.09	6.9	-0.9	6.2	14.9	7.6	12446	1213	0.0	10.0	89.0	10.0	0	100	0	0	0	0	36	n.a.	8	19		
18	Schwarze	SCH	1046 46 40' 10" N	7° 17' 06" E	9.5	0.46	0	19.70	6.0	-1.8	5.1	14.0	6.7	10671	1620	7.1	53.2	2.2	27.0	10.5	0	15	66	0	0	49	6	19	22		
19	Rotsee	ROT	419 47 04' 18" N	8° 19' 01" E	16.0	0.50	2	4.60	9.1	0.9	8.6	17.3	9.5	17190	1179	0.5	36.1	35.1	18.5	9.8	0	10	90	0	0	40	11	22	9		
20	Mattensee	MAU	504 47 10' 20" N	8° 04' 55" E	9.0	0.60	2	4.30	8.7	0.5	8.1	16.9	9.1	16258	1110	2.0	76.5	8.2	12.2	1.0	0	85	15	0	0	38	16	21	20		
21	Seelbisg See	SEL	738 46 57' 32" N	8° 34' 16" E	37.5	0.18	1	2.70	7.3	-0.6	6.6	15.3	8.0	13301	1591	4.1	46.3	3.6	46.0	0.0	0	100	0	0	0	18	15	20	24		
22	Lac Brenet	BRE	1002 46 50' 29" N	6° 19' 31" E	17.0	0.63	0	2.85	6.3	-1.1	5.0	14.0	7.4	10710	1515	2.2	31.9	7.2	55.9	2.7	0	30	70	0	0	66	n.a.	20	24		
23	Lac des Taillores	TAI	1036 46 57' 57" N	6° 34' 07" E	8.5	0.44	0	33.16	5.5	-2.1	4.4	13.4	6.4	9691	1603	0.2	44.6	2.0	52.7	0.5	0	4	96	0	0	51	27	11	19		
24	Schwendisee	SCW	1159 47 11' 19" N	9° 19' 55" E	9.5	0.04	2	5.06	5.1	-2.6	4.2	12.7	6.2	8865	1793	7.3	48.5	0.5	37.4	6.3	0	13	84	0	3	42	16	13	27		
25	Voralpsee	VOR	1123 47 09' 30" N	9° 22' 43" E	3.3	0.15	5	13.52	5.3	-2.5	4.4	12.9	6.3	9184	1881	12.2	49.8	1.0	28.1	9.0	0	16	84	0	0	41	n.a.	4	7		
26	Tschingelsee	TSC	1150 46 33' 10" N	7° 44' 37" E	1.6	0.11	2	3.665	5.6	-2.0	4.6	13.4	6.4	9798	1304	57.0	25.6	1.2	10.1	6.1	8	13	55	0	24	55	n.a.	1	6		
27	Lac des Chavornes	CHV	1690 46 20' 05" N	7° 05' 09" E	29.5	0.05	1	0.74	3.7	-3.4	2.1	11.1	4.8	6179	1665	1.0	26.5	1.0	67.3	4.1	0	0	22	0	78	53	14	9	6		
28	Lac Retard	RET	1685 46 21' 41" N	7° 12' 00" E	4.5	0.01	0	0.22	3.5	-3.7	2.1	11.0	4.7	6057	1762	8.9	44.6	5.0	9.9	31.7	0	59	0	0	41	46	14	18	11		
29	Fälensee	FAL	1452 47 15' 08" N	9° 24' 59" E	31.0	0.15	0	4.25	3.5	-3.9	2.2	10.9	4.7	5887	2018	28.9	44.8	0.0	5.5	20.9	0	15	85	0	0	13	12	7	10		
30	Sealpsee	SAL	1141 47 16' 10" N	9° 33' 56" E	15.0	0.14	1	11.33	5.3	-2.4	4.3	12.9	6.3	9044	1874	29.3	51.9	0.5	3.5	14.9	0	18	82	0	0	40	n.a.	8	7		
31	Grossee	GRO	1618 47 04' 48" N	9° 14' 53" E	11.5	0.05	2	2.20	2.9	-4.5	1.6	10.3	4.2	5142	1824	3.0	79.4	1.0	14.5	2.0	0	43	57	0	0	61	n.a.	8	2		
32	Engstensee	ENG	1850 46 46' 27" N	8° 21' 32" E	49.0	0.45	2	7.40	1.9	-5.1	0.2	9.0	3.3	3470	1793	58.5	29.3	0.3	4.0	8.0	11	10	54	0	25	31	n.a.	9	21		
33	Seebensee	SEB	1831 46 34' 41" N	7° 26' 38" E	15.5	0.06	0	0.23	2.2	-4.9	0.6	9.7	3.5	4163	1683	15.2	42.3	0.0	15.2	27.3	0	8	46	0	46	48	13	7	13		
34	Tannensee	TAN	1976 46 46' 30" N	8° 18' 22" E	16.0	0.34	10	1.12	1.3	-5.6	-0.5	8.4	2.7	2697	1861	17.8	70.3	2.0	0.0	9.9	0	100	0	0	92	20	9	18			
35	Melchsee	MEL	1891 46 46' 19" N	8° 16' 07" E	15.5	0.49	7	5.92	1.7	-5.2	0.1	8.9	3.2	3279	1843	19.2	71.6	1.2	2.0	6.0	0	26	74	0	0	45	n.a.	7	11		
36	Seewensee	SEW	1689 46 53' 21" N	8° 05' 15" E	4.5	0.03	2	0.21	3.3	-4.0	1.8	10.7	4.5	5671	1744	0.0	23.8	0.0	70.3	5.9	0	65	0	0	35	47	15	9	11		
37	Lac de Bret	BRE	674 46 30' 55" N	6° 46' 26" E	18.0	0.50	1	2.97	8.2	0.3	7.5	16.3	8.8	15131	1278	0.3	83.3	5.1	10.3	1.0	0	89	11	0	0	43	n.a.	16	11		
38	Lac Tannay	TAY	1408 46 20' 47" N	6° 50' 33" E	31.0	0.18	1	7.93	5.0	-2.2	3.5	12.5	6.0	8265	1500	21.5	35.4	0.8	25.3	17.2	0	1	99	0	0	36	n.a.	9	14		
39	Lac de Nervaux	NER	1493 46 22' 44" N	6° 59' 07" E	10.0	0.01	1	0.92	4.3	-2.9	2.9	11.9	5.4	7287	1609	8.0	44.0	0.0	30.0	18.0	0	0	95	0	5	35	16	10	17		
40	Stigistalsee	SAG	1935 46 40' 51" N	7° 58' 39" E	9.7	0.07	3	3.85	1.7	-5.3	-0.1	7.6	2.1	3290	1663	39.5	41.5	0.0	2.2	16.8	0	1	100	0	0	48	18	5	13		
41	Wännishordsee	WAN	2103 46 40' 58" N	8° 17' 58" E	14.0	0.02	1	1.64	0.5	-6.2	-1.4	7.6	4.5	1878	1530	53.0	30.0	0.0	17.0	0	12	88	0	0	35	n.a.	4	4			
42	Bannalpsee	BAN	1587 46 25' 12" N	8° 25' 42" E	17.0	0.16	2	8.23	3.3	-3.9	1.9	10.7	4.1	5659	1674	58.4	32.2	0.5	2.0	7.0	2	29	69	0	0	49	15	6	14		
43	Iffigsee	IFF	2065 46 23' 16" N	7° 24' 33" E	30.0	0.10	1	4.61	1.5	-5.5	-0.3	8.8	2.9	3152	1666	73.1	18.0	0.0	0.0	9.0	13	18	43	0	26	35	21	6	11		
44	Flusssee	FLU	2045 46 24' 38" N	7° 29' 59" E	8.5	0.04	1	0.79	1.5	-5.5	-0.3	8.9	2.9	3181	1487	92.0	8.0	0.0	0.0	0.0	0	100	0	0	100	0	0	47	n.a.	2	9
45	Lämmereisee	LAM	2296 46 24' 08" N	7° 35' 13" E	2.5	0.07	1	1.05	2.4	-6.4	-1.6	7.6	1.9	1878	1530	53.0	30.0	0.0	0.0	17.0	0	12	88	0	0	35	n.a.	4	4		
46	Trübssee	TRÜ	1764 46 47' 33" N	8° 33' 38" E	7.0	0.26	1	7.07	2.3	-4.7	0.8	9.6	3.7	4111	1749	60.8	31.2	0.3	4.8	3.0	19	7	48	0	26	44	n.a.	6	14		
47	Buchsee	BAC	2265																												

Table 1. Continued

Lakes Number Name in Fig. 1	Geography		Catchment		Climate		Land-use				Geology			Biology															
	Abbre- viation	Eleva- tion [m]	Longi- tude [E]	Maximum depth [m]	Open water area [km ²]	Inflowing streams area [km ²]	Annual temperature [°C]	Winter temperature [°C]	Spring temperature [°C]	Summer temperature [°C]	Autumn temperature [°C]	Degree Annual precipita- tion [mm]	Bare land [%]	Agri- land [%]	Urban [%]	Wooded [%]	Green unwooded [%]	Cliffters [%]	Loose rock [%]	Carbonate bedrock [%]	Siliceous bedrock [%]	Mixed bedrock [%]	Dia-Chryso-Clado-Chiro- nomid taxa	Clado-Chiro- nomid taxa	Chironomid taxa				
50	Lag Grand	GRD	1016	46°48'32"/9°15'29"/	5.0	0.02	1.89	6.3	-1.4	5.5	13.9	7.2	10999	1200	1.0	49.0	22.4	25.5	2.0	0	92	0	8	0	52	15	18		
51	Schwellsee	SCE	1933	46°45'56"/9°38'55"/	12.0	0.03	4	9.58	1.8	-5.0	8.9	3.3	3267	1162	58.3	25.7	0.0	0.2	15.8	0	57	29	14	0	67	n.a.	2	15	
52	Obersee	OB	1734	46°47'07"/9°40'53"/	14.5	0.08	1	2.71	2.7	-4.4	1.2	9.9	4.0	4895	1140	2.3	62.8	6.3	25.6	3.0	0	75	18	7	0	38	11	10	18
53	Türtersee	TÜR	643	47°16'17"/8°30'02"/	21.0	0.50	5	5.19	7.9	-0.2	7.3	16.0	8.4	14495	1139	0.2	58.0	15.0	25.0	1.8	0	57	43	0	0	35	10	20	20
54	Seewilsee	SWL	2028	46°48'45"/8°43'02"/	16.0	0.08	1	2.70	0.8	-0.0	-1.0	7.9	2.4	2224	1729	57.0	27.0	0.0	1.0	15.0	0	61	33	0	6	42	n.a.	3	11
55	Bichelsee	BIC	590	47°27'32"/8°54'04"/	6.5	0.09	5	2.70	6.8	-1.1	6.1	14.9	7.3	12317	1437	0.0	28.2	3.2	68.5	0.0	0	1	99	0	0	28	12	14	20
56	Egelsee	EGE	667	47°24'08"/8°21'39"/	10.0	0.02	0	0.29	7.6	-0.4	7.0	15.7	8.1	13923	1247	3.0	0.0	0.0	80.0	17.0	0	100	0	0	0	30	18	16	18
57	Drittligsee	DIT	652	46°45'25"/7°32'09"/	16.5	0.07	0	3.13	7.9	-0.2	7.3	16.0	8.4	14582	1169	3.1	69.4	5.9	21.4	0.3	0	100	0	0	0	17	8	14	21
58	Inkwiensee	INK	461	47°11'58"/7°39'50"/	5.0	0.12	1	2.13	8.8	0.7	8.2	17.1	9.3	16663	1073	1.0	67.9	9.3	20.6	1.3	0	100	0	0	0	30	n.a.	15	17
59	Hänsensee	HAS	434	47°36'29"/8°49'58"/	5.5	0.11	0	2.52	8.6	0.3	8.3	17.0	8.9	16336	926	0.3	75.9	5.4	17.4	1.0	0	100	0	0	0	39	21	15	20
60	Nusshaussee	NUS	434	47°36'29"/8°49'58"/	8.2	0.25	1	5.87	8.6	0.2	8.3	16.9	8.8	16263	927	0.5	68.7	7.2	23.6	0.0	0	94	6	0	0	40	n.a.	20	19
61	Gantler Waldweiher	GAW	545	47°16'48"/8°33'35"/	5.5	0.03	1	1.88	8.3	0.2	7.8	16.5	8.8	15463	1265	0.0	27.3	2.0	70.7	0.0	0	96	4	0	0	53	16	14	20
62	Hüntensee	HÜN	658	47°11'05"/8°40'36"/	12.0	0.17	1	2.33	7.7	-0.4	7.0	15.8	8.2	14087	1574	1.0	81.6	9.2	6.1	2.0	0	100	0	0	0	39	n.a.	18	12
63	Lac des Roussets	ROU	1088	46°30'12"/6°05'11"/	11.5	0.89	4	15.68	5.9	-1.6	4.6	13.4	6.8	10314	1976	0.2	39.8	10.0	49.8	0.2	0	25	75	0	0	60	n.a.	20	19
64	Lac de l'Abbaye	ABB	871	46°31'48"/5°54'42"/	18.0	0.80	1	25.93	6.6	-0.9	5.3	14.1	7.5	10800	1884	0.0	50.0	10.0	40.0	0.0	0	25	75	0	0	41	19	16	18
65	Lago di Montorfano	MON	394	45°46'59"/9°08'23"/	6.5	0.52	0	1.57	13.2	4.2	12.0	21.8	14.1	24995	1592	1.0	49.0	14.7	34.3	1.0	0	55	35	0	10	48	24	15	19
66	Lago del Segrino	SEG	374	45°49'51"/9°16'02"/	8.5	0.34	1	2.66	11.7	2.9	10.4	20.1	13.0	23900	1586	5.1	25.3	8.1	60.6	1.0	0	25	70	0	5	41	n.a.	21	27
67	Lago di Endine	END	334	45°46'55"/9°56'50"/	8.0	0.49	3	8.34	12.2	4.0	10.2	20.6	13.8	24000	1425	0.0	39.6	9.9	49.5	1.0	0	20	20	50	10	37	15	16	17
68	Lac Lison	LIO	1848	46°23'14"/7°07'46"/	26.0	0.07	0	1.50	2.6	-4.4	1.0	10.0	3.9	4659	1777	28.0	30.0	1.0	14.0	27.0	0	13	0	0	87	52	n.a.	5	18
Maximum			2339		49.0	0.89	3665	13.2	4.2	12.0	21.8	14.1	24995	2018	92.0	89.8	50.5	89.0	31.7	19	100	100	99	87	92	30	22	31	
Mean			1094		13.8	0.20	5.07	5.9	-1.8	4.9	13.7	6.8	11039	1467	16.3	46.2	5.8	25.1	6.7	1	43	43	7	7	43	16	12	16	16
Median			945		11.8	0.12	2.70	6.4	-1.1	5.4	14.1	7.3	10900	1552	4.0	44.6	3.0	19.2	3.5	0	25	40	0	0	41	15	13	17	17
Minimum			334		1.6	0.01	0.09	-0.4	-7.0	-2.4	6.6	1.3	1046	892	0.0	0.0	0.0	0.0	0.0	0	0	0	0	0	13	6	1	2	2

of the head shield, species such as *Alona rustica* are possibly underestimated.

For chironomid analysis, the fractions >200 μm and 100–200 μm were examined separately under a stereo microscope at 20–25 × magnification. The results of both analyses were then combined for the numerical treatment of the data. The larval head-capsules were picked out, dehydrated in 96% alcohol, and mounted in Euparal (Hofmann, 1986). The head capsules were identified at 200–400 × magnification. Densities were calculated as numbers per gram dry weight. In 46 of the 68 lakes, numbers of specimens per sample were <50 and examination of the topmost 2 cm of sediment was therefore necessary. For identification, the keys by Hofmann (1971), Wiederholm (1983), and Moller Pillot (1984) were used. Nomenclature follows Wiederholm (1983). The Pentaneurini were separated by the positions of the pores SSm, S9, S10, and VP on the submental surface (Kowalyk, 1985). With respect to pore arrangement, Pentaneurini sp. A, B, and C correspond to *Paramerina-*, *Zavrelimyia-*, and *Telopelopia-*types, respectively. The distinction of *Orthocladius* with six lateral mentum teeth from *Cricotopus* is uncertain: brownish head capsules in which the lateral mentum teeth were equal in size are associated with *Orthocladius*. *Orthocladius* sp. A has more than six pairs of lateral mentum teeth and refers to the subgenus *Euorthocladius*. *Tanytarsus* sp. A is characterized by a short, distally rounded spur at the antennal pedestal.

Numerical analyses

To determine whether to use linear- or unimodal-based numerical techniques (ter Braak & Prentice, 1988), each biological data-set was initially analysed by detrended correspondence analysis (DCA; Hill & Gauch, 1980) with detrending-by-segments, non-linear rescaling, and downweighting of rare taxa to estimate the lengths of the compositional gradients in each data-set. As all the data-sets have compositional gradient lengths of 2 or more standard deviation units, all subsequent numerical analyses involved techniques that are based on an underlying unimodal species-response model (ter Braak & Prentice, 1988; Birks, 1995), namely canonical correspondence analysis (CCA), detrended CCA, weighted-averaging (WA) regression and calibration, and WA-partial least squares regression (WA-PLS; ter Braak & Juggins, 1993).

Table 2. Percentage variance explained by each environmental variable in CCA (999 unrestricted Monte Carlo permutations) when that environmental variable was the sole constraining variable. * significant at the 95% level ($p \leq 0.05$)

Variables	Diatoms	Chrysophytes	Benthic cladocera	Planktonic cladocera	All cladocera	Chironomids
Limnology						
Maximum water depth	2.5*	3.5	4.1*	11.2*	4.4*	2.9
Open water area	1.6	3.3	5.5*	4.2	3.5*	2.4
Number of inflows	1.4	2.1	0.9	2.3	1.1	1.7
Catchment area	1.7	1.6	0.7	0.3	0.7	1.3
Fish farming	1.8	2.4	3.7*	1.0	1.5	1.8
Hydroelectric power	1.7	3.2	1.9	12.9*	4.5*	1.9
Lake restoration	2.9*	2.2	1.8	1.2	1.1	1.2
Karst outflow	1.8	4.5*	1.7	0.8	1.6	1.5
Geography						
Elevation	6.6*	7.7*	6.7*	21.6*	14.9*	10.4*
Longitude	1.3	2.6	1.3	0.2	0.3	2.0
Latitude	2.0*	3.1	2.2	1.2	1.4	2.0
Catchment						
Area of glaciers	3.6*	3.5	5.8*	3.2	1.5	4.9*
Area of loose rocks	1.5	3.2	1.5	2.4	1.7	1.8
Area of carbonate bedrock	1.9	1.8	0.9	0.8	0.7	0.9
Area of silicate bedrock	1.2	2.7	2.0	4.6*	2.7	2.7
Area of mixed bedrock	2.9	2.4	3.3*	0.1	0.6	4.4
Area of agricultural land	1.9	2.2	0.7	0.4	1.6	1.1
Area of urban land	1.5	0.2	1.5	1.6	2.0	1.4
Wooded areas	1.1	1.4	1.4	1.4	1.5	1.1
Unwooded green areas	1.4	1.5	1.2	1.9	0.9	1.0
Area of bare ground	3.8*	5.4*	4.3*	12.6*	0.7	5.3*
Climate						
Mean annual temperature	6.2*	6.8*	6.3*	21.1*	14.1*	9.5*
Mean winter temperature	6.2*	6.7*	6.2*	20.6*	13.8*	9.5*
Mean spring temperature	6.4*	7.2*	6.4*	21.7*	14.5*	9.9*
Mean summer temperature	6.3*	6.9*	6.3*	21.4*	14.2*	9.5*
Mean autumn temperature	6.0*	6.3*	6.1*	20.1*	13.4*	9.1*
Number of degree days	6.3*	6.1*	6.1*	19.9*	12.9*	9.0*
Annual precipitation	3.6*	5.1*	5.3*	8.3*	5.1*	4.5*
Winter precipitation	4.3*	5.6*	5.1*	8.5*	6.0*	5.4*
Summer precipitation	2.5*	4.1*	4.1*	5.9*	3.2*	2.7*
Chemistry						
Conductivity	5.5*	4.7*	5.5*	12.0*	9.1*	7.5*
pH	2.5*	3.1	3.4*	4.9*	3.9*	2.7
Alkalinity	5.1*	4.5*	5.9*	11.4*	9.1*	6.9*
DOC	5.1*	5.1*	4.8*	15.6*	8.7*	6.9*
NO ₃	2.8*	3.5	2.0	3.5	3.2	3.8*
TN	3.0*	3.6	2.4	5.7	4.4*	4.8*
PO ₄	3.4*	3.9	1.4	1.0	1.3	2.7
TP	4.7*	4.4*	3.9*	6.2*	4.5	5.4*
Ca	4.4*	4.1*	5.5*	11.5*	9.1*	6.9*
Mg	3.5*	2.7	2.8*	4.4	3.6*	3.7*
Na	4.8*	6.6*	3.4*	9.0*	5.8*	4.6*
K	5.9*	6.6*	3.6*	10.0*	7.6*	6.9*
Si	1.6	1.9	2.3	1.2	1.2	1.8

In an attempt to estimate the explanatory power of each of the 43 environmental variables individually (marginal effects) for each biological data-set, a series of CCAs (ter Braak, 1986, 1990) were done using each environmental variable as the sole constraining variable. The percentage of the variance in the biological data explained by each variable was calculated (Table 2) and the statistical significance of each model was assessed by an unrestricted Monte Carlo permutation test involving 999 unrestricted permutations (ter Braak, 1990).

As 19–29 environmental variables have statistically significant marginal relationships with the different biological data-sets (Table 2), an attempt was made to find a minimal set of statistically significant environmental variables that explain, in a statistical sense, the biological data almost as well as when all 43 environmental variables are used to model the taxon-environment relationships. A forward-selection procedure (ter Braak, 1990; ter Braak & Verdonschot, 1995) was used for variable selection, and the statistical significance of each variable added was assessed by a Monte Carlo permutation test (999 unrestricted permutations) with a Bonferroni-type adjustment for significance levels (Manly, 1991; Miller, 1990).

Because a range of environmental predictors (climate, water chemistry, elevation, limnology, longitude and latitude, catchment variables) were selected in these CCA models, we assessed the relative statistical strength and independence of the six different groups of environmental variables (Table 3). This was done by a series of CCAs and partial CCAs (ter Braak, 1988) to estimate the marginal effects of the six groups of variables and to partition the total variance in each biological data-set into fractions representing: (a) the unique, independent contribution of variables reflecting the complex gradients of water chemistry, climate, elevation, latitude and longitude, catchment characteristics, and limnological features; (b) the covariances or conditional effects between these gradients; and (c) the unexplained variance (Borcard et al., 1992; Qinghong & Bråkenhielm, 1995; Table 3). Marginal effects for a group of variables (e.g. the eight limnology variables) were estimated by using this group of variables as the sole predictor variables in CCA. All other variables are ignored, hence the variance explained represents marginal effects. Unique effects for a group of variables were estimated by using the group of variables as the sole predictor variables and all other groups of variables as covariables in partial CCA (Borcard et al., 1992; Qinghong & Bråkenhielm, 1995). The statistical

significance of the marginal and the unique effects of each group of explanatory variables was assessed by Monte Carlo permutation tests (99 unrestricted permutations).

Of the various climatic variables considered (Table 2), we selected summer temperature for our inference models because it is highly correlated with the duration of ice-free season and epilimnetic water temperature (Patalas, 1990; Livingstone & Lotter, in press). Furthermore, mean summer temperature by itself explains the largest (or nearly the largest) amount of the variance in the individual data-sets (Table 2). All the biological percentage data were transformed to square-roots (Prentice, 1980) in an attempt to optimize the 'signal' to 'noise' ratio in the data. The inference models were developed using WA-PLS (ter Braak & Juggins, 1993; ter Braak, 1995). The optimal number of components to include in the model was assessed by leave-one-out jack-knifing (ter Braak & Juggins, 1993). The final model was selected that gave the lowest root mean squared error of prediction (RMSEP), as assessed by jack-knifing, the highest coefficient of determination (r^2) between observed and predicted values, again assessed by jack-knifing, and the lowest mean and maximum biases (ter Braak & Juggins, 1993) in the leave-one-out cross-validations. Ter Braak & Juggins (1993) and Birks (1995) discuss the important distinction between estimated and predicted values and between statistics based on the observed and estimated values ('apparent' statistics) and on the observed and predicted values ('cross-validation derived' statistics). The latter statistics provide more reliable measures of the true predictive ability of the transfer functions as they are less biased by sample resubstitution (Birks, 1995). Some of the final transfer functions derived by WA-PLS only involve one component, in which case the WA-PLS transfer function is identical to a WA regression and calibration with inverse deshrinking (ter Braak & Juggins, 1993).

Large biological and environmental data-sets invariably contain some samples that may show a poor relationship to the environmental variable of interest. Such outliers or 'rogue' observations can strongly affect the transfer function coefficients and may markedly decrease the predictive ability of the transfer function (Martens & Naes, 1989; Birks et al., 1990; Jones & Juggins, 1995). The concept of an outlying observation is very much model dependent (Hamilton, 1992). An observation may appear as an outlier in one statistical model but not in another statistical model. Outliers were first identified as samples hav-

Table 3. Marginal (M) effects of major groups of environmental variables (see Table 2) and partitioning of the total variance for each organism group into unique (U) effects

	Diatoms		Chrysophytes ¹⁾	Benthic cladocera		Planktonic cladocera		Chironomids	
	Unique	Marginal	M	U	M	U	M	U	M
Limnology	11.51*	13.75*	20.32	10.97	27.43*	9.62	15.21*	11.00	13.52*
Elevation	1.32	6.56*	7.65*	0.08	21.64*	1.94	6.75*	1.48	10.43*
Lat. & long.	3.22	3.51	5.62	2.78	1.47	4.59*	3.60	3.14	3.99*
Catchment	14.59*	19.68*	28.49	13.60	27.82	14.10*	19.52*	16.37	22.52
Climate	13.43*	19.18*	27.37*	8.73	41.04*	13.16*	21.24*	14.59	22.99*
Chemistry	14.60	21.81	36.69	11.28	27.13	15.21	25.61*	16.45	23.42
Total unique effects	58.67		–	47.44		58.62		63.03	
Total explained variance (including covariance between groups of variables)	67.33		84.56	80.14		71.68		71.74	
Sum of covariance terms	8.66		–	32.70		13.06		8.71	
Unexplained variance	32.67		15.44	19.86		28.32		28.26	

* Statistically significant, $p \leq 0.05$

¹⁾ Because of the small number of samples (37) relative to the number of environmental variables (43), it is not possible to estimate the unique contributions of the different groups of environmental variables for the chrysophyte data.

ing an absolute residual (observed – predicted) higher than the standard deviation of the environmental variable of interest (Jones & Juggins, 1995). The statistical influence *sensu* Hamilton (1992) of each potential outlier was estimated by Cook's D, which measures the change in the regression coefficient if a particular sample is deleted (Rawlings, 1988). If Cook's $D > 4/n$, where n is the number of samples, the sample is considered to have a high influence *sensu* Hamilton (1992). If a sample has a large absolute residual and a low Cook's $D (< 4/n)$, namely the sample has a low influence on the model, the sample was deleted as an outlier, as it has biotic assemblages that are poorly related to the environmental variable of interest and has little influence on the model coefficients (Jones & Juggins, 1995). Samples with a large absolute residual, a high influence (Cook's $D > 4/n$), and a very high squared residual chi-squared distance in a CCA (ter Braak, 1990) using the environmental variable of interest as the sole constraining variable in the analysis (Birks et al., 1990) were examined and usually deleted as outliers in the WA-PLS as they too appear to have biotic assemblages that are poorly related to the environmental variable of interest in the particular statistical model.

The final screened training sets for summer temperature are characterized in Table 4 by DCCA with

the environmental variable of interest as the only explanatory variable (detrending-by-segments, non-linear rescaling, square root transformed percentage data, rare taxa downweighted). The gradient length of DCCA axis 1 is the gradient length of the environmental variable in standard deviation units (ter Braak & Juggins, 1993). The gradient length of the second unconstrained axis is also presented, along with the eigenvalues and percentage variance of the biological data explained by each axis, as a guide to the presence of any large secondary gradients in the data. The biological data-sets used in the final training sets are summarized in terms of the ranges and medians of the effective number of taxa per sample and the effective number of occurrences per taxon, as estimated by Hill's (1973) N_2 diversity measure (ter Braak, 1990; ter Braak & Verdonschot, 1995). The environmental variable (summer temperature) is characterized in terms of its range, mean, median, and standard deviation (Table 4). The transfer function prediction models are summarized in terms of the optimal number of WA-PLS components, the apparent r^2 and RMSE, the jack-knifed r^2 and RMSEP, and the mean and maximum bias.

The statistical relationship of each individual taxon in the final screened training sets for the five taxonomic

Table 4. Descriptive statistics for the modern training sets in relation to summer temperature inference models after screening for outliers

	Diatoms	Chrysophytes	Benthic cladocera	Planktonic cladocera	Chironomids
Number of samples	64	34	61	48	50
Number of taxa	345	78	30	5	58
N2 for samples					
minimum	5.56	2.68	1.18	1.00	3.25
median	18.11	11.60	7.08	1.55	13.12
maximum	48.77	24.55	14.82	3.68	23.11
N2 for taxa					
minimum	1.00	1.00	1.00	3.05	1.00
median	2.94	1.99	12.53	12.96	6.62
maximum	40.97	20.12	51.68	42.19	37.81
DCCA axis 1					
λ_1	0.288	0.308	0.129	0.277	0.447
Gradient length (SD)	2.303	2.454	1.460	1.485	2.613
% variance	8.4	9.4	12.2	29.0	18.4
DCA axis 2					
λ_2	0.205	0.233	0.119	0.251	0.195
Gradient length (SD)	2.631	2.544	1.976	1.842	2.643
% variance	6.0	5.1	11.2	26.3	8.0
λ_1/λ_2	1.405	1.322	1.084	1.104	2.292
Summer temperature (°C)					
minimum	7.0	8.4	6.6	7.0	6.6
mean	13.8	14.3	13.7	14.3	13.0
median	14.5	15.5	14.0	15.8	13.7
maximum	20.6	21.8	21.8	20.6	17.3
standard deviation	3.56	3.31	3.75	3.32	3.51
Prediction model					
Number of (WA-)PLS components	2	1	2	2	2
apparent r^2	0.962	0.789	0.900	0.773	0.930
RMSE (°C)	0.694	1.328	1.191	1.583	0.929
jack-knifed r^2	0.799	0.551	0.821	0.715	0.849
RMSEP (°C)	1.619	2.229	1.597	1.773	1.370
mean bias (°C)	-0.069	0.124	0.139	0.003	0.006
maximum bias (°C)	3.505	6.486	3.375	2.984	1.668
Taxon response models (maximum likelihood) for all taxa in >20% of the samples					
Skewed unimodal model	0	0	0	0	1
Symmetric unimodal model	20	4	8	0	12
Sigmoidal model	30	5	8	4	10
Null model	19	13	3	1	7

groups was assessed using a hierarchical set of taxon response models (Huisman et al., 1993). This hierarchical set consists of a skewed unimodal response model, a symmetric (Gaussian) unimodal response model,

a monotonically increasing or decreasing sigmoidal response model, and a null model of no relationship to the environmental variable. The simplest statistically significant response model for each taxon was found by

fitting the most complex model first and progressively removing parameters from the regression model. This was done until the model could not be simplified without a significant change ($p < 0.05$) in the deviance of the model. Deviance is a goodness-of-fit statistic based on a likelihood ratio that can be used in F-ratio tests (Crawley, 1993). Taxon response models were fitted by maximum likelihood with a Poisson error structure and a logarithmic link function and were restricted to all taxa with occurrences in 20% or more of the samples in the screened training sets. The number of taxa in each training set with statistically significant fits to the four types of response models are given in Table 4.

All DCA, CCA, partial CCA, and DCCAs were implemented by the program CANOCO version 3.12 (ter Braak, 1987–1992, 1990). The WA-PLS and data-screening analyses were done by means of the programs CALIBRATE version 0.61 and WAPLS version 1.0 (S. Juggins & C. J. F. ter Braak, unpublished programs), and the taxon response modelling was done using the program HOF (J. Oksanen, unpublished program).

Results and discussion

Diatoms

The surface-sediment diatom flora of the 68 lakes includes a total of 353 taxa. The most abundant diatom taxa are arranged along the altitudinal gradient in Figure 2. Below an elevation of 1000 m a.s.l. planktonic taxa dominate the surface-sediment assemblages, whereas above 1000–1500 m a.s.l. periphytic taxa such as *Fragilaria* spp. become more important. There are, however, exceptions, mainly involving small centric taxa such as *Cyclotella comensis* and *C. radiosa* (Figure 2).

After transformation to percentages of total diatoms, all taxa were used in the numerical analyses. DCA revealed a compositional gradient length of 3.96 standard deviations (SD) suggesting the use of unimodal methods. CCA with forward selection and statistical evaluation by Monte Carlo permutation tests involving 999 unrestricted permutations shows that elevation, the presence of glaciers in the catchment, $[PO_4]$, water depth, alkalinity, and the area of bare ground in the catchment are the minimum set of environmental variables that best explain (in a statistical sense) the variance in the full diatom data.

The groups of environmental variables with the largest, statistically significant unique or independent explanatory powers (Table 3) are the catchment (14.59%, $p = 0.03$) and the climate variables (13.43%, $p = 0.01$), closely followed by the limnological variables (11.51%, $p = 0.04$). Although the set of chemical variables uniquely explains 14.60% of the total variance in the diatom data, the resulting model is not statistically significant ($p = 0.85$). A total of 67.33% variance in the diatom data is captured by all the environmental variables, of which 8.66% consists of covariances or conditional effects between the various groups of predictor variables.

Out of the 68 sites initially used for the diatom-summer temperature-inference model, two sites have high absolute residuals and low leverage (FÄL, HAG) and were therefore deleted as outliers. Two sites (TRÜ, MON) have high residuals and high leverage values (Cook's D). As TRÜ also has a very high squared residual distance in a CCA with mean summer temperature as the only constraining variable, it was deleted along with MON. The WA-PLS model of square-root transformed diatom percentage data and summer temperature thus includes 64 sites and 345 taxa (Figure 7). It has a $r^2_{(jack)} = 0.799$, a $RMSEP_{(jack)} = 1.619$ °C, a maximum bias of 3.505 °C, and a mean bias of -0.069 °C (Table 4).

In the final diatom-summer temperature training set, summer temperature explains 8.4% of the variance in the diatom data (Table 4). Summer temperature clearly is a major gradient (eigenvalue = 0.288), as the second, unconstrained axis is smaller (eigenvalue = 0.205) than the first constrained axis. There are, however, large secondary gradients in the diatom data. As catchment and limnology variables have statistically significant large marginal effects (Table 3), it is likely that factors such as water depth, nutrients, competition, or UV radiation may form important secondary gradients (e.g. Kilham et al., 1996; Vinebrooke & Leavitt, 1996).

Based on palaeolimnological studies, several authors have suggested that diatoms may be used as indirect palaeoclimatic indicators through changes in salinity (e.g. Fritz et al., 1991) or through the extent of ice cover (e.g. Smol, 1988). Furthermore, an altitudinal zonation in diatom assemblages has also been observed (e.g. Servant-Vildary, 1982; Arzet, 1987; Vyverman & Sabbe, 1995; Wunsam et al., 1995) which suggests some relationship between the occurrence and relative abundance of diatoms and water temperature. Similar studies on latitudinal climatic gradients strongly

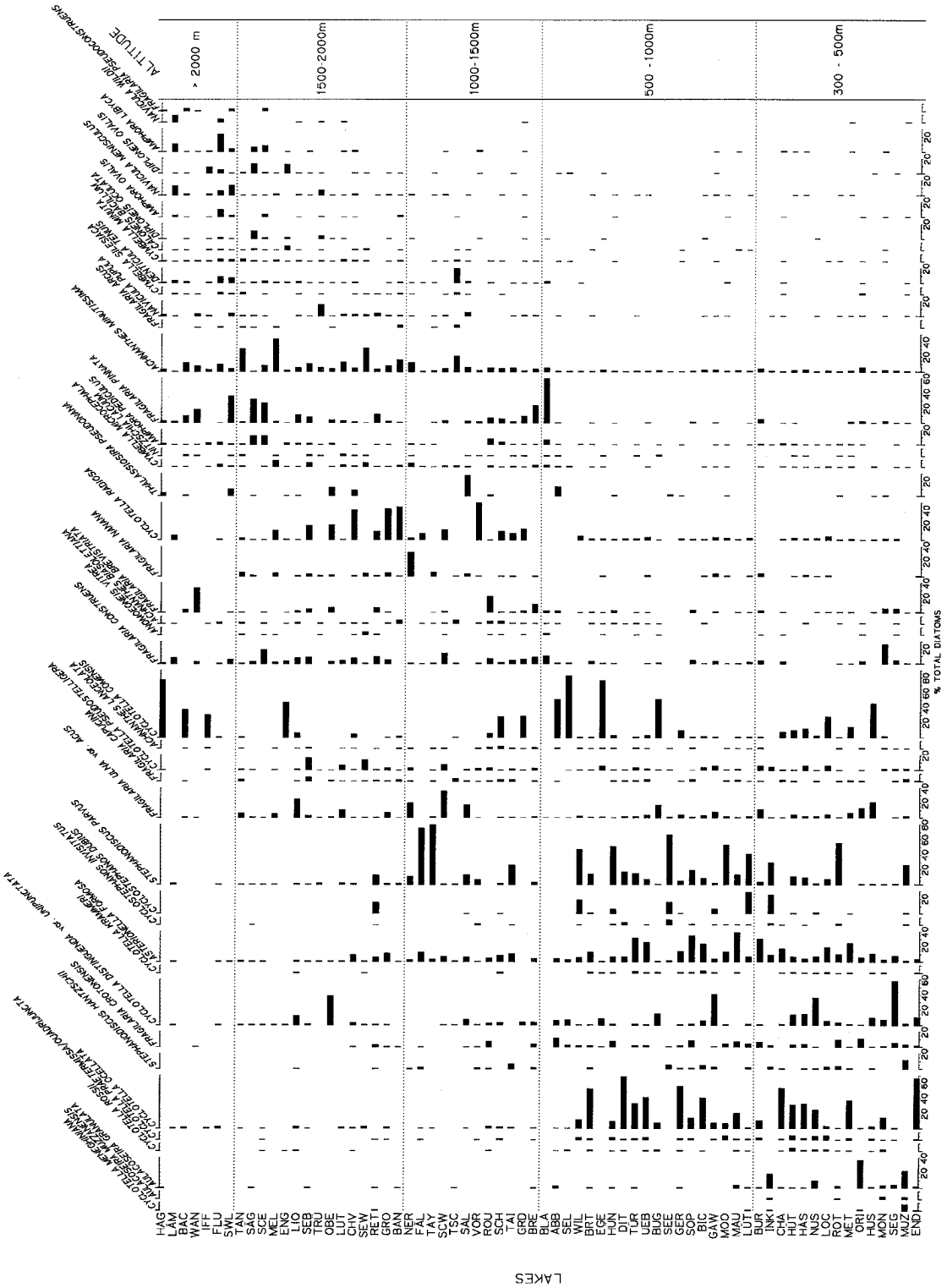


Figure 2. Distribution of diatoms along the altitudinal gradient of the lakes. Only selected major taxa are shown. The lakes are ordered according to their elevation and the lake abbreviations are given in Table 1.

support the importance of some temperature relationship in diatoms (Pienitz et al., 1995a, b; Weckström et al., 1997). Furthermore, Psenner & Schmidt (1992) have suggested that shifts in air temperature can affect the composition of diatom assemblages indirectly via changes in alkalinity and pH at high-elevation sites in the Alps.

There are at present only two available quantitative inference models for diatoms and surface-water temperature: Wunsam et al.'s (1995) data-set from the Alps includes 86 lakes but only using 26 *Cyclotella* taxa it yields an apparent $r^2=0.62$ and a bootstrap RMSEP=1.32 °C, whereas Pienitz et al.'s (1995b) data-set from Canada includes 56 surface sediments with 126 taxa that yield an apparent $r^2=0.63$ and a bootstrapped RMSEP=1.84–2.0 °C. Our alpine inference model for summer air temperature with its apparent $r^2=0.96$, a jack-knifed $r^2=0.79$, and a RMSEP_(jack)=1.62 °C (Table 4) compares very favourably with these two data-sets. Further temperature calibration sets from Fennoscandia (Weckström et al., 1997) are currently being assembled and evaluated.

Chrysophyte cysts

Cyst types were analysed in 37 samples in which the C/D ratio was higher than 0.02. A minimum of 50 cysts were counted. Chrysophyte cysts were classified according to morphological features such as collar, pore, surface texture, spines, etc. following the taxonomy proposed by Duff et al. (1995). One morphotype not described in this flora has been newly described by Marchetto (1995). A total of 104 morphotypes were identified using scanning electron microscopy. However, 14 of these morphotypes had to be amalgamated with other taxa because Duff et al. (1995) report these morphotypes not to be distinguishable using the light microscope. Twelve samples were excluded because they included only a single taxon. Relative abundances for 78 morphotypes were estimated and these were then used for numerical analyses. Figure 3 shows the distribution of the most abundant chrysophyte cysts types in relation to the altitudinal gradient.

Trophic state as well as the length of the growing season have been suggested to be factors that influence the C/D ratio (Smol, 1985). In our data-set, the C/D ratio shows a significant (Kendall test, $p<0.01$) positive correlation with altitude and a negative correlation with temperature, alkalinity, conductivity, and [TN]. Using a parametric test, the logarithm of C/D still

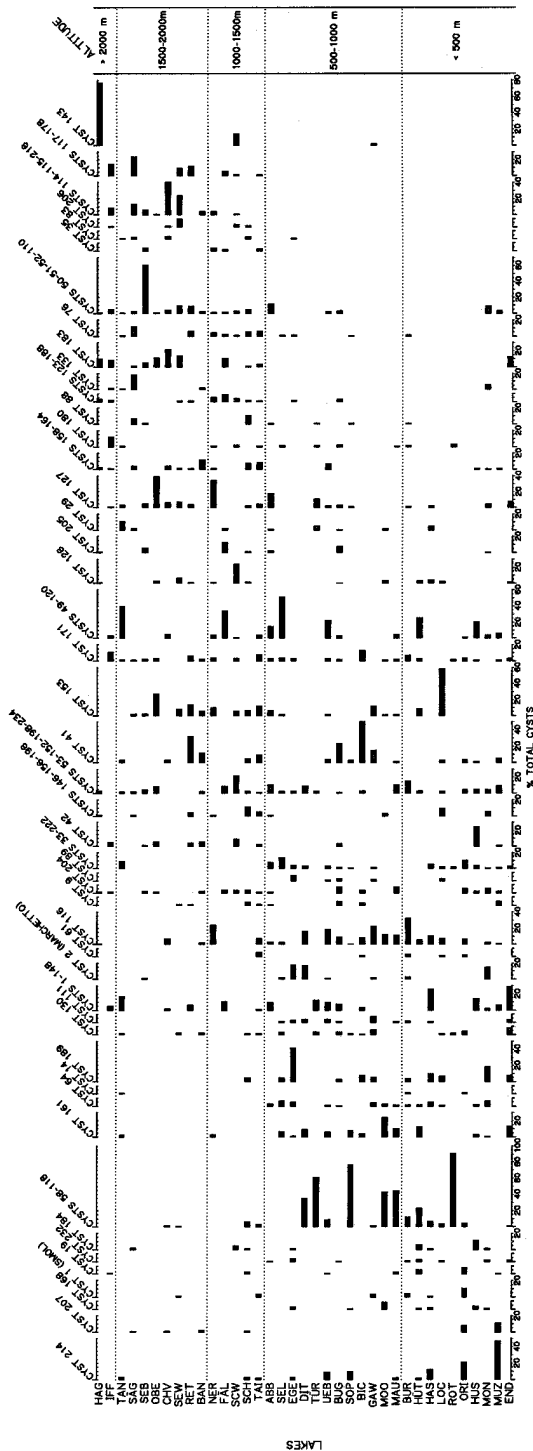


Figure 3. Distribution of chrysophyte cysts along the altitudinal gradient of the lakes. Only selected taxa are shown. The lakes are ordered according to their elevation and the lake abbreviations are given in Table 1. Nomenclature follows Duff et al. (1995).

shows a correlation with altitude and summer temperature (Figure 4), but the relationship is weak ($r=0.26$ and -0.24 , respectively). The correlation between C/D and temperature agrees with results by Zeeb & Smol (1993) from Elk Lake, where high C/D ratios were observed during the 'Little Ice Age' and before 8500 years BP, when colder conditions have been inferred from the terrestrial vegetation record. High C/D ratios were also found by Smol (1985) in three southern Ontario lakes during the early Holocene. From our data-set it is, however, not possible to ascertain whether the observed relationship is directly due to temperature effects or due to a higher proportion of chrysophyte cysts in high mountain lakes. Facher & Schmidt (1996) observed a high abundance of chrysophyte cysts in the sediment of Alpine lakes, whereas in the sediment of the large deep lakes on the southern slope of the Alps virtually no cysts can be found (Marchetto, 1995). Reasons for the high abundance of chrysophytes in many high mountain lakes in the Alps may be related to low water temperature, but other factors such as oligotrophy, morphometry, under-ice growth (e.g. Rott, 1988; Pugnetti & Bettinetti, 1995), or the ability of flagellate cells to avoid photo-inhibition may also play an important role (Cronberg, 1986; Duff et al., 1995; Smol, 1995). Furthermore, because of their similarity Alpine lakes may share the presence of periphytic chrysophytes with arctic lakes (Douglas & Smol, 1995).

The floristic gradient length in the chrysophyte cyst data is 4.37 SD units. CCA with forward selection identifies elevation and the area of bare ground in the catchment as the two environmental variables that explain most of the variance in this data set. In the Alps the area of bare ground is closely related to altitude.

It was not possible to estimate the unique contributions of the six groups of environmental variables in explaining the observed patterns in the chrysophyte cysts because there were less samples with cysts in sufficient quantity than environmental variables. When all environmental variables are included in a CCA (Table 3), 84.56% of the variance in the cyst data is explained. The climatic variables form a statistically significant model ($p=0.02$) and explain 27.37% (marginal effect). Elevation, not surprisingly, also has a statistically significant marginal effect ($p=0.01$) that explains 7.65%. None of the other groups of environmental variables have statistically significant marginal effects (Table 3).

Three samples were deleted as outliers as they had residuals higher than the standard deviation of mean summer temperature (MUZ, END) or had a

high leverage value and the highest squared residual distances in a CCA with mean summer temperature as the only constraining variable (HAG). This screening left 34 samples in the WA-PLS model of square-root transformed chrysophyte cyst percentage data and summer temperature (Figure 8), giving a $r^2_{(jack)}=0.551$, a $RMSEP_{(jack)}=2.229$ °C, a maximum bias of 6.486 °C, and a mean bias of 0.124 °C (Table 4).

With the current knowledge of fossil chrysophyte taxonomy it is often not possible to attribute certain cyst types to individual species. Moreover, it is possible that the same cyst type may originate from several taxa with different ecological preferences. In particular, the common types characterized by little or no ornamentation are probably produced by several chrysophyte species (Duff et al., 1995). This fact may explain the high proportion (60%) of common cysts whose distribution follows the null response model (Table 4). Furthermore, some important morphological features are not visible in the light microscope (Duff et al., 1995) and 22 types had to be amalgamated into 8 counting units (Figure 3). These two important factors may decrease the ecological indicator value of our chrysophyte data-set. Additionally, the selection of samples with high C/D ratios may largely bias the data-set towards lakes in which chrysophytes have a competitive advantage over diatoms.

Cladocera

The cladoceran assemblages in the surface sediments of 67 lakes include 35 taxa, of which 30 taxa are benthic chydorids and 5 are planktonic (*Bosmina* spp. and *Daphnia*). The altitudinal zonation of the cladoceran assemblages indicates the major compositional change between 1000–1500 m a.s.l. (Figure 5).

The compositional gradient length for the entire, unscreened cladoceran data-set is 3.22 SD, whereas it is only 2.34 SD for the benthic cladocera and 1.59 SD for the planktonic cladocera. For the cladocera-summer temperature inference models, these two life-forms have been analysed separately.

A CCA with forward selection for the entire cladoceran data-set suggests that the area of bare ground in the catchment, the area of open water, the area of silicate bedrock, and lake-water Ca concentration best explain the variance in the total cladocera data. For the benthic cladocera, elevation, area of glaciers in the catchment, presence of fish farming, water depth, winter precipitation, number of degree days, pH, lat-

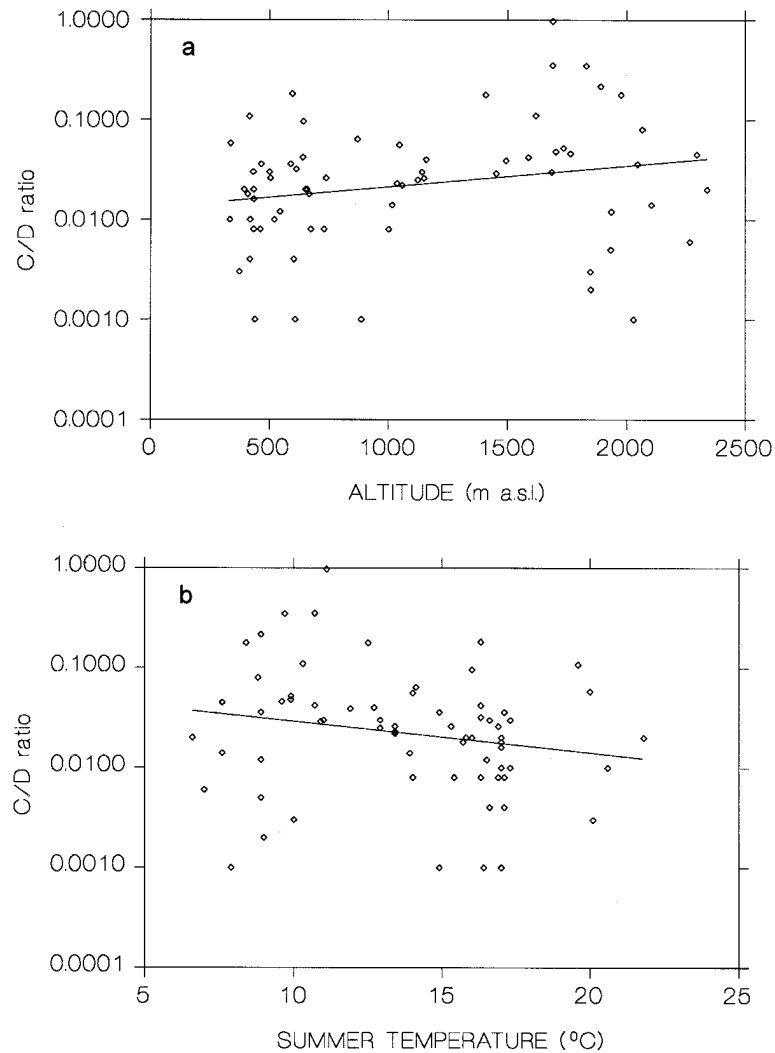


Figure 4. Altitude of lakes ($r=0.26$) (a) and mean summer temperature ($r=0.24$) (b) in relation to the chrysophyte cyst to diatom (C/D) ratio in the surface sediments of the 68 sampled lakes. Note the logarithmic scale on the y-axes.

itude, and annual temperature are the best predictors, whereas for planktonic cladocera it is spring temperature, hydroelectric use of the lake, water depth, area of silicate bedrock, and longitude.

None of the groups of environmental variables have a statistically significant unique relationship with the benthic cladocera (Table 3), even though elevation and the climatic and limnological variables all have statistically significant ($p=0.01$) marginal effects. Although all the environmental variables together explain 80.14% of the variance in the benthic cladocera, a large part of this (32.7%) consists of conditional, covariance terms, leaving only 47.44% of the variance explained by unique, independent groups of variables.

Climate and catchment variables and latitude and longitude have statistically significant ($p=0.01$, 0.03, 0.02, respectively), unique, independent relationships with the planktonic cladoceran data. A total of 71.68% of the variance is explained by all the environmental variables, consisting of 58.62% unique components and 13.06% covariance terms between the different groups of environmental variables (Table 3).

For the derivation of temperature inference models, the percentages of benthic cladocera were square-root transformed. One lake (TSC) did not contain any benthic cladocerans and six lakes showed high absolute residuals (ORI, SEE, BLA, RET, LÄM, TÜR) and were therefore deleted. WA-PLS for benthic

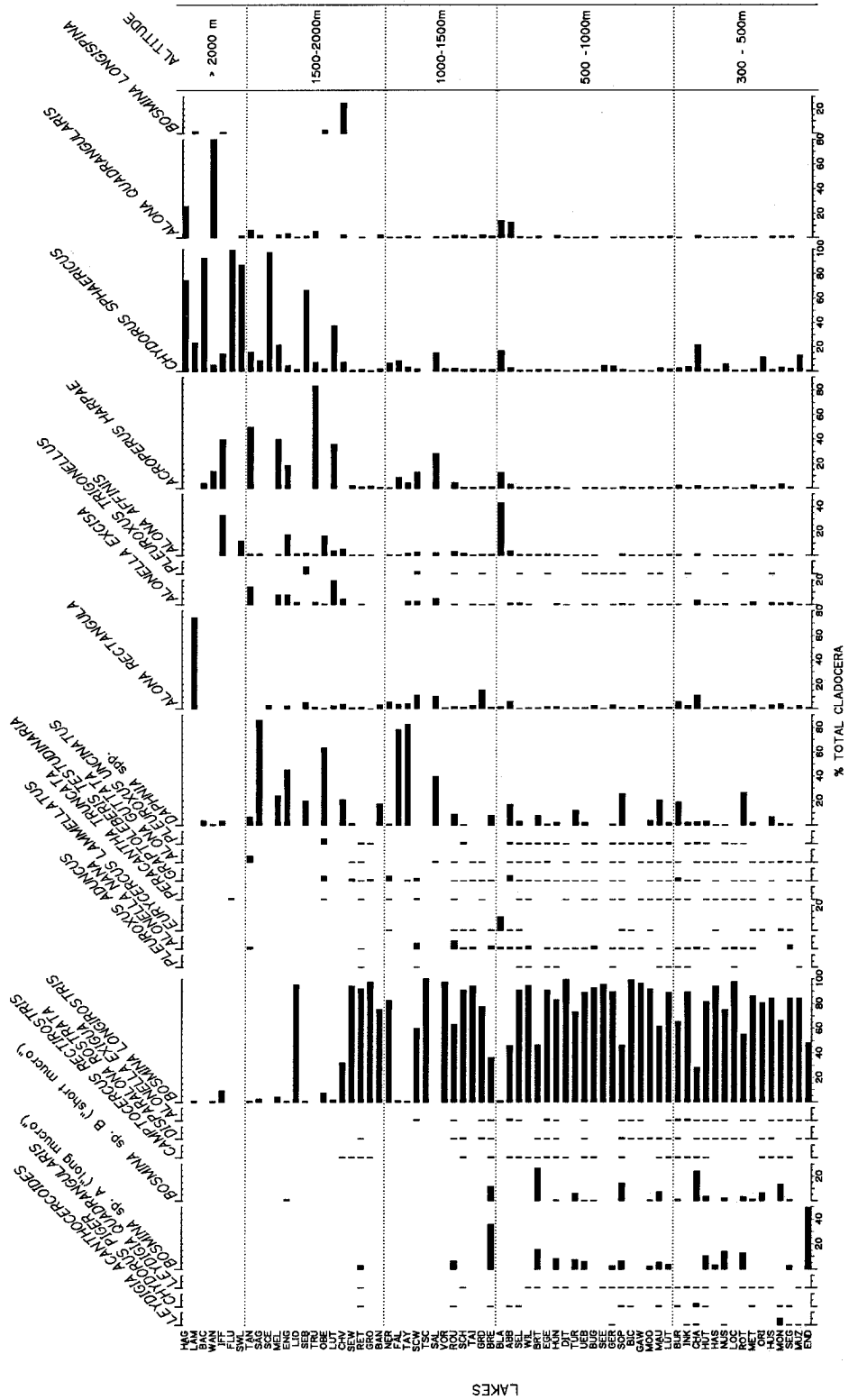


Figure 5. Distribution of cladocera along the altitudinal gradient. Only selected taxa are shown. The lakes are ordered according to their elevation and the lake abbreviations are given in Table 1.

cladocera and summer temperatures for the remaining 61 sites (Figure 9) gave a $r^2_{(jack)} = 0.821$, a $RMSEP_{(jack)} = 1.597$ °C, and a maximum bias of 3.375 °C, and a mean bias of 0.139 °C (Table 4).

Planktonic cladocera were present in 61 of the 68 lakes. The compositional gradient length of these 61 lakes is 1.59 SD as assessed by DCCA, suggesting the use of linear models (Birks, 1995). After square-root transformation of their percentage values, screening for outliers indicated 14 lakes with high absolute residuals (MUZ, BUR, BLA, RET, SAL, GRO, SEW, TAY, NER, WAN, LUT, MON, SEG, LIO). These were deleted. The remaining 48 lakes were used in a linear PLS model of planktonic cladocera and mean summer temperature (Figure 10; $r^2_{(jack)} = 0.715$; $RMSEP_{(jack)} = 1.773$ °C; maximum bias = 2.984 °C, mean bias = 0.003 °C, Table 4).

Although there are large secondary gradients in the benthic and planktonic cladocera (Table 4) unrelated to mean summer temperature, the summer temperature gradient is larger than the remaining secondary gradients in both data-sets, with eigenvalues of 0.129 (benthic) and 0.277 (planktonic) for DCCA axis 1 compared to 0.119 (benthic) and 0.251 (planktonic) for the first unconstrained secondary gradient (DCA axis 2 in Table 4).

DeCosta (1964) found a latitudinal pattern in the present-day distribution of chydorid cladocera species. In a study on Canadian lakes, Patalas (1990) concluded that climate is the single most important factor controlling zooplankton diversity. George & Harris (1985) showed a strong correlation between water temperature and crustacean zooplankton biomass in Windermere, whereas Stemberger et al. (1996) found a decrease in small cladocera species richness as a reaction to climatic cooling. According to their latitudinal affinities, Harmsworth (1968) characterized European chydorid species as 'arctic', 'sub-arctic', 'north temperate', and 'south temperate'. In contrast to chironomids, cladocera taxa predominating under arctic/subarctic conditions may frequently occur under temperate conditions as well. Hence, they may not be regarded as cold stenothermal but as cold-tolerant taxa (Meijering, 1983). Under conditions of a cool climate, chydorid species diversity is commonly low because of the absence of less cold-tolerant taxa. Several palaeoecological case studies of temperate lakes have shown that chydorid assemblages consisted only of a few species generally associated with arctic/subarctic conditions (Harmsworth, 1968) during the Late-Glacial (Hofmann, 1987; Frey, 1988). In the case of Belauer

See (Northern Germany), climatic cooling during the Younger Dryas coincided with a minimum of chydorid species diversity (Hofmann, 1993). Throughout the Pleniglacial of a French maar lake, only two taxa of the arctic elements were present (Hofmann, 1991). Climatic warming at the onset of the Holocene is indicated by an increase in species diversity due to the appearance of less cold-tolerant taxa (Hofmann, 1987; Frey, 1988).

As there are no true stenotherms among the chydorids which could be used as indicators, qualitative palaeoecological interpretations should not be based on single taxa but on the overall structure and composition of the assemblage, e.g. species diversity and presence/absence of temperate species. Quantitative temperature reconstructions using the entire assemblage, however, take account of these features. The present surface-sediment cladocera assemblages provide the first modern quantitative cladoceran training-set and show that these animals have considerable potential as quantitative climate indicators.

Chironomids

The altitudinal zonation of the chironomid assemblages (Figure 6) reveals major changes above ca. 1500 m a.s.l. The chironomid fauna in the surface sediments of all 68 investigated lakes includes 68 taxa. However, only 58 surface samples contained more than 45 occurrences and were used for the numerical analyses. DCA gave a compositional gradient length of 4.95 SD units. Elevation is the environmental variable in CCA with forward selection that explains most of the variance in the chironomid data-set.

None of the groups of environmental variables make a statistically significant unique contribution to explaining the total variance in the chironomid data (Table 3). Elevation, latitude and longitude, and the limnological and climatic variables all have statistically significant ($p \leq 0.05$) marginal effects, but when the effects of all the other groups of environmental variables are partialled out, none of the resulting models are statistically significant ($p = 0.17-0.95$). All environmental variables explain 71.74% of the total variance in the chironomid data. This includes 8.71% of covariances between the various groups of environmental variables.

The percentage data were square-root transformed for the chironomid-summer temperature inference model. Seven samples (MUZ, BLA, RET, SEB, SEG, MON, END) were deleted as outliers because

Diatoms

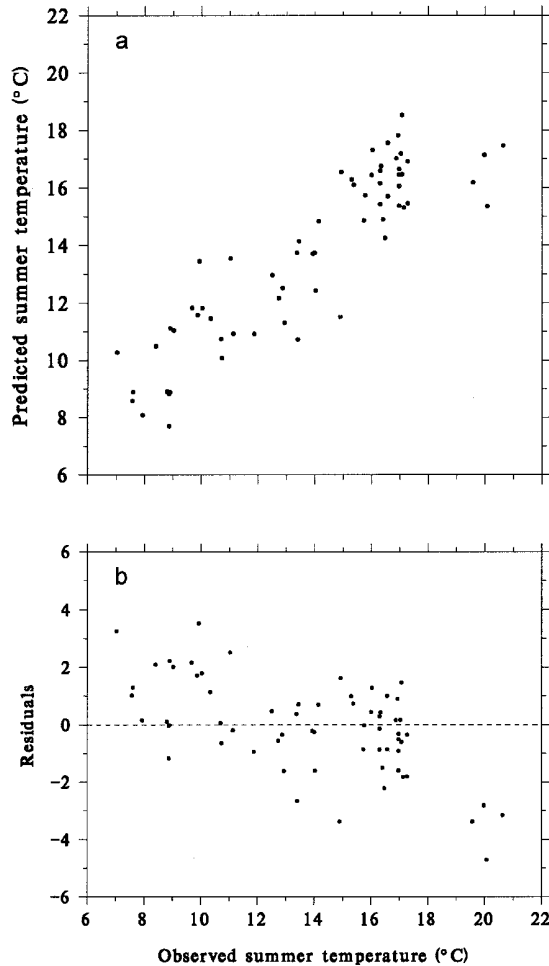


Figure 7. Diatom – mean summer temperature training set: (a) plot of predicted mean summer temperature against observed mean summer temperature based on a 2-component WA-PLS model and (b) plot of residuals (predicted – observed) against observed mean summer temperature.

of their high absolute residuals, whereas one sample (TSC) was deleted despite its high Cook's D because of its high residuals and a high squared residual distance in CCA with mean summer temperature as the only explanatory variable. The WA-PLS model for chironomids and summer temperature of the remaining 50 lakes (Figure 11) gave a $r^2_{(jack)} = 0.849$, a $RMSEP_{(jack)} = 1.370$ °C, a maximum bias of 1.668 °C, and a mean bias of 0.006 °C (Table 4).

Chrysophyte Cysts

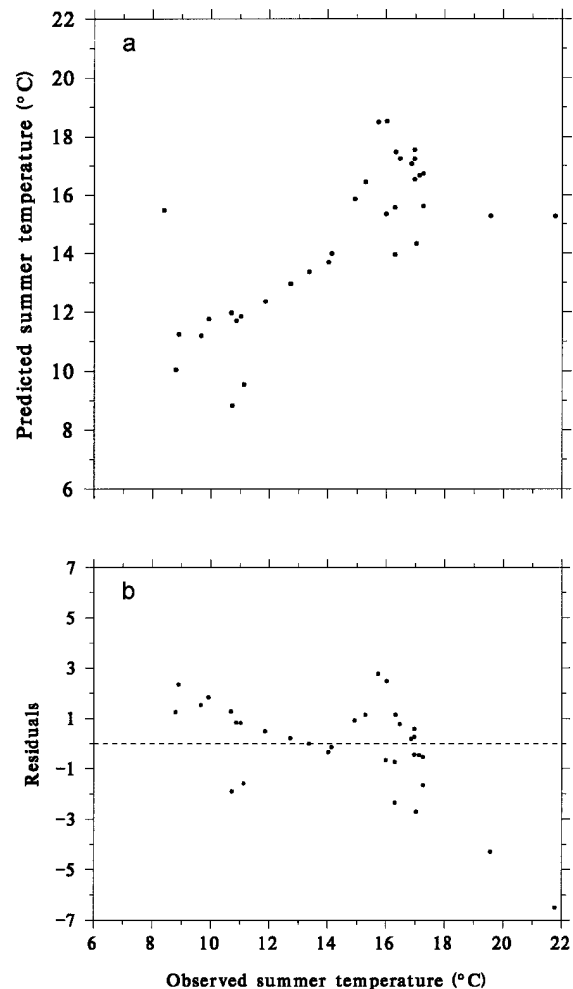


Figure 8. Chrysophyte cyst – mean summer temperature training set: (a) plot of predicted mean summer temperature against observed mean summer temperature based on a 1-component WA-PLS model (= WA with inverse deshrinking) and (b) plot of residuals (predicted – observed) against observed mean summer temperature.

The gradient of mean summer temperature clearly reflects a strong gradient in the chironomid data with the first DCCA axis having an eigenvalue of 0.447 (explaining 18.4% of the variance in the chironomid data), in contrast to the largest unconstrained axis of 0.195 (8.0% of the variance, Table 4).

On the basis of material from Scandinavian lakes, Brundin (1949, 1956) concluded that temperature is an important and often underestimated factor determining chironomid species distributions. The fauna from northern Scandinavia is dominated by true

Benthic Cladocera

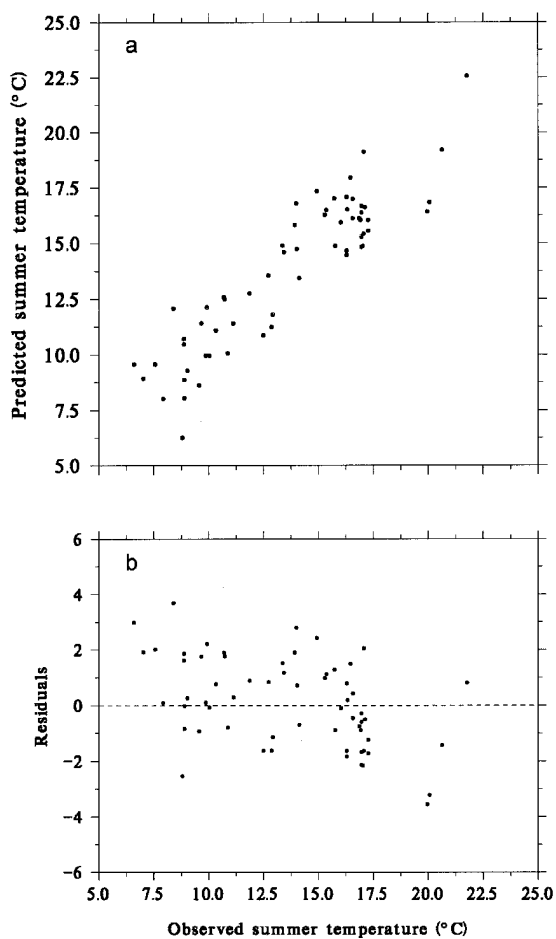


Figure 9. Benthic cladocera – mean summer temperature training set: (a) plot of predicted mean summer temperature against observed mean summer temperature based on a 2-component WA-PLS model and (b) plot of residuals (predicted – observed) against observed mean summer temperature.

cold stenothermal taxa, while in more southern regions, eurythermal and warm stenothermal taxa occur. Brundin (1949) defined the '*Tanytarsus lugens*'-community consisting of ten cold stenothermal, polyoxybiontic, and eurybathic species, which are found in the littoral zone of lakes only under subarctic/arctic conditions. In temperate lakes, they are restricted to the profundal zone, i.e. the region below the thermocline.

Thienemann (1954) noted a high degree of similarity between the Scandinavian and Alpine chironomid faunas due to the boreo-alpine distribution of several cold-stenotherms. Our results indicate that members of

Planktonic Cladocera

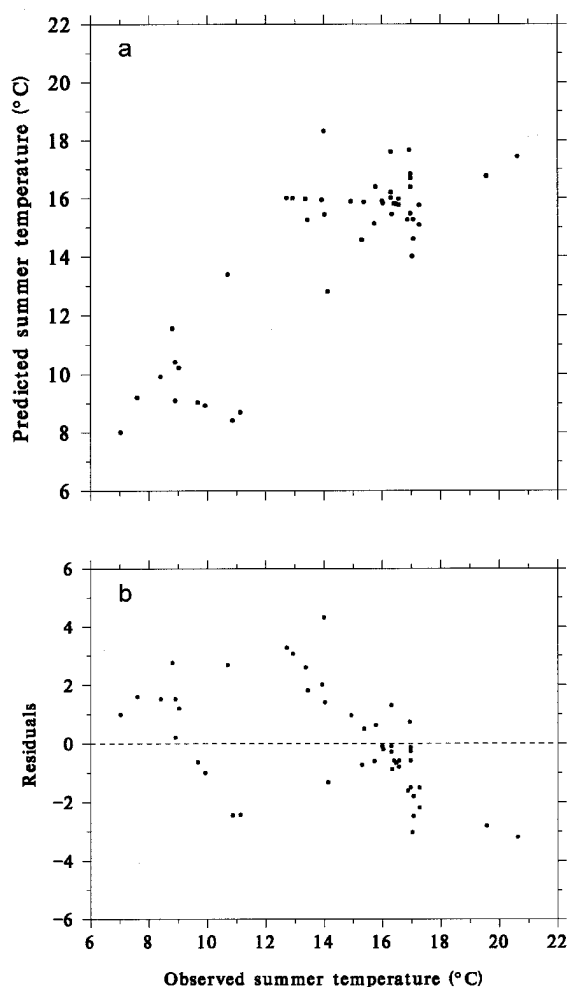


Figure 10. Planktonic cladocera – mean summer temperature training set: (a) plot of predicted mean summer temperature against observed mean summer temperature based on a 2-component WA-PLS model and (b) plot of residuals (predicted – observed) against observed mean summer temperature.

the '*Tanytarsus lugens*'-community are most abundant in high-elevation Swiss lakes. A recent study of the altitudinal distribution of chironomids in the Canadian Cordillera (Walker & Mathewes, 1989), as well as an Italian study of chironomid distributions in relation to stream temperature (Rossaro, 1991), similarly points to temperature as a major determinant of chironomid distributions.

Moreover, using CCA, Walker et al. (1991b) found summer surface-water temperature to be the variable which best accounted for chironomid distributions

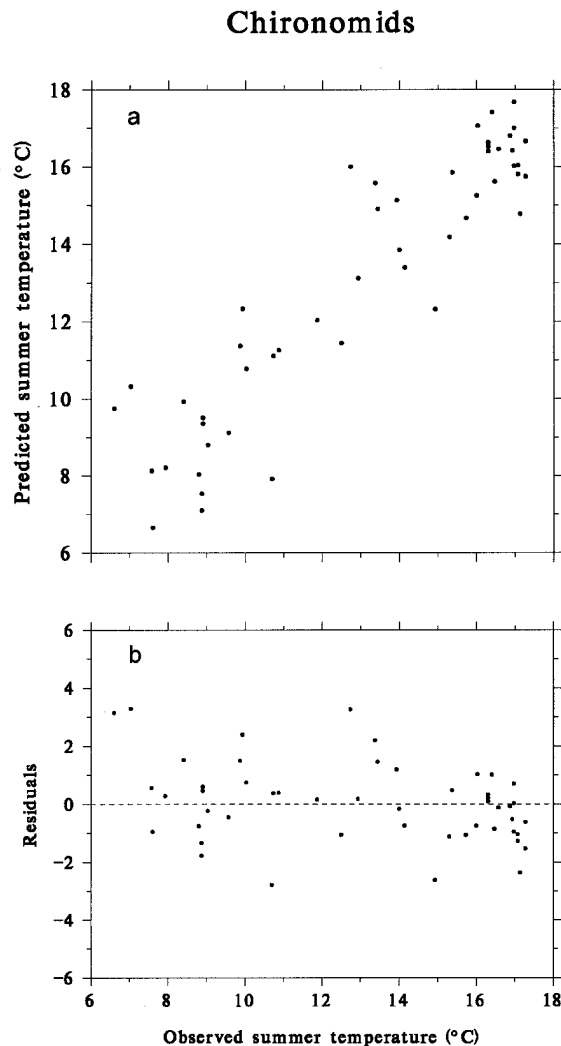


Figure 11. Chironomid – mean summer temperature training set: (a) plot of predicted mean summer temperature against observed mean summer temperature based on a 2-component WA-PLS model and (b) plot of residuals (predicted – observed) against observed mean summer temperature.

among lakes in Labrador, Canada. They also presented the first quantitative model for inferring summer surface-water temperatures from chironomids. Their latest, expanded training set (Walker et al., 1997) produces an WA-PLS inference model that yields a jack-knifed $r^2 = 0.88$ and a RMSEP = 2.26 °C, whereas Olander et al.'s (1997) WA inference model for chironomids and July lake water temperature gives a jack-knifed $r^2 = 0.58$ and a RMSEP = 0.12 log(temp + 1) °C. Our results from the Alps with a jack-knifed $r^2 = 0.84$ and a RMSEP = 1.37 °C (Table 4) compare well with

both of these chironomid-based inference models. Hann et al. (1992), however, were highly critical of Walker et al.'s (1991b) original study. They argued that the results and interpretation of the CCA tended to overestimate the importance of temperature relative to other factors, such as depth, transparency, turbidity, and sediment composition. Hann et al. (1992) also argued that chironomids from below the thermocline should have been excluded from the analysis. In responding to these criticisms, Walker et al. (1992) indicated the importance of scale, noting that temperature was probably most important in regulating the broad-scale geographic distribution of chironomids, but that other factors were likely to be more important at finer scales (e.g., within a small lake, or among lakes within a small geographic region). They noted that it was not feasible to separate littoral from profundal head capsules.

Palaeoecological studies have revealed that Brundin's '*Tanytarsus lugens*'-community were more abundant in Maar lakes during the Weichselian Pleniglacial (Hofmann, 1990, 1991) and also more abundant in lakes during the Late-Glacial (Hofmann, 1988; Walker, 1995), particularly in sediments deposited prior to the Allerød, as well as in sediments of Younger Dryas age (e.g. Walker et al., 1991a, 1997). In the temperate zone, they disappeared from shallow lakes at the beginning of the Holocene and were confined to the profundal zone in the case of dimictic lakes (Hofmann, 1988; Walker, 1995). These patterns support the contention that temperature has a strong influence, directly or indirectly on chironomid distributions, but only to the extent that these climatic episodes are well-documented through independent evidence.

Where chironomids have been used as quantitative palaeotemperature indicators (e.g. Walker et al., 1991a, b; Levesque et al., 1993, 1994; Cwynar & Levesque, 1995), the inferred temperatures are generally consistent with other lines of evidence. Our evidence provides a further indication that chironomids can serve as useful palaeoclimate indicators. This may not end the discussion, but as Walker (1995) states, 'the controversy will inspire research by a new generation of palaeoecologists'.

General discussion

Distinct changes in the composition of surface-sediment assemblages of diatoms, chrysophyte cysts, cladocera, and chironomids have been observed along an altitudinal sampling gradient in the Alps (Figures 2,

3, 5, and 6). The major changes in all the investigated biota occur around 1500 m a.s.l. Present-day timberline in the investigated part of the Alps lies at elevations of between 1900–2000 m a.s.l. This suggests that the major changes in the assemblage compositions are not related to catchment-related limnological features, such as, for example, changes in the DOC content of the water (Pienitz & Smol, 1993). The altitudinal gradient reflects a major climate gradient with temperature decreasing (Figure 12) and precipitation increasing with increasing altitude. The overall gradient in summer temperature in our data-set includes more than 15 °C (Tables 1 and 3) and is therefore comparable to (Walker et al., 1997), or distinctly larger than the temperature gradients sampled in other quantitative studies (e.g. Wunsam et al., 1995; Pienitz et al., 1995b; Weckström et al., 1997).

All the above mentioned studies have used summer surface-water temperatures for their inference models, whereas we have used mean summer air temperatures. Given the day-to-day variability in surface-water temperatures, the use of mean seasonal air temperatures may be a more reliable measure for remote lakes where no temperature monitoring data are available. Moreover, there is a close linear relationship between air and surface-water temperatures during the summer months (e.g. Forester, 1987; Livingstone & Schanz, 1994; Livingstone & Lotter, in press) that helps justify the use of the more readily available mean air temperatures. By taking advantage of this fact, we can circumvent possible problems and criticisms arising by single surface-water temperature measurements (Hann et al., 1992).

There is a strong linear relationship between altitude and mean summer temperature, except for the five lakes located on the foothills of the southern Alps (MUZ, ORI, MON, SEG, END, see Figure 12). For most inference models these five were deleted as outliers. The insubric climate (high temperatures and high precipitation) of the southern Alpine foreland may create a different environment than the more temperate climate on the northern side of the Alps. It is, therefore, likely that our inference models may not be applicable to the southern side of the Alps.

Limnological variables such as maximum water depth or lake surface-area are not significantly correlated with altitude, whereas water chemistry variables such as TP, conductivity, and alkalinity (Figure 12), not surprisingly, show a weak but significant ($p < 0.01$) correlation with altitude (see also Müller et al., in press). This may, to some extent, explain the strong secondary

gradients present in the diatom and cladocera data-sets. However, by restricting our modern training-set to hardwater lakes, effects of pH and pH-related variables can be excluded. Nevertheless, unmeasured factors such as mixing regimes and oxygen concentrations, increasing UV radiation with altitude, length of ice cover, competition, grazing, and predation may also strongly influence the distribution and abundance of the organisms studied.

A consistent feature of the residual (predicted-observed values) in this study (Figures 7–11) is the tendency for the predicted values to be over-estimated at the low end of the sampled gradient and to be under-estimated at the high end. This feature occurs with several other training sets when WA-PLS is used for developing transfer-function models (Birks, unpublished; ter Braak & Juggins, 1993; Bennion et al., 1996) and appears to be characteristic of WA-PLS. The likely explanation for this bias is that WA-PLS and its linear counterpart PLS use an inverse deshrinking regression (ter Braak & Juggins, 1993). In classical deshrinking, which is often used in single WA (Birks et al., 1990) where the initial inferred values are regressed on the observed values of the environmental variable being calibrated, the residuals are orthogonal to the inferred values and are thus uncorrelated with the original observed values. In contrast, in inverse regression in WA, where the observed values are regressed on the initial inferred values, the residuals are orthogonal to the initial inferred values and not uncorrelated to the original observed values. There is thus a tendency for the inferred values to be pulled towards the means of the observed values, leading to an over-prediction at the low end and an under-prediction at the high end of the gradient of observed values (ter Braak & Juggins, 1993). In classical deshrinking, which deshrinks more than inverse regression, the net effect is to pull the inferred values further away from the mean of the training set and lower residuals generally arise at the low and high ends of the sampled gradient. WA-PLS utilises the residual structure in the biological part of a training set to improve the estimates of the optima of the taxa in the final transfer function so as primarily to maximise the predictive power of the model (lowest RMSEP) and secondarily to reduce, as far as possible, any bias in the residuals. Inverse deshrinking is, however, implicit in PLS and WA-PLS (ter Braak & Juggins, 1993), and there is thus an in-built bias resulting from inverse deshrinking (Martens & Naes, 1989). In many cases, as in this study, the in-built bias is not completely removed, even when two components

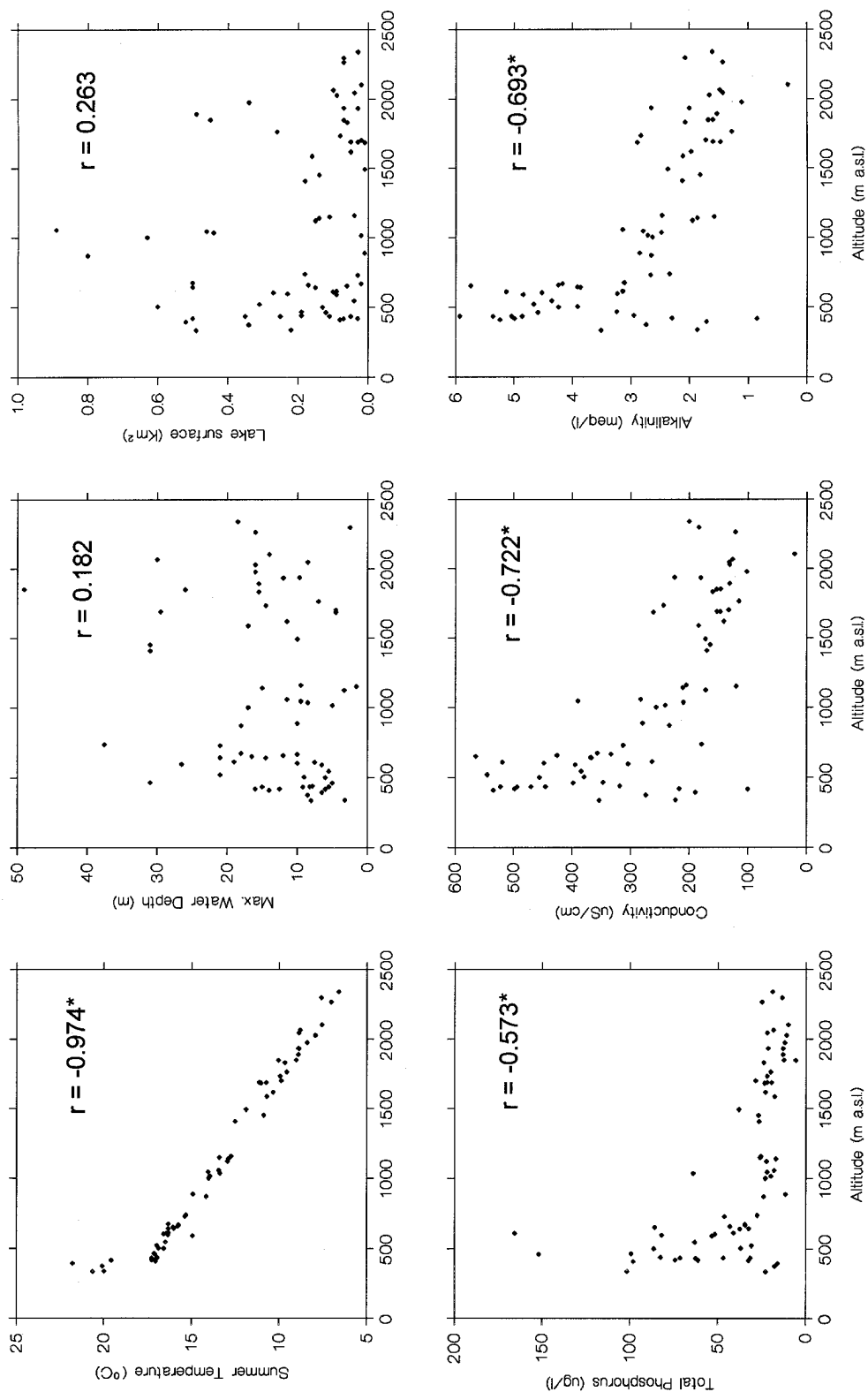


Figure 12. Relationship between selected limnological and chemical environmental variables. r = correlation coefficient; * $p < 0.01$, $n = 68$.

are used in the final transfer function. Introducing further components often helps to reduce this bias but at the expense of decreasing the predictive power (higher RMSEP of the final model). The final transfer functions (Table 4) are thus, to some degree, a compromise between the lowest possible RMSEP, as assessed by cross-validation, and the lowest maximum bias. Other models (e.g. WA, WA-PLS with 3 or more components) have higher RMSEP (WA [classical or inverse deshrinking], WA-PLS) but lower maximum bias (WA [classical deshrinking], WA-PLS with 3 or more components) than the models presented in Table 4 and Figures 7–11.

Conclusions

Our study of surface-sediment assemblages clearly reveals that the abundance of aquatic organisms shows a strong statistical relationship to climate, especially the mean temperature of the summer season. These data represent the first multi-proxy modern training set for aquatic organisms available for the Alps. As each set of organisms was studied by only one analyst, they form high-quality training sets as are required for reliable palaeoclimatic reconstructions (Birks, 1994, 1995). In combination with similar pollen-climate inference models these modern training sets will make an independent reconstruction of past climatic change possible. Rigorous numerical and biological evaluations are necessary to quantify the errors inherent in inferences from all kinds of proxy data and to assess the statistical reliability and ecological realism of all quantitative palaeoenvironmental reconstructions (Birks, 1995).

Interestingly, over 70% of the taxa (except chrysophyte cysts), that occur in 20% or more of the samples in the individual training sets, have statistically significant relationships to mean summer temperature (Table 4), either as unimodal or sigmoidal responses (72.5% diatoms, 84.2% benthic cladocera, 80% planktonic cladocera, 76.7% chironomids). This compares with diatoms and lake-water pH in the Surface Water Acidification Project (SWAP) training sets of 167 lakes, where 74% of the diatom taxa had statistically significant relationships with pH (Birks et al., 1990).

With the available data it is not possible to decide whether the distribution of these organisms is directly related to ambient temperature or is indirectly controlled by temperature through changes in physical,

chemical, and/or biological lake dynamics. Nevertheless, one of the basic assumptions of any quantitative palaeoecological reconstruction is, that ‘the environmental variable to be reconstructed is, or is linearly related to, an ecologically important determinant in the ecological system of interest’ (Birks, 1995). The training sets presented here indicate strong empirical relationships with mean summer temperature. The ecological explanations for such relationships require detailed knowledge of the dynamics of the taxa concerned in response to the multitude of environmental and biotic factors that covary with mean summer temperature and with altitude. At present, such basic ecological information is, however, largely lacking.

Acknowledgments

This project would not have been possible without the help of the following persons during field work and laboratory analyses: A. Ammann, F. Bürgi, J. Hürlimann, B. Müller, T. Rüttimann, M. Sturm, Y. Weidmann, B. Wilke. Special thanks are due to the core members of the field team for their patience and endurance: E. Grieder, C. Stengel and A. Zwyssig. We thank F. Kienast of the Swiss Federal Institute for Forest, Snow, and Landscape Research for providing the modern climate data, S. J. Brooks, J. Hürlimann and S. Wunsam for valuable discussions on taxonomic problems in relation to chironomids and small centric diatoms, R. W. Battarbee, H. H. Birks, and C. J. F. ter Braak for discussions, B. Cumming, R. Pienitz, J. P. Smol and I. R. Walker for comments on earlier versions of the manuscript, S. Juggins and C. J. F. ter Braak for providing pre-release copies of their CALIBRATE and WAPLS programs and J. Oksanen for his HOF program.

This project was supported by the Swiss Priority Programme Environment through grant 5001-34876.

References

- Arzet, K., 1987. Diatomeen als pH-Indikatoren in subrezentem Sedimenten von Weichwasserseen. Ph.D. Dissertation. University of Innsbruck, 266 pp.
- Bennion, H., S. Juggins & N. J. Anderson, 1996. Predicting epilimnetic phosphorus concentrations using an improved diatom-based transfer function and its application to lake eutrophication management. *Envir. Sci. Technol.* 30: 2004–2007.
- Birks, H. J. B., 1992. Some reflections on the application of numerical methods in Quaternary palaeoecology. *Publications of the Karelian Institute* 102: 7–20.

- Birks, H. J. B., 1993. Quaternary palaeoecology and vegetation science – current contributions and possible future developments. *Revue Palaeobot. Palynol.* 79: 153–177.
- Birks, H. J. B., 1994. The importance of pollen and diatom taxonomic precision in quantitative palaeoenvironmental reconstructions. *Revue Palaeobot. Palynol.* 83: 107–117.
- Birks, H. J. B., 1995. Quantitative palaeoenvironmental reconstructions. In Maddy, D. & J. S. Brew (eds), *Statistical modelling of Quaternary science data*. *Quat. Res. Assoc.*, Cambridge: 161–254.
- Birks, H. J. B., J. M. Line, S. Juggins, A. C. Stevenson & C. J. F. Ter Braak, 1990. Diatoms and pH reconstruction. *Phil. Trans. r. Soc. Lond. B* 327: 263–278.
- Borcard, D., P. Legendre & P. Drapeau, 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045–1055.
- Brundin, L., 1949. Chironomiden und andere Bodentiere der südschwedischen Urgebirgsseen. *Rep. Inst. Freshwat. Res. Drottningholm* 30: 1–914.
- Brundin, L., 1956. Die bodenfaunistischen Seentypen und ihre Anwendbarkeit auf die Südhalbkugel. *Rep. Inst. Freshwat. Res. Drottningholm* 37: 186–235.
- Charles, D. F., 1990. A checklist for describing and documenting diatom and chrysophyte calibration data sets and equations for inferring water chemistry. *J. Paleolimnol.* 3: 175–178.
- Crawley, M. J., 1993. *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- Cronberg, G., 1986. Chrysophycean cysts and scales in lake sediments: a review. In Kristiansen, J. & R. A. Andersen (eds), *Chrysophytes. Aspects and Problems*. Cambridge University Press, Cambridge: 281–315.
- Cwynar, L. C. & A. J. Levesque, 1995. Chironomid evidence for late-glacial climatic reversals in Maine. *QR* 43: 405–413.
- DeCosta, J. J., 1964. Latitudinal distribution of chydorid cladocera in the Mississippi valley, based on their remains in surficial lake sediments. *Inv. Ind. Lakes and Streams* 6: 65–101.
- Douglas, M. S. V. & J. P. Smol, 1995. Paleolimnological significance of observed distribution patterns of chrysophyte cysts in arctic pond environments. *J. Paleolimnol.* 13: 79–83.
- Duff, K. E., B. A. Zeeb & J. P. Smol, 1995. *Atlas of Chrysophycean cysts*. Kluwer Academic Publishers, Dordrecht, 189 pp.
- Facher, E. & R. Schmidt, 1996. A siliceous chrysophycean cyst-based pH transfer function for Central European lakes. *J. Paleolimnol.* 16: 275–321.
- Flössner, D., 1972. Branchiopoda, Branchiura. *Die Tierwelt Deutschlands* 60: 1–501.
- Forester, R. M., 1987. Late Quaternary paleoclimate records from lacustrine ostracods. In Ruddiman, W. F. & H. E. Wright (eds), *North America and adjacent oceans during the last deglaciation*. *Geol. Soc. Am. K-3*: 261–276.
- Frey, D. G., 1958. The late-glacial cladoceran fauna of a small lake. *Arch. Hydrobiol.* 54: 209–275.
- Frey, D. G., 1959. The taxonomic and phylogenetic significance of the head pores of the Chydoridae (Cladocera). *Int. Revue ges. Hydrobiol.* 44: 27–50.
- Frey, D. G., 1986. Cladocera analysis. In Berglund, B. E. (ed.), *Handbook of Holocene Palaeoecol. Palaeohydrolog.* J. Wiley & Sons, Chichester, 667–692.
- Frey, D. G., 1988. Littoral and offshore communities of diatoms, cladocerans and dipterous larvae, and their interpretation in paleolimnology. *J. Paleolimnol.* 1: 179–191.
- Fritz, S. C., 1996. Paleolimnological records of climatic change in North America. *Limnol. Oceanogr.* 41: 882–889.
- Fritz, S. C., S. Juggins, R. W. Battarbee & D. R. Engstrom, 1991. Reconstruction of past changes in salinity and climate using a diatom-based transfer function. *Nature* 352: 706–708.
- George, D. G. & G. P. Harris, 1985. The effect of climate on long-term changes in the crustacean zooplankton biomass of Lake Windermere, UK. *Nature* 316: 536–539.
- Hamilton, L. C., 1992. *Regression with graphics*. Brooks/Cole Publishing Co., Pacific Grove, 363 pp.
- Hann, B. J., B. G. Warner & W. F. Warwick, 1992. Aquatic invertebrates and climatic change: A comment on Walker et al. (1991). *Can. J. Fish. aquat. Sci.* 49: 1274–1276.
- Harmsworth, R. V., 1968. The developmental history of Blelham Tarn (England) as shown by animal microfossils, with special reference to the Cladocera. *Ecol. Monogr.* 38: 223–241.
- Hill, M. O., 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54: 427–432.
- Hill, M. O. & H. G. Gauch, 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47–58.
- Hofmann, W., 1971. Zur Taxonomie und Palökologie subfossiler Chironomiden (Dipt.) in Seesedimenten. *Arch. Hydrobiol. Beih.* 6: 1–50.
- Hofmann, W., 1986. Chironomid analysis. In Berglund, B. E. (ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*. J. Wiley & Sons, Chichester, 715–727.
- Hofmann, W., 1987. Cladocera in space and time: Analysis of lake sediments. *Hydrobiologia* 14: 315–321.
- Hofmann, W., 1988. The significance of chironomid analysis (Insecta: Diptera) for paleolimnological research. *Palaeogeogr., Palaeoclim., Palaeoecol.* 62: 501–509.
- Hofmann, W., 1990. Weichselian chironomid and cladoceran assemblages from maar lakes. *Hydrobiologia* 214: 207–211.
- Hofmann, W., 1991. Stratigraphy of Chironomidae (Insecta: Diptera) and Cladocera (Crustacea) in Holocene and Wurm sediments from Lac du Bouchet (Haute Loire, France). *Documents du C.E.R.L.A.T.* 2: 363–386.
- Hofmann, W., 1993. Dynamics of a littoral Cladocera assemblage under the influence of climatic and water depth changes from Alleröd to Subboreal. *Verh. int. Ver. Limnol.* 25: 1095–1101.
- Huisman, J., H. Olff & L. F. M. Fresno, 1993. A hierarchical set of models for species response analysis. *Journal of Vegetation Science* 4: 37–46.
- Huntley, B. & I. C. Prentice, 1988. July temperatures in Europe from pollen data, 6000 years before present. *Science* 241: 687–690.
- Huntley, B. & I. C. Prentice, 1993. Holocene vegetation and climates of Europe. In Wright, H. E., J. E. Kutzbach, T. Webb, W. F. Ruddiman, F. A. Street-Perrott & P. J. Bartlein (eds), *Global Climate since the Last Glacial Maximum*. University of Minnesota Press, Minneapolis, 136–168.
- Imbrie, J. & N. G. Kipp, 1971. A new micropalaeontological method for quantitative paleoclimatology: application to late Pleistocene Caribbean core V28-238. In Turekian, K. K. (ed.), *The late Cenozoic Glacial Ages*. Yale University Press, New Haven, 77–181.
- Iversen, J., 1944. *Viscum, Hedera* and *Ilex* as climatic indicators. *Geologiska Föreningen i Stockholm Förhandlingar* 66: 463–483.
- Jones, V. J. & S. Juggins, 1995. The construction of a diatom-based chlorophyll *a* transfer function and its application at three lakes on Signy Island (maritime Antarctic) subject to differing degrees of nutrient enrichment. *Freshwat. Biol.* 34: 433–445.
- Kilham, S. S., E. C. Theriot & S. C. Fritz, 1996. Linking planktonic diatoms and climate change in the large lakes of the Yellowstone ecosystem using resource theory. *Limnol. Oceanogr.* 41: 1052–1062.

- Kowalyk, H. E., 1985. The larval cephalic setae in the Tanypodinae (Diptera: Chironomidae) and their importance in generic determinations. *Can. Ent.* 117: 67–106.
- Krammer, K. & H. Lange-Bertalot, 1986–1991. *Bacillariophyceae*, 1–4. G. Fischer Verlag, Stuttgart.
- Levesque, A. J., F. E. Mayle, I. R. Walker & L. C. Cwynar, 1993. A previously unrecognized late-glacial cold event in eastern North America. *Nature* 361: 623–626.
- Levesque, A. J., L. C. Cwynar & I. R. Walker, 1994. A multiproxy investigation of late-glacial climate and vegetation change at Pine Ridge Pond, southwest New Brunswick, Canada. *Quat. Res.* 42: 316–327.
- Lieder, U., 1983. Introgression as a factor in the evolution of polytypical plankton Cladocera. *Int. Revue ges. Hydrobiol.* 68: 269–284.
- Livingstone, D. M. & F. Schanz, 1994. The effects of deep-water siphoning on a small, shallow lake: a long-term case study. *Arch. Hydrobiol.* 132: 15–44.
- Livingstone, D. M. & A. F. Lotter, 1997. The relationship between air and water temperature in lakes of the Swiss Plateau: a case study with palaeolimnological implications. *J. Paleolimnol.*: in press.
- Lotter, A. F., H. J. B. Birks, W. Hofmann & A. Marchetto, in press. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. *J. Paleolimnol.*
- Manly, B. F. J., 1991. Randomization and Monte Carlo methods in biology. Chapman & Hall, London.
- Marchetto, A., 1995. Light- and electron microscopic evaluation of chrysophycean remains in surface samples of 62 lakes in the Alps and establishing a calibration set for environmental variables transfer functions. Report Österreichische Akademie der Wissenschaften, Institut für Limnologie Mondsee.
- Martens, H. & T. Naes, 1989. Multivariate calibration. J. Wiley & Sons, Chichester.
- Meijering, M. P. D., 1983. On the occurrence of 'arctic' Cladocera with special reference to those along the Strait of Belle Isle (Québec, Labrador, Newfoundland). *Int. Revue ges. Hydrobiol.* 68: 885–893.
- Miller, A. J., 1990. Subset selection in regression. Chapman & Hall, London.
- Moller Pillot, K. M., 1984. De larven der Nederlandse Chironomidae (Diptera), Part B (Orthocladinae). *Nederl. Faun. Meded.* 2.
- Müller, B., A. F. Lotter, M. Sturm & A. Ammann, in press. The influence of catchment and geographic location on the water and sediment composition of 68 small circumalpine lakes. *Aquat. Sci.*
- Munro, M. A. R., A. M. Kreiser, R. W. Battarbee, S. Juggins, A. C. Stevenson, N. J. Anderson, F. Berge, R. B. Davis, R. J. Flower, S. C. Fritz, E. Y. Haworth, V. J. Jones, J. C. Kingston & I. Renberg, 1990. Diatom quality control and data handling. *Phil. Trans. r. Soc. Lond. B* 327: 257–261.
- Olander, H., A. Korhola & T. Blom, 1997. Surface sediment Chironomidae (Insecta: Diptera) distributions along an ecotonal transect in subarctic Fennoscandia: developing tools for palaeotemperature reconstructions. *J. Paleolimnol.*: in press.
- Patalas, K., 1990. Diversity of the zooplankton communities in Canadian lakes as a function of climate. *Verh. int. Ver. Limnol.* 24: 360–368.
- Pienitz, R. & J. P. Smol, 1993. Diatom assemblages and their relationship to environmental variables in lakes from the boreal-tundra ecotone near Yellowknife, Northwest Territories, Canada. *Hydrobiologia* 269/270: 391–404.
- Pienitz, R., M. S. V. Douglas, J. P. Smol, P. Huttunen & J. Meriläinen, 1995a. Diatom, chrysophyte and protozoan distributions along a latitudinal transect in Fennoscandia. *Ecography* 18: 429–439.
- Pienitz, R., J. P. Smol & H. J. B. Birks, 1995b. Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. *J. Paleolimnol.* 13: 21–49.
- Prentice, I. C., 1980. Multidimensional scaling as a research tool in Quaternary palynology: a review of theory and methods. *Revue Palaeobot. Palynol.* 31: 71–104.
- Psenner, R. & R. Schmidt, 1992. Climate-driven pH control of remote alpine lakes and effects of acid deposition. *Nature* 356: 781–783.
- Pugnetti, A. & R. Bettinetti, 1995. The phytoplankton communities of two acid sensitive alpine lakes (lakes Paione, Central Alps, Italy). *Mem. Ist. ital. Idrobiol.* 53: 39–52.
- Qinghong, L. & S. Bråkenhielm, 1995. A statistical approach to decompose ecological variation. *Wat. Air Soil Pollut.* 85: 1587–1592.
- Rawlings, J. O., 1988. Applied regression analysis. A research tool. Wadsworth & Brooks, Pacific Grove.
- Renberg, I. & T. Hellberg, 1982. The pH history of lakes in southwestern Sweden, as calculated from the subfossil diatom flora of the sediments. *Ambio* 11: 30–33.
- Rossaro, B., 1991. Chironomids and water temperature. *Aquat. Insects.* 13: 87–98.
- Rott, E., 1988. Some aspects of the seasonal distribution of flagellates in mountain lakes. *Hydrobiologia* 161: 159–170.
- Servant-Vildary, S., 1982. Altitudinal zonation of mountainous diatom flora in Bolivia: application to the study of the Quaternary. *Acta Geol. Acad. Sci. Hungaricae* 25: 179–210.
- Smol, J. P., 1985. The ratio of diatom frustules to chrysophycean statospores: a useful paleolimnological index. *Hydrobiologia* 123: 199–208.
- Smol, J. P., 1988. Paleoclimate proxy data from freshwater arctic diatoms. *Verh. int. Ver. Limnol.* 23: 837–844.
- Smol, J. P., 1995. Application of Chrysophytes to problems in paleoecology. In Sandgren, C. J. P. Smol & J. Kristiansen (eds), *Chrysophyte algae: Ecology, Phylogeny and Development*. Cambridge University Press, Cambridge, 303–329.
- Stemberger, R. S., A. T. Herlihy, D. L. Kugler & S. G. Paulsen, 1996. Climate forcing on zooplankton richness in lakes of the northeastern United States. *Limnol. Oceanogr.* 41: 1093–1101.
- ter Braak, C. J. F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167–1179.
- ter Braak, C. J. F., 1987. Unimodal models to relate species to environment. Wageningen.
- ter Braak, C. J. F., 1987–1992. CANOCO – a FORTRAN program for canonical community ordination. Microcomputer Power, Ithaca, New York.
- ter Braak, C. J. F., 1988. Partial canonical correspondence analysis. In Bock, H. H. (ed.), *Classification methods and related methods of data analysis*. North-Holland, Amsterdam, 551–558.
- ter Braak, C. J. F., 1990. Update notes: CANOCO version 3.10. Agricultural Mathematics Group, Wageningen.
- ter Braak, C. J. F., 1995. Non-linear methods for multivariate statistical calibration and their use in palaeoecology: a comparison of inverse (*k*-nearest neighbours, partial least squares and weighted averaging partial least squares) and classical approaches. *Chemo-metrics and Intelligent Laboratory Systems* 28: 165–180.
- ter Braak, C. J. F. & S. Juggins, 1993. Weighted averaging partial least squares regression (WA-PLS): an improved method

- for reconstructing environmental variables from species assemblages. *Hydrobiologia* 269/270: 485–502.
- ter Braak, C. J. F. & L. G. Barendregt, 1986. Weighted averaging of species indicator values: its efficiency in environmental calibration. *Mathematical Biosciences* 78: 57–72.
- ter Braak, C. J. F. & C. W. N. Looman, 1986. Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio* 65: 3–11.
- ter Braak, C. J. F. & C. W. N. Looman, 1987. Regression. In Jongman, R. H. G., C. J. F. ter Braak & O. F. R. van Tongeren (eds), *Data Analysis in Community and Landscape Ecology*. Pudoc, Wageningen, 29–77.
- ter Braak, C. J. F. & I. C. Prentice, 1988. A theory of gradient analysis. *Advances in Ecological Research* 18: 271–317.
- ter Braak, C. J. F. & H. van Dam, 1989. Inferring pH from diatoms: a comparison of old and new calibration methods. *Hydrobiologia* 178: 209–223.
- ter Braak, C. J. F. & P. F. M. Verdonschot, 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquat. Sci.* 57: 255–289.
- Thienemann, A., 1954. *Chironomus*. Die Binnengewässer 20, Schweizerbart, Stuttgart.
- Vinebrook, R. D. & P. R. Leavitt, 1996. Effects of ultraviolet radiation on periphyton in an alpine lake. *Limnol. Oceanogr.* 41: 1035–1040.
- Vyverman, W. & K. Sabbe, 1995. Diatom-temperature transfer functions based on the altitudinal zonation of diatom assemblages in Papua New Guinea: a possible tool in the reconstruction of regional palaeoclimatic changes. *J. Paleolimnol.* 13: 65–77.
- Walker, I. R., 1995. Chironomids as indicators of past environmental change. In Armitage, P. D., P. S. Cranston & L. C. V. Pinder (eds), *The Chironomidae: Biology and ecology of non-biting midges*. Chapman & Hall, 405–422.
- Walker, I. R. & R. W. Mathewes, 1989. Chironomid (Diptera) remains in surficial lake sediments from the Canadian Cordillera: analysis of the fauna across an altitudinal gradient. *J. Paleolimnol.* 2: 61–80.
- Walker, I. R., R. J. Mott & J. P. Smol, 1991a. Alleröd-Younger Dryas lake temperatures from midge fossils in Atlantic Canada. *Science* 253: 1010–1012.
- Walker, I. R., J. P. Smol, D. R. Engstrom & H. J. B. Birks, 1991b. An assessment of Chironomidae as quantitative indicators of past climatic change. *Can. J. Fish. aquat. Sci.* 48: 975–987.
- Walker, I. R., J. P. Smol, D. R. Engstrom & H. J. B. Birks, 1992. Aquatic invertebrates, climate, scale, and statistical hypothesis testing: a response to Hann, Warner, and Warwick. *Can. J. Fish. aquat. Sci.* 49: 1276–1280.
- Walker, I. R., A. J. Levesque, L. C. Cwynar & A. F. Lotter, 1997. An expanded surface-water palaeotemperature inference model for use with fossil midges from eastern Canada. *J. Paleolimnol.*: in press.
- Weckström, J., A. Korhola & T. Blom, 1997. The relationship between diatoms and water temperature in 30 subarctic Fennoscandian lakes. *Arctic and Alpine Research* 29: 75–92.
- Wiederholm, R., 1983. Chironomidae of the holarctic region. Part 1: Larvae. *Ent. Scand. Suppl.* 19.
- Wunsam, S., R. Schmidt & R. Klee, 1995. *Cyclotella*-taxa (Bacillariophyceae) in lakes of the Alpine region and their relationship to environmental variables. *Aquat. Sci.* 57: 360–386.
- Zeeb, B. A. & J. P. Smol, 1993. Postglacial chrysophycean record from Elk Lake, Minnesota. In Bradbury, J. P. & W. Dean (eds), *Elk Lake, Minnesota: Evidence for Rapid Climate Change in the North-Central United States*. Geological Society of America Special Paper 276: 239–249.