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

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Abstract

Surface sediments from 68 small lakes in the Alps and 9 well-dated sediment core samples that cover a gradient of total phosphorus (TP) concentrations of 6 to 520 μg TP l^{-1} were studied for diatom, chrysophyte cyst, cladocera, and chironomid assemblages. Inference models for mean circulation $\log_{10}$ TP were developed for diatoms, chironomids, and benthic cladocera using weighted-averaging partial least squares. After screening for outliers, the final transfer functions have coefficients of determination (r^2), as assessed by cross-validation, of 0.79 (diatoms), 0.68 (chironomids), and 0.49 (benthic cladocera). Planktonic cladocera and chrysophytes show very weak relationships to TP and no TP inference models were developed for these biota. Diatoms showed the best relationship with TP, whereas the other biota all have large secondary gradients, suggesting that variables other than TP have a strong influence on their composition and abundance. Comparison with other diatom – TP inference models shows that our model has high predictive power and a low root mean squared error of prediction, as assessed by cross-validation.

Introduction

Nutrient enrichment in aquatic systems due to soil erosion, fertilizer runoff from agricultural land, and especially sewage disposal has been identified as a major environmental problem for many decades (Likens, 1972; OCDE, 1982). Effects of such eutrophication are an increased lake productivity and closely related to this is a loss of aquatic organism diversity. Furthermore, substantial structural changes in the aquatic ecosystem (e.g. plankton, fish, and macrophyte communities) also occur as a consequence of eutrophication. Besides these biological effects that are of concern to nature conservationists, enrichment in phosphorus, nitrogen, and carbon, and the consequent loss of oxygen, also have economic consequences with respect to water-sports, tourism, the quality of drinking water, and the quantitative and qualitative yield of fisheries. Many countries have realized the importance of this issue and have, consequently, taken legal measures against nutrient enrichment of aquatic systems. However, in order to set realistic legal or management goals (Rast & Holland, 1988), it is important to differentiate between the natural trophic state and

Table 1. Major variables characterizing the catchments and limnology of the investigated lakes. The water chemistry variables refer to mean circulation concentrations (n.a.: not analysed)

Lake			Catchment				Limnology													Biology			
number in Fig. 1	name	abbreviation	elevation [m asl]	maximum depth [m]	open water area [km2]	catchment area [km2]	conductivity [µS/cm at 20°C]	pH	alkalinity [mg/l]	DOC [mg C/l]	NO3 [mg/l]	TN [mg/l]	PO4 [µg/l]	TP [µg/l]	Ca [mg/l]	Mg [mg/l]	Na [mg/l]	K [mg/l]	Si [mg/l]	Diatom taxa	Chrysophyte taxa	Cladocera taxa	Chironomid taxa
1	Lago di Muzzano	MUZ	337	3.2	0.22	2.20	223	8.6	1.87	10.5	0.58	1.91	7	102	40.3	10.1	6.4	3.3	1.2	48	15	12	16
2	Lago d'Origlio	ORI	416	6.0	0.07	1.19	100	7.9	0.85	4.2	0.59	1.40	2	32	14.0	5.6	3.0	1.2	2.6	48	18	10	8
3	Burgäschisee	BUR	465	31.0	0.19	4.29	347	8.3	3.24	9.6	4.22	4.22	11	99	78.5	8.8	4.5	1.9	2.8	40	18	20	25
4	Moossee	MOO	521	21.0	0.31	10.41	545	8.1	4.66	5.0	5.40	6.16	4	31	114.0	13.7	9.0	3.1	2.5	45	11	18	12
5	Le Loclat	LOC	432	9.2	0.05	0.88	494	8.3	5.37	4.9	2.43	3.38	18	63	106.2	13.8	3.5	2.3	0.8	34	14	13	27
6	Lac de Seedorf	SEE	609	7.5	0.10	7.38	519	8.5	5.13	6.3	3.34	5.23	62	166	103.6	15.9	9.7	4.8	0.1	24	n.a.	6	17
7	Gerzensee	GER	603	10.0	0.27	2.70	448	8.3	4.52	5.9	1.53	2.82	3	52	93.3	12.3	6.2	2.8	0.2	32	n.a.	17	26
8	Uebeschisee	UEB	641	14.5	0.15	2.16	367	8.3	3.86	6.4	1.18	2.55	3	37	86.0	4.4	4.3	3.0	0.5	37	18	21	22
9	Lützelsee	LÜT	500	6.0	0.13	6.02	456	8.1	4.24	4.4	0.97	2.72	11	86	74.2	16.7	4.2	1.8	0.8	41	n.a.	19	8
10	Wilersee	WIL	730	21.0	0.03	0.50	313	8.1	2.67	3.6	0.54	1.44	7	46	52.2	3.3	20.1	2.2	0.7	35	n.a.	16	24
11	Hüttwilersee	HÜT	434	15.0	0.35	3.71	470	8.0	5.04	7.3	1.88	5.72	8	47	95.1	19.9	4.8	2.6	4.6	35	14	20	18
12	Husemersee	HUS	409	14.0	0.08	1.33	535	8.0	5.24	5.5	3.10	8.36	8	98	115.2	22.2	5.7	2.5	1.6	36	16	19	16
13	Mettmenhasler See	MET	418	12.5	0.03	0.50	498	7.8	4.99	3.0	1.27	3.68	4	61	87.0	23.0	11.5	2.2	0.7	46	n.a.	17	26
14	Unterer Chatzensee	CHA	439	7.8	0.19	1.29	318	8.1	2.95	6.9	0.08	1.40	5	82	54.4	10.1	6.7	1.5	0.5	51	n.a.	22	31
15	Soppensee	SOP	596	26.5	0.23	1.59	304	7.9	3.23	4.3	0.76	1.91	30	82	55.4	5.8	4.2	3.5	0.4	40	11	22	9
16	Burgseeli	BUG	613	19.0	0.09	1.18	263	8.1	3.14	4.6	0.27	1.21	4	41	67.8	2.4	2.5	1.4	0.5	28	30	15	22
17	Blausee	BLA	887	10.0	0.01	0.09	280	8.1	2.85	1.0	0.39	0.96	5	12	53.4	10.9	0.9	0.5	1.8	36	n.a.	8	19
18	Schwarzsee	SCH	1046	9.5	0.46	19.70	390	8.3	2.79	2.6	0.29	0.84	5	22	88.1	6.8	1.8	1.1	1.4	58	29	14	8
19	Rotsee	ROT	419	16.0	0.50	4.60	217	8.4	2.30	2.1	0.35	1.38	16	74	44.0	5.2	3.5	1.7	0.4	49	6	19	22
20	Mauensee	MAU	504	9.0	0.60	4.30	379	7.9	3.92	4.9	0.77	1.99	2	37	72.5	11.2	6.2	2.8	0.3	38	16	21	20
21	Seelisberg Seeli	SEL	738	37.5	0.18	2.70	179	8.3	2.34	2.2	0.45	0.94	4	28	42.7	2.2	0.8	0.7	1.0	18	15	20	20
22	Lac Brenet	BRE	1002	17.0	0.63	2.85	256	8.4	2.64	3.5	0.13	0.56	4	23	58.0	2.4	3.5	0.9	0.3	66	n.a.	20	24
23	Lac des Tailleres	TAI	1036	8.5	0.44	33.16	210	8.1	2.48	5.8	0.24	0.44	4	64	86.9	1.4	1.2	1.5	0.7	51	27	11	19
24	Schwendisee	SCW	1159	9.5	0.04	5.06	205	7.7	2.47	3.5	0.07	0.66	1	26	36.7	0.9	0.7	0.7	0.7	42	16	13	27
25	Voralpsee	VOR	1123	3.3	0.15	13.52	172	8.6	1.95	1.6	0.19	1.48	5	22	36.5	1.8	0.4	0.4	0.4	41	n.a.	4	7
26	Tschingelsee	TSC	1150	1.6	0.11	36.65	n.a.	8.2	1.58	0.8	0.26	0.56	3	26	33.8	2.4	0.3	0.3	0.6	55	n.a.	1	6
27	Lac des Chavonnes	CHV	1690	29.5	0.05	0.74	153	8.2	1.60	2.0	0.13	0.51	7	22	31.7	3.3	0.4	0.3	0.6	53	14	9	6

Table 1. Continued

28	Lac Retaud	RET	1685	4.5	0.01	0.22	261	8.2	2.89	1.3	0.03	0.80	4	24	62.9	1.6	1.0	0.8	1.1	46	14	18	11
29	Fälensee	FÄL	1452	31.0	0.15	4.25	164	8.1	1.82	0.9	0.87	0.54	4	27	36.4	2.2	0.5	0.3	0.9	13	12	7	10
30	Seealpsee	SAL	1141	15.0	0.14	11.33	211	8.2	1.87	1.0	0.98	0.54	4	17	36.3	2.6	0.6	0.2	1.3	40	n.a.	8	7
31	Grosssee	GRO	1618	11.5	0.05	2.20	141	8.9	1.97	2.3	0.53	1.83	3	23	28.1	6.3	0.7	0.7	0.9	61	n.a.	8	2
32	Engstlensee	ENG	1850	49.0	0.45	7.40	147	8.5	1.60	1.5	0.21	0.50	3	13	31.5	1.7	0.3	0.4	0.6	31	n.a.	9	21
33	Seebergsee	SEB	1831	15.5	0.06	0.23	160	8.4	2.07	1.7	0.03	0.50	3	24	27.8	7.1	0.5	0.4	0.7	48	13	7	13
34	Tannensee	TAN	1976	16.0	0.34	1.12	102	8.2	1.11	0.8	0.08	0.20	3	12	22.4	0.8	0.3	0.5	0.3	92	20	9	18
35	Melchsee	MEL	1891	15.5	0.49	5.92	132	8.2	1.53	0.9	0.08	0.43	3	13	28.7	1.5	0.4	0.3	0.4	45	n.a.	7	11
36	Sewenseeli	SEW	1689	4.5	0.03	0.21	147	8.1	1.47	2.9	0.05	0.56	4	20	27.7	0.8	1.2	0.5	0.9	47	15	9	11
37	Lac de Bret	BRT	674	18.0	0.50	2.97	357	8.1	3.11	3.2	1.62	2.25	7	35	57.8	9.2	8.2	2.8	1.5	43	n.a.	16	11
38	Lac Tanay	TAY	1408	31.0	0.18	7.93	170	8.5	2.12	1.4	0.24	0.59	8	27	38.3	2.1	0.4	0.4	0.7	36	n.a.	9	14
39	Lac de Nervaux	NER	1493	10.0	0.01	0.92	173	8.2	2.37	2.0	0.05	0.69	4	38	40.6	3.7	0.8	0.5	1.2	35	16	10	17
40	Sägistalsee	SÄG	1935	9.7	0.07	3.85	225	8.4	2.65	0.9	0.06	0.39	2	22	51.6	2.9	0.4	0.3	0.6	48	18	5	13
41	Wannisbordsee	WAN	2103	14.0	0.02	1.64	21	7.7	0.33	0.6	0.19	0.44	3	10	3.6	0.2	0.4	0.2	0.7	59	n.a.	5	16
42	Bannalpsee	BAN	1587	17.0	0.16	8.23	184	8.3	2.11	0.6	0.26	0.60	3	18	43.2	2.8	0.3	0.2	0.5	49	15	6	14
43	Iffigsee	IFF	2065	30.0	0.10	4.61	127	8.5	1.48	0.7	0.23	0.60	2	19	23.4	3.6	0.2	0.1	0.6	35	21	6	11
44	Flueseeli	FLU	2045	8.5	0.04	0.79	132	8.4	1.43	1.2	0.28	0.56	3	22	23.2	4.1	0.5	0.2	0.7	47	n.a.	2	9
45	Lämmerensee	LÄM	2296	2.5	0.07	1.55	184	8.4	2.07	1.1	0.11	0.53	4	14	37.7	2.9	0.3	0.2	0.5	35	n.a.	4	4
46	Trüebsee	TRÜ	1764	7.0	0.26	7.07	115	8.5	1.28	0.9	0.25	0.64	2	20	27.1	0.9	0.3	0.2	0.6	44	n.a.	6	14
47	Bachsee	BAC	2265	16.0	0.07	1.87	122	8.7	1.43	1.2	0.05	0.62	2	25	28.8	1.0	0.4	0.2	0.5	55	n.a.	3	9
48	Lutersee	LUT	1702	4.5	0.02	0.59	133	8.2	1.72	2.9	0.04	0.68	2	29	29.3	1.3	0.2	0.4	0.3	53	n.a.	6	11
49	Hagelseewli	HAG	2339	18.5	0.03	0.36	200	8.3	1.61	0.9	0.17	0.47	4	19	33.3	3.7	0.8	0.2	1.5	40	11	2	6
50	Lag Grond	GRD	1016	5.0	0.02	1.89	241	8.1	2.71	2.3	0.36	1.48	2	20	48.6	3.1	2.2	0.7	2.3	52	n.a.	15	18
51	Schwellisee	SCE	1933	12.0	0.03	9.58	181	8.4	2.00	0.5	0.23	1.53	2	13	28.7	9.4	0.7	0.5	2.6	67	n.a.	2	15
52	Obersee	OBE	1734	14.5	0.08	2.71	244	8.5	2.83	1.1	0.13	3.74	5	22	33.7	19.7	1.0	0.9	4.4	38	11	10	18
53	Türlersee	TÜR	643	21.0	0.50	5.19	368	7.9	3.92	3.8	0.69	1.58	5	32	56.7	17.0	5.6	1.6	0.7	35	10	10	20
54	Seewli See	SWL	2028	16.0	0.08	2.70	132	8.5	1.66	1.5	0.18	0.61	3	11	26.6	1.9	0.3	0.2	0.7	42	n.a.	3	11
55	Bichelsee	BIC	590	6.5	0.09	2.70	395	8.3	4.84	5.0	0.79	1.28	3	53	63.4	23.3	4.1	1.3	2.1	28	12	14	20
56	Egelsee	EGE	667	10.0	0.02	0.29	334	8.0	4.17	4.7	0.10	1.24	3	34	70.7	6.3	1.1	0.8	2.3	30	18	16	18
57	Dittligsee	DIT	652	16.5	0.07	3.13	565	8.1	5.74	9.6	2.60	4.36	5	86	129.9	7.3	5.0	3.0	1.2	17	8	14	21
58	Inkwilersee	INK	461	5.0	0.12	2.13	398	7.9	4.59	5.0	1.18	4.50	48	152	100.3	9.0	5.7	2.4	3.2	30	n.a.	15	17
59	Hasensee	HAS	434	5.5	0.11	2.52	522	8.0	5.93	6.6	3.79	6.88	4	71	113.4	20.7	4.5	2.0	6.9	39	21	15	20
60	Nussbaumsee	NUS	434	8.2	0.25	5.87	445	8.0	4.87	6.0	1.69	5.08	5	31	94.4	20.6	4.8	3.0	3.3	40	n.a.	20	19
61	Gattiker Waldweiher	GAW	545	5.5	0.03	1.88	384	8.1	4.35	4.0	0.50	1.51	9	63	80.0	10.0	2.4	0.5	3.3	53	16	14	20
62	Hüttnersee	HÜN	658	12.0	0.17	2.33	426	8.1	4.24	5.2	0.89	2.09	15	43	78.9	7.5	7.7	2.5	0.5	39	n.a.	18	12
63	Lac des Rousses	ROU	1058	11.5	0.89	15.68	283	8.5	3.14	2.7	0.06	0.41	2	18	57.6	1.3	4.4	0.5	0.2	60	n.a.	20	19
64	Lac de l'Abbaye	ABB	871	18.0	0.80	25.93	234	8.4	2.65	3.4	0.05	0.47	2	24	45.2	1.2	2.7	1.0	0.1	41	19	16	18
65	Lago di Montorfano	MON	394	6.5	0.52	1.57	190	7.8	1.71	4.3	0.08	0.90	2	16	31.0	3.5	2.9	0.7	0.2	48	24	15	19

Table 1. Continued

66	Lago del Segrino	SEG	374	8.5	0.34	2.66	274	8.2	2.75	2.7	1.05	1.77	2	18	42.6	4.9	2.2	0.5	0.7	41	n.a.	21	27
67	Lago di Endine	END	334	8.0	0.49	8.34	354	8.1	3.51	2.7	0.50	0.93	2	23	48.4	11.8	2.7	0.6	1.5	37	15	16	17
68	Lac Lioson	LIO	1848	26.0	0.07	1.50	153	8.3	1.68	1.8	0.10	0.22	2	6	33.2	2.6	0.4	0.5	0.8	52	n.a.	5	18
69	Baldeggersee 1988	BA1988	463	67.0	5.20	73.00	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	153	n.a.	n.a.	n.a.	n.a.	n.a.	21	n.a.	10	1
69	Baldeggersee 1982	BA1982	463	67.0	5.20	73.00	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	309	n.a.	n.a.	n.a.	n.a.	n.a.	13	n.a.	7	1
69	Baldeggersee 1979	BA1979	463	67.0	5.20	73.00	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	390	n.a.	n.a.	n.a.	n.a.	n.a.	30	n.a.	3	1
69	Baldeggersee 1973	BA1973	463	67.0	5.20	73.00	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	520	n.a.	n.a.	n.a.	n.a.	n.a.	25	n.a.	3	0
69	Baldeggersee 1972	BA1972	463	67.0	5.20	73.00	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	325	n.a.	n.a.	n.a.	n.a.	n.a.	14	n.a.	4	2
69	Baldeggersee 1967	BA1967	463	67.0	5.20	73.00	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	380	n.a.	n.a.	n.a.	n.a.	n.a.	10	n.a.	5	2
69	Baldeggersee 1958	BA1958	463	67.0	5.20	73.00	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	211	n.a.	n.a.	n.a.	n.a.	n.a.	20	n.a.	5	1
19	Rotsee 1986	ROT1986	419	16.0	0.50	4.60	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	112	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	19	16
19	Rotsee 1979/80	ROT1979/80	419	16.0	0.50	4.60	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	140	n.a.	n.a.	n.a.	n.a.	n.a.	31	n.a.	17	11
19	Rotsee 1969/70	ROT1969/70	419	16.0	0.50	4.60	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	460	n.a.	n.a.	n.a.	n.a.	n.a.	33	n.a.	18	9
Maximum			2339	49.0	0.89	36.65	565	9	5.93	10.5	5.40	8.36	62	520	129.9	23.3	20.1	4.8	6.9	92	30	22	31
Mean			1094	13.8	0.20	5.07	274	8	2.87	3.3	0.78	1.76	6	73	55.1	7.1	3.0	1.2	1.2	43	16	12	16
Median			945	11.8	0.12	2.70	241	8	2.65	2.8	0.29	1.08	4	31	46.8	4.3	2.0	0.7	0.7	41	15	13	17
Minimum			334	1.6	0.01	0.09	21	8	0.33	0.5	0.03	0.20	1	6	3.6	0.2	0.2	0.1	0.1	13	6	1	2

anthropogenically-induced nutrient enrichment. Limnological monitoring data assessing water chemistry or biological data are rarely available for more than the last few decades (e.g. Maberly et al., 1994) and, therefore very rarely document the onset of eutrophication. Baseline lake-nutrient data therefore have to be evaluated by use of palaeolimnological methods (Schindler, 1987; Anderson, 1993).

Furthermore, processes governing the natural trophic ontogeny of lake systems have long interested limnologists, and are of fundamental importance to aquatic science (Whiteside, 1983). Various classification systems relating the occurrence of different indicators to the trophic state of a lake have been developed. For example, macrophytes (e.g. Birks, 1980; Krause, 1981; Lotter, 1988), algal pigments (e.g. Züllig, 1981, 1989), saprobic indices using different organisms (Kolkwitz, 1950), diatoms (Lange-Bertalot, 1978, 1979), and chironomids (e.g. Sæther, 1979) have all been used as indicators of trophic state. Moreover, sediment geochemistry has also been used to assess lake trophic state (e.g. Engstrom et al., 1985; Schelske et al., 1986; Brenner & Binford, 1988, Anderson & Rippey, 1994, Rippey & Anderson, 1996). All these methods provide qualitative insights into the long-term development of an aquatic system in relation to its nutrient history. It is only recently that quantitative diatom-based inference models have been developed to reconstruct the past trophic state of lakes (e.g. Whitmore, 1989; Agbeti & Dickman, 1989; Anderson et al., 1993; Christie & Smol, 1993) and thus provide realistic baseline conditions that may be used for legislative and lake-management purposes (Anderson, 1995). Such quantitative reconstructions of past trophic state not only give insights into the long-term history of a lake, but also provide important information about the onset, the rate, and the magnitude of eutrophication.

The aims of the present study are to examine the present-day relationship between the distribution of different aquatic organisms in the Alps in relation to nutrients, with special reference to phosphorus, and to develop quantitative inference models that permit the reconstruction of total phosphorus values from subfossil assemblages of aquatic organisms.

Methods

Surface sediments from the deepest part of 68 lakes had previously been sampled and analysed for organic remains by Lotter et al. (1997a) in order to develop

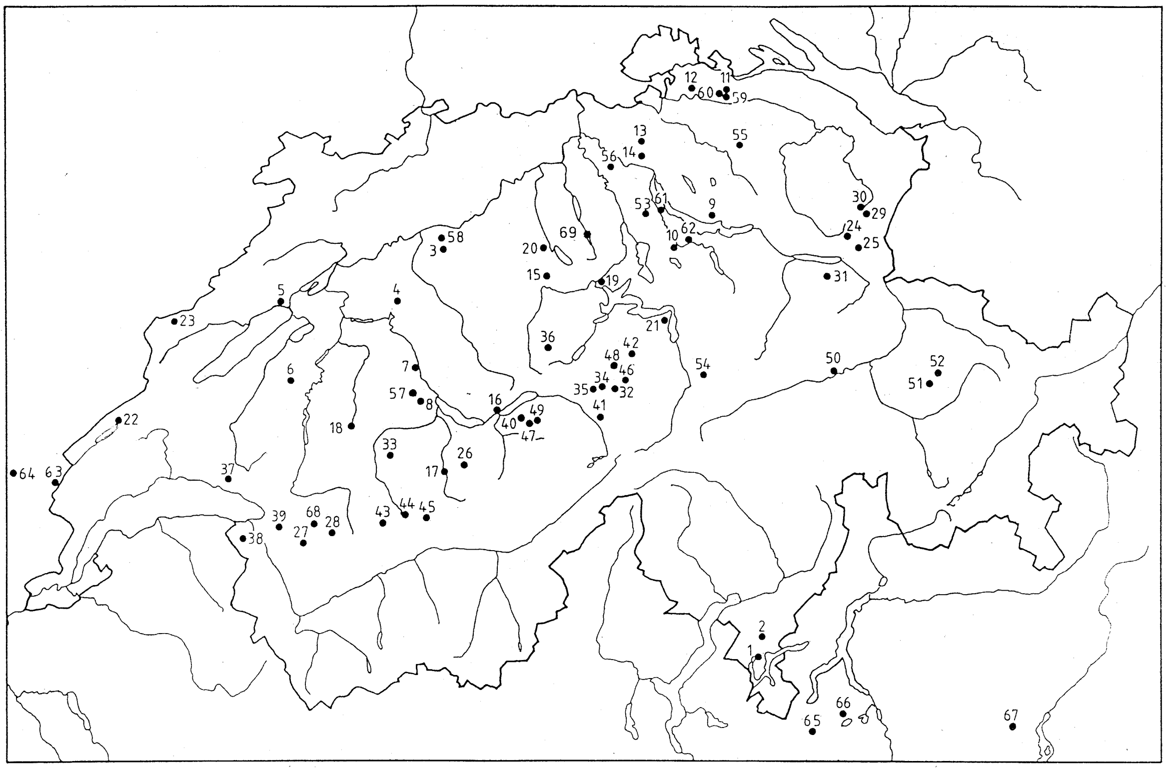

Figure 1. Map of Switzerland showing the location of the sampled lakes. The numbers refer to the lake names in Table 1.

quantitative palaeoecological climate-inference models. Statistical analyses of these data also revealed significant nutrient effects; thus in this paper we make use of these data to derive nutrient inference models.

The lakes are situated on the Swiss Plateau, in the Jura mountains and in the Alps, as well as in the foreland of the southern Alps (Figure 1) at elevations between 300 and 2350 m above sea level (a.s.l., see Table 1). To minimize the effects of low pH that might override the effects of other important environmental variables on aquatic organisms, only lakes in calcareous bedrock regions were chosen. As a consequence, the resulting inference models are not likely to be applicable to lakes underlain by non-calcareous bedrock. Geographical lake and catchment data are given in Table 1.

Continuous temperature and conductivity profiles were recorded before sampling in spring 1993 or 1994 at the deepest point to assess lake stratification. In the non-stratified lakes, three water samples (surface, mid depth, 1 m above bottom) were taken, whereas in thermally stratified lakes, four water samples were taken (surface, above and below the thermocline, 1 m above bottom). The pH was determined in the field, whereas oxygen content, alkalinity, dissolved organic carbon (DOC), nitrate (NO_3), total nitrogen (TN), orthophosphate (PO_4), total phosphorus (TP), calcium (Ca), magnesium (Mg), sodium (Na), potassium (K), and silica (Si) were measured in the laboratory at EAWAG (for details see Müller et al., in press). For most of the lowland lakes, additional water chemistry data obtained through the regional environmental protection agencies allowed an estimate of interannual variability in water chemistry (Håkanson, 1992). Lakes without such monitoring data, especially at higher elevations, were revisited for surface-water sampling under the ice during the winter. A depth-weighted average was estimated using the three to four water chemistry determinations. An arithmetical mean of this value and the circulation value (lowland lakes) or the winter value (alpine lakes) was then calculated for the nutrient parameters. These data are used as an estimate of the mean water chemistry for the circulation period (Table 1) and are assumed to represent the maximum available epilimnetic nutrient concentrations in these lakes.

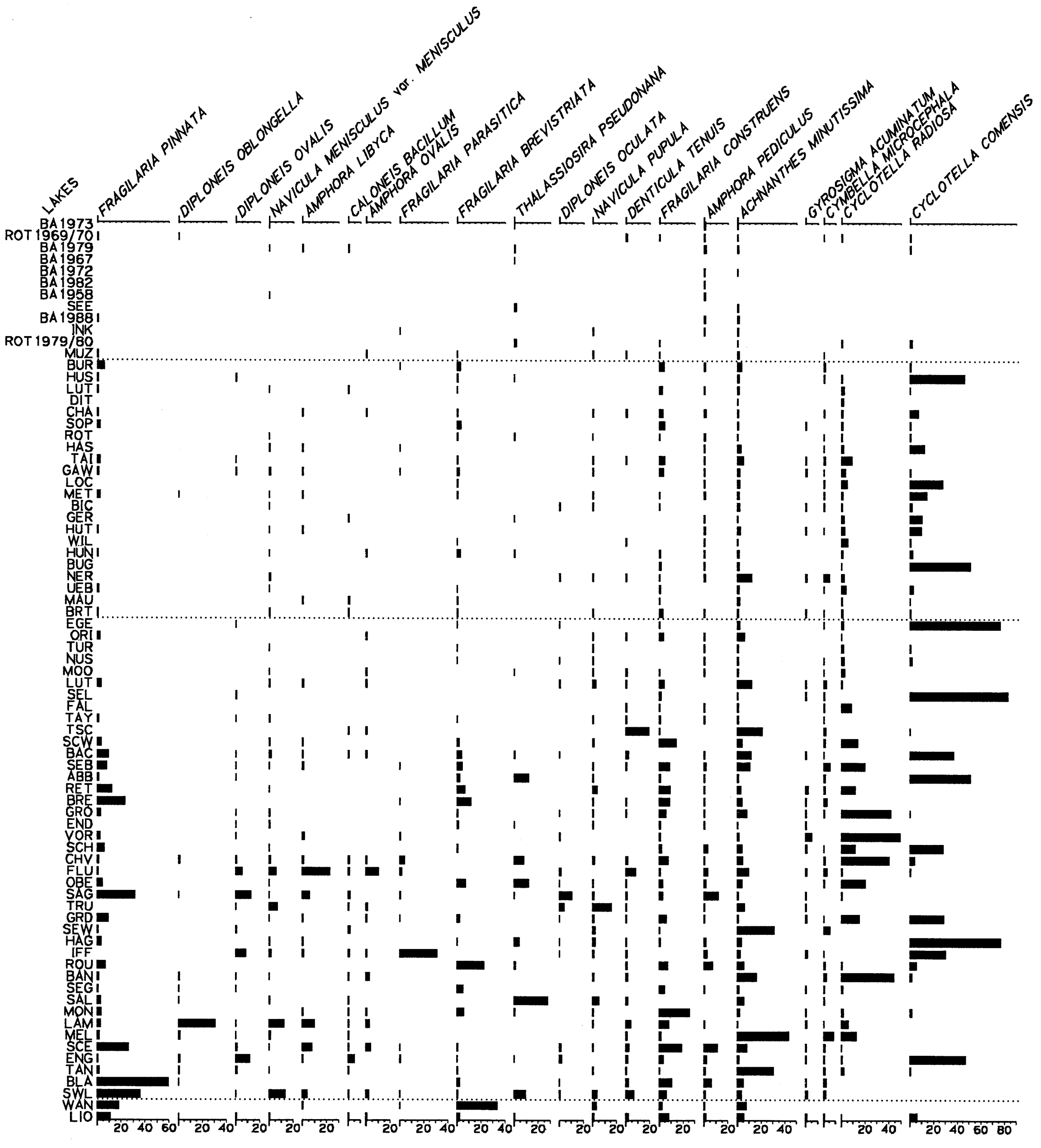

Figure 2. Distribution of diatoms along the TP gradient. Only selected taxa are shown. Classification of trophic status is according to OCDE (1982).

For this study the uppermost centimetre of two Kajak-cores taken ca 0.5 m apart in the deepest part of the basin was used for analysis. In certain lakes the top 2 cm were needed because of the scarcity of chironomid head capsules (for details see Lotter et al., 1997a). The methods used for the analyses of the different biological microfossils are described in Lotter et al. (1997a). Each set of organisms has been analysed by one analyst only, thus providing a potentially high-quality modern training-set with consistent taxonomy and nomenclature (Birks, 1994).

Percentages were calculated for each set of organisms. In an attempt to optimize the ‘signal’ to ‘noise’ ratio in the data (Prentice, 1980), all percentage data were transformed to square-roots. The inference models were developed, as described in Lotter et al.

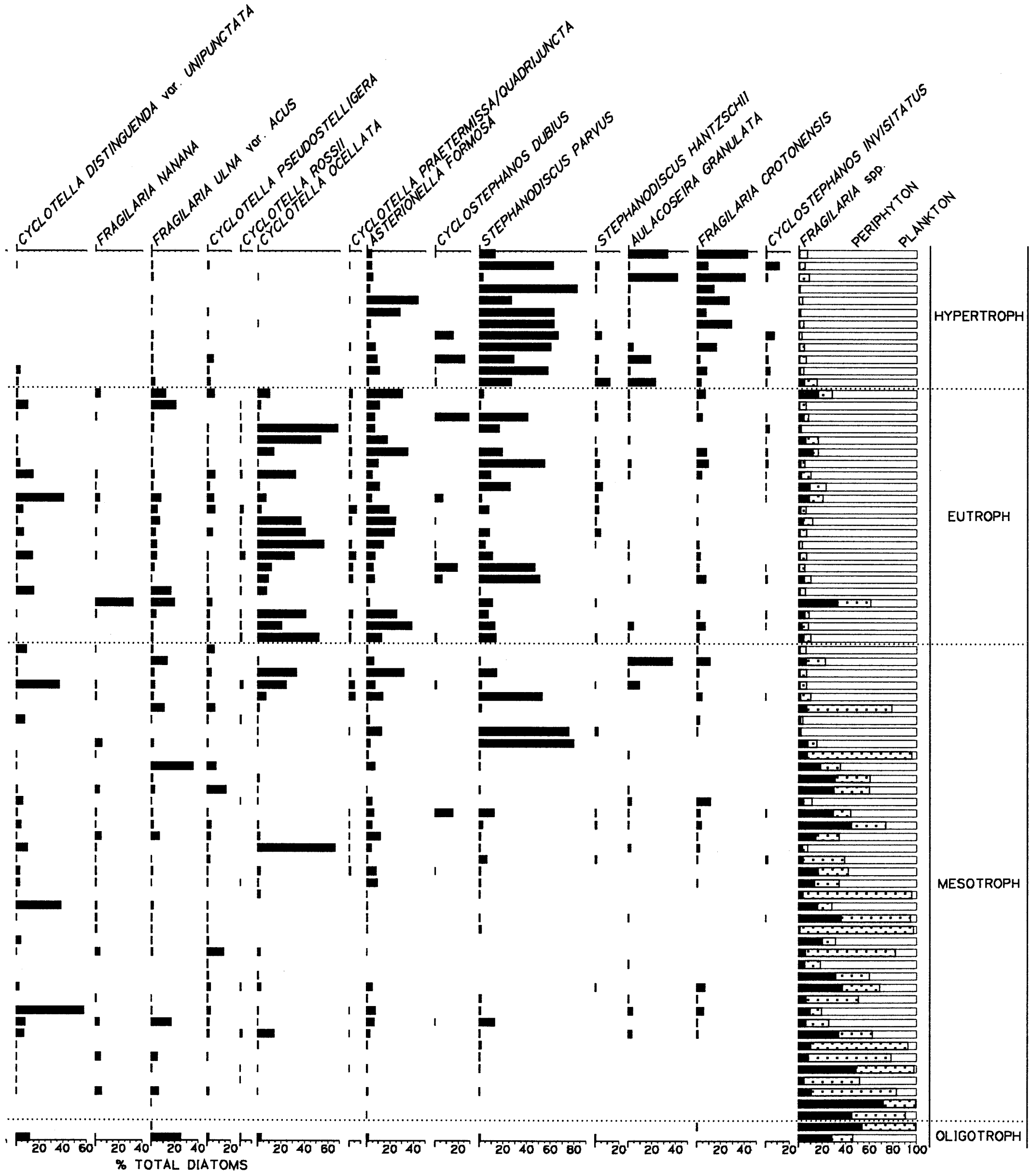

Figure 2. Continued

(1997a) using weighted averaging partial least squares regression (WA-PLS). Model assessment using cross-validation, data screening, outlier detection, and summarisation of the final screened training-sets (Table 2) follow Lotter et al. (1997a). As the distribution of the TP values is right-skewed, a $\log_{10}$-transformation was applied to normalize its distribution. All results are reported as $\log_{10}$ μg TP l^{-1}.

The final screened training-sets for $\log_{10}$ TP are characterized in Table 2 by detrended canonical correspondence analysis (DCCA), with TP as the only explanatory variable (detrending-by-segments, non-linear rescaling, rare taxa downweighted). The gradient length of the DCCA axis 1 is the gradient length of the environmental variable in standard deviation (SD) units (ter Braak & Juggins, 1993; ter Braak et al.,

Table 2. Descriptive statistics for the screened modern training-sets in relation to $\log_{10}$ TP inference models after screening for outliers

	Diatoms	Benthic Cladocera	Chironomids
Number of samples	72	69	48
Number of taxa	341	30	59
N2 for samples			
minimum	3.25	1.00	2.06
median	16.89	6.19	12.50
maximum	45.67	14.82	22.91
N2 for taxa			
minimum	1.00	1.00	1.00
median	3.90	13.85	9.22
maximum	47.20	58.67	37.93
DCCA axis 1			
λ_1	0.295	0.088	0.285
gradient length (SD)	2.901	1.478	2.351
% variance	8.4	8.0	11.4
DCA axis 2			
λ_2	0.207	0.123	0.356
gradient length (SD)	2.346	2.141	3.455
% variance	5.9	11.3	14.2
Total inertia	3.510	1.092	2.506
λ_1/λ_2	1.425	0.715	0.800
$\mathbf{Log_{10}}$ TP			
minimum	1.000	0.780	1.000
mean	1.588	1.601	1.450
median	1.380	1.430	1.380
maximum	2.720	2.590	2.010
standard deviation	0.408	0.391	0.245
Prediction model			
Number of WA-PLS components	2	1	2
apparent r^2	0.927	0.625	0.838
RMSE (apparent)	0.110	0.240	0.099
jack-knifed r^2	0.786	0.487	0.679
RMSEP (jack–knifed)	0.191	0.280	0.139
mean bias	0.011	0.004	−0.003
maximum bias	0.329	0.568	0.206
Taxon response models (maximum likelihood) for all taxa in $>$20% of the samples			
skewed unimodal model	2	2	0
symmetric unimodal model	20	7	10
sigmoidal model	28	4	7
null model	14	5	12

1993). The gradient length of the second unconstrained axis is also presented, along with the eigenvalues and percentage variance of the biological data explained for each axis, as a guide to the presence of any large secondary gradients in the data. The biological datasets 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) N2 diversity measure (ter Braak, 1990; ter Braak & Verdonschot, 1995). The environmental variables are characterized in terms of their ranges, means, medians, and standard deviations. The transfer function prediction models are summarized in terms of the optimal number of WA-PLS components, the apparent r^2 and root mean squared error (RMSE), the jack-knifed r^2 and root mean squared error of prediction (RMSEP), and the mean and maximum bias (Table 2). Details of these statistics and the difference between apparent r^2 and jack-knifed r^2, RMSE and RMSEP, and mean and maximum bias are given by ter Braak & Juggins (1993) and Birks (1995).

All 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). Species response models were fitted using the program HOF (J. Oksanen, unpublished program).

In Figures 2, 4, and 6, the distribution of the biological assemblages in the surficial sediments are shown along a TP gradient, from low TP values at the bottom of the diagrams to high TP values in the top part. The OCDE (1982) classification system with respect to TP was adopted, in which concentrations ≤ 10 μg TP l^{-1} are termed as oligotrophic, concentrations between 10–35 μg TP l^{-1} mesotrophic, 35–100 μg TP l^{-1} eutrophic, and concentrations ≥ 100 μg TP l^{-1} hypertrophic.

Results

Diatoms

The TP gradient of the original 68 lake training-set is relatively short (6–166 μg l^{-1}) compared to other European studies (Table 3). Due to the lack of modern high TP lakes in the Alps, ten additional sediment core samples with known measured circulation TP values have been added to the modern training-set to extend

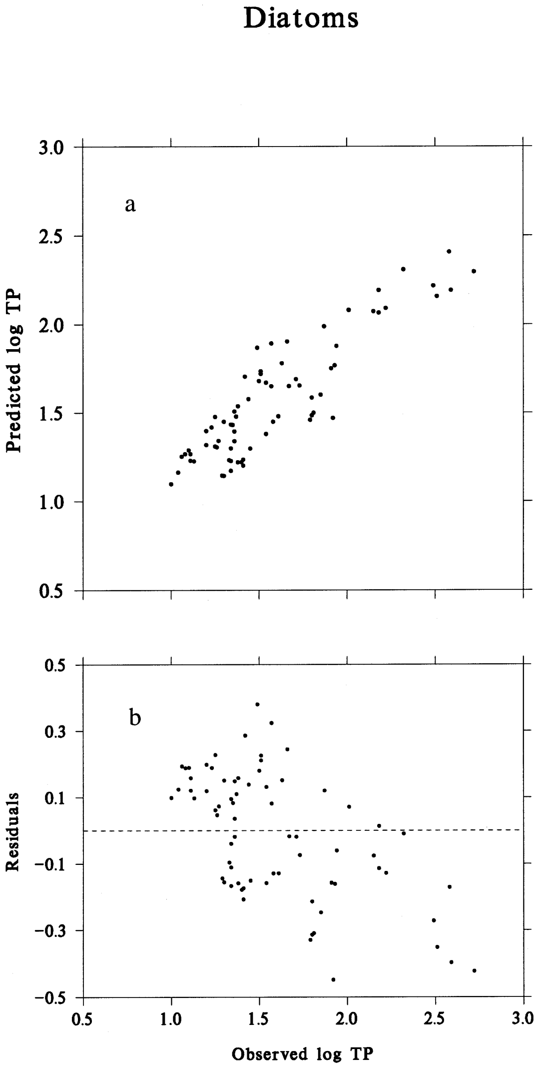

Figure 3. Diatom – $\log_{10}$TP training-set: (a) plot of predicted $\log_{10}$TP against observed $\log_{10}$TP based on a 2-component WA-PLS model, and (b) plot of residuals (predicted – observed) against observed $\log_{10}$TP.

the gradient (6–520 μg l^{-1}, see Table 1). Three of these samples (ROT1986, ROT1979/80, and ROT1969/70; Table 1) come from the well dated (^{137}Cs) sediments of Rotsee (Lotter, 1988, 1989), whereas the other seven samples (BA1988; BA1982; BA1979; BA1973; BA1972; BA1967; BA1958) originate from the annually laminated sediments of Baldeggersee (Lotter et al., 1997b; Lotter, in press).

The diatom data-set thus consists of 68 surface sediment samples and ten core samples. Oligotrophic and mesotrophic sites are mainly characterized by *Fragilaria* spp. and *Cyclotella radiosa*, whereas eutrophic and hypertrophic sites show a dominance of *C. ocellata*, *Asterionella formosa*, *Stephanodiscus parvus*, and *Fragilaria crotonensis* (Figure 2). The life-form spectra are generally dominated by benthic *Fragilaria* spp. and periphytic diatoms in low to medium TP lakes, whereas planktonic diatoms dominate at higher TP concentrations.

In relation to TP, the diatom data have a gradient length of 2.90 SD units. Log_{10} TP explains 8.4% of the variance in the diatom data, whereas the second unconstrained axis explains 5.9%, indicating a relatively strong relationship between the diatom assemblages and $\log_{10}$ TP. A preliminary WA-PLS model using all 77 samples gave an optimal two-component model with a RMSEP of 0.24 $\log_{10}$ μg TP l^{-1}, a jack-knifed r^2 of 0.69, a mean bias of 0.008, and a maximum bias of 0.58. Five samples (BUR, HUS, FÄL, LIO, ROT1969/70) have very high absolute residuals, and these were deleted. The resulting training-set of 72 samples and 341 taxa gives a RMSEP of 0.19, a jack-knifed r^2 of 0.79, a mean bias of 0.01, and a maximum bias of 0.33 for a two-component WA-PLS model (Table 2). Further data screening failed to produce a significant improvement in the predictive power of the model.

Of the 64 diatom taxa occurring in 20% or more of the samples, two show a statistically significant skewed unimodal response to $\log_{10}$ TP, 20 have a statistically significant symmetric unimodal response, and 28 show a statistically significant increasing or decreasing sigmoidal monotonic response to $\log_{10}$ TP, whereas 14 diatom taxa show no significant response to $\log_{10}$ TP (Table 2), as assessed by a hierarchical set of species response models (Huisman et al., 1993). These models are a series of generalised linear models fitted by maximum likelihood using a Poisson error distribution and a log link function.

Cladocera

The cladoceran assemblages are generally dominated by planktonic taxa (Figure 4). The relative abundances of the chydorids are, therefore, very low. The latter are composed mainly of *Alona quadrangularis*, *A. affinis*, *Acroperus harpae*, and *Chydorus sphaericus* that are more abundant in oligo- and mesotrophic lakes. The planktonic cladocera show no clear pattern in relation to the TP gradient.

The planktonic cladocera data-set consists of 72 samples containing only five taxa (*Bosmina* spp.,

Table 3. Performance of different diatom – TP calibration data-sets based on a WA or WA-PLS model. The RMSEP are based on either leave-one-out jack-knifing (WA-PLS) or bootstrapping (WA). n = number of lakes, WA = weighted averaging; WA-PLS = weighted averaging partial least squares

Authors	TP range μg TP l^{-1}	lakes n	r^2 apparent	app. RMSE log μg TP l^{-1}	RMSEP log μg TP l^{-1}	model
Agbeti (1992)	2–63	28	0.86	0.15		WA
Hall & Smol (1992)	5–28	37	0.73	0.25		WA
Anderson et al. (1993)	25–800	43	0.75/0.77	0.17/0.16		WA
Fritz et al. (1993)	1–31	41	0.73	0.41		WA
Anderson & Rippey (1994)	15–800	49	0.80	0.19	0.24	WA
Anderson & Odgaard (1994)	25–1000	27	0.80	0.15		WA
Bennion (1994)	25–646	30	0.79	0.16	0.28	WA
Dixit & Smol (1994)	1–154	64	0.62	0.66		WA
Wunsam & Schmidt (1995)	5–266	86	0.57	0.32	0.35	WA
Wunsam et al. (1995)	2–266	86	0.61/0.65	0.12/0.22	0.35/0.36	WA
Bennion et al. (1995)	2–263	44	0.60	0.32	0.37	WA
Reavie et al. (1995)	5–85	59	0.73	0.33*		WA
Bennion et al. (1996a)	5–1190	147	0.80	0.24	0.27	WA
Bennion et al. (1996b)	5–1190	152	0.91	0.15	0.21	WA
Hall & Smol (1996)	3–24	54	0.62	3.5*	4.2*	WA-PLS
Lotter et al. (this study)	6–520	72	0.93	0.11	0.19	WA-PLS

* RMSE and RMSEP in μg TP l^{-1}

Daphnia). There is a very weak, statistically non-significant relationship with $\log_{10}$ TP (0.7% of the variance explained in a DCCA with $\log_{10}$ TP as the sole constraining variable). The WA-PLS model (one-component) is correspondingly poor with a RMSEP of 0.439 and a jack-knifed r^2 of 0.001. In view of the poor predictive power of this data-set, no further work was done with the planktonic cladocera.

The benthic cladocera data consist of 74 samples (68 surface-sediments, six subfossil samples) containing 30 taxa. There is a moderately strong and statistically significant relationship between the benthic cladoceran assemblages and $\log_{10}$ TP as the sole constraining variable (8% of the variance explained by the first, constrained axis, 11.3% explained by the unconstrained axis 2). A one-component WA-PLS model has a RMSEP of 0.35 and a jack-knifed r^2 of 0.33. Five samples had high absolute residuals and/or high leverage statistics (IFF, FLU, MON, LIO, BA1967). When they were deleted the predictive power of the one-component WA-PLS model increased to a RMSEP of 0.28 and a jack-knifed r^2 of 0.49 (Table 2). Subsequent deletions of samples with high residuals and/or high leverage values gave small improvements in the model but no major improvement.

Of the 18 benthic cladocerans present in 20% or more of the samples in the screened training-set, two show statistically significant skewed unimodal responses to $\log_{10}$ TP, seven show significant symmetric unimodal responses, and four have significant sigmoidal responses. Five taxa have no significant responses to $\log_{10}$ TP (Table 2).

If the benthic and planktonic cladocera are combined (72 samples, 35 taxa), the resulting two-component WA-PLS model for all 72 samples has a RMSEP of 0.35 and a jack-knifed r^2 of 0.35. Screening and deletion of the six samples with absolute residuals greater than the standard deviation of $\log_{10}$ TP result in a two-component WA-PLS model with a RMSEP of 0.29 and jack-knifed r^2 of 0.46. In view of the better predictive power of the benthic cladoceran model, we have discarded the total cladocera - TP model.

Chironomids

The distribution of the chironomids along the TP gradient is illustrated in Figure 6. There is a grouping of taxa such as *Parachironomus*, *Glyptotendipes*, *Nanocladius*, and *Polypedilum sordens* with higher percentages in the eu- and hypertrophic lakes. *Cricotopus* has the highest relative abundance in the hypertrophic lakes, whereas *Micropsectra*, *Chironomus* gr. *anthracinus*, *Tanypus* gr. *lugens*, *Heterotrissocladius*,

Figure 4. Distribution of benthic Cladocera along the TP gradient. Only selected taxa are shown. Classification of trophic status is according to OCDE (1982).

and *Parakiefferiella* spp. dominate the meso- and oligotrophic lakes.

The chironomid data-set consists of 60 taxa in 58 surface sediments. The analyses of additional subfossil samples did not yield enough head capsules for further statistical analyses. There is a statistically significant relationship between the modern chironomid assemblages and $\log_{10}$ TP, as assessed in a DCCA with $\log_{10}$ TP as the sole constraining variable. Log_{10} TP explains 9.7% of the variance in the unscreened chironomid data, whereas the second unconstrained DCA axis captures 14.3% of the variance. A two-component WA-PLS model gives a RMSEP of 0.21 and jack-knifed r^2 of 0.53. Two iterations of data-screening, identifying samples with high absolute residuals and/or high leverage values, identified ten outliers (ORI, MOO, WIL, LÄM, HAG, EGE, DIT, INK [iteration 1]; and BAN, BRT [iteration 2]). When these are deleted $\log_{10}$ TP explains 11.4% of the variance and the resulting two-component WA-PLS model has a high predictive power with a RMSEP of 0.14 and a jack-knifed r^2 of 0.68 (Table 2).

Of the 29 chironomid taxa present in 20% or more of the final screened data-set, 10 have statistically significant symmetric unimodal responses to $\log_{10}$ TP and seven have statistically significant sigmoidal responses. Twelve taxa have no statistical relationship to $\log_{10}$ TP.

Chrysophyte cysts

The chrysophyte cyst data consist of 78 taxa in 37 samples. The additional subfossil samples did not contain a high enough number of cysts to permit useful statistical analyses. The $\log_{10}$ TP constrained DCCA axis has an eigenvalue (0.184) and gradient length (1.62 SD) which are less than the first unconstrained axis (eigenvalue = 0.256, gradient length = 2.54 SD). Although $\log_{10}$ TP explains 5.4% of the variance in these data, the second unconstrained axis explains 7.4%, suggesting that the $\log_{10}$ TP relationship is weak (ter Braak, 1987–1992) and that there are large gradients in the cyst data unrelated to TP. Not surprisingly, the resulting one-component WA-PLS model has a poor predictive ability with a RMSEP of 0.24, jack-knifed r^2 of 0.18, mean bias of 0.002, and a maximum bias of 0.51. Attempts at data-screening failed to improve the predictive power of the model.

Discussion

TP concentrations are, amongst other variables, widely used in limnology to define boundaries between different trophic states (e.g. Forsberg & Ryding, 1980; OCDE, 1982). Inference models were developed for $\log_{10}$ TP for the biological data-sets because $\log_{10}$ TP explains a large and statistically significant part of the variance in the individual data-sets (between 6.2 and 3.9% of the variance in the species data, see Lotter et al., in press). Several modern training-sets for diatom – TP inference have been described from Europe and North America (see Table 3). We, therefore, decided to focus on TP as a major nutrient and to assess TP inference models for the different biological organisms. Nevertheless, we are aware that TP is a summary variable that is composed of soluble (reactive and unreactive) and particulate phosphorus fractions (e.g. Tarapchak & Nalewajko, 1986).

Diatoms

Many of the common planktonic (e.g. Vollenweider, 1950; Rosen, 1981; Kilham et al., 1986, 1996) and periphytic (e.g. Salden, 1978; Hofmann, 1994) diatoms have defined nutrient requirements and have, therefore, been used as sensitive trophic indicators. Qualitative approaches using sedimentary diatom assemblages (e.g. Bradbury, 1975) have traditionally used the occurrence of some indicator diatoms (see e.g. Lowe, 1974; De Wolf, 1982; van Dam et al., 1994) to interpret diatom changes in terms of nutrient enrichment. Early semi-quantitative approaches include the use of the Centrales/Pennales ratio (Nygaard, 1956) or the Araphidineae/Centrales ratio (Stockner & Benson, 1967; Stockner, 1971) to track the trophic history of a lake. The first quantitative inference models for TP used linear regression (e.g. Whitmore, 1989; Agbeti & Dickman, 1989), whereas later models took account of the non-linear unimodal relationship of diatom abundances in relation to TP. Weighted averaging (WA) and recently WA-PLS regression and calibration models have been employed (see Table 3). In comparison to these published models, our newly developed WA-PLS model for diatoms and TP compares well, as the apparent statistics are better than these statistics reported for the previously published models. With its high jack-knifed r^2 (0.79) as well as a low RMSEP (0.19, see Table 2) our model has high predictive power. Our model encompasses a larger TP gradient (6–520 μg TP l^{-1}) than most of the North American models. The integration of well-dated sediment samples with known water chemistry helps to extend the gradient of interest and helps to reduce the problems of truncated species distributions near the ends of the environment gradient for some species.

Besides TP, however, other factors such as basin morphometry, mixing, light, grazing, and the availability of other nutrients such as silica, nitrogen, and carbon are also important for the distribution of diatoms. Indirect effects of increased TP concentrations on diatoms may also include a rise in pH and alkalinity through enhanced aquatic productivity. Furthermore, diatom growth may be affected by interspecific competition (see also Kilham et al., 1986, 1996), as well as inhibition through other algae by shading, allelopathy (Keating, 1978), or nutrient competition (Tilman et al., 1986).

Cladocera

Apart from pH (Krause-Dellin & Steinberg, 1986), summer temperatures (Lotter et al., 1997a), and salinity (Bos 1996; Bos et al., 1996), cladocera have so far not been used as quantitative environmental indicators. In palaeolimnological studies the succession of planktonic cladocera, from *Bosmina longispina* to *B. longirostris* or from *B. longispina* to *B. coregoni* (or *B. kessleri*) dominated assemblages are commonly interpreted as a change from nutrient-poor to nutrient-rich conditions (e.g. Frey, 1969, 1988; Boucherle & Züllig, 1983; Hofmann, 1987, 1990). However, changes from large planktonic forms to smaller ones (*Daphnia* → *B. longispina* → *B. longirostris*) may also be controlled by fish and copepod predation (Brooks & Dodson, 1965; Zaret & Kerfoot, 1975; Stenson,

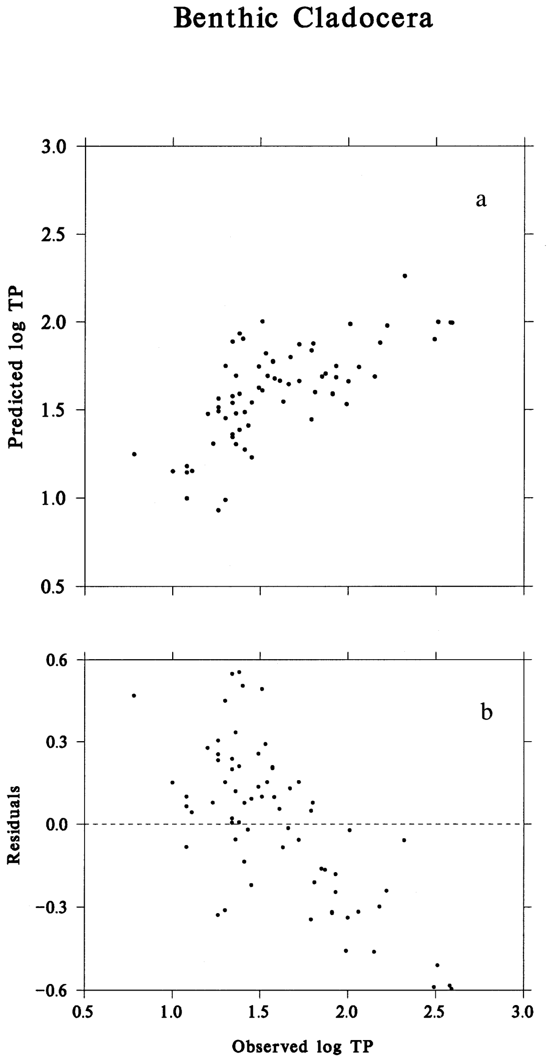

Figure 5. Benthic Cladocera (chydorids) – $\log_{10}$TP training-set: (a) plot of predicted $\log_{10}$TP against observed $\log_{10}$TP based on a 1-component WA-PLS model, and (b) plot of residuals (predicted – observed) against observed $\log_{10}$TP.

1976; Kerfoot, 1978). Jeppesen et al. (1996), in a recent study on planktivorous fish and trophic structure in Danish lakes, concluded that the influence of TP on planktonic cladocerans is insignificant, which agrees well with our results. Harmsworth & Whiteside (1968) found decreasing chydorid species diversity with increasing primary production in lakes, whereas Crisman & Whitehead (1978) discovered a marked response of planktonic cladocera to changes in primary production.

On the basis of 80 Danish lakes, Whiteside (1969, 1970) categorized the surface-sediment cladocera assemblages into three groups of lakes: oligotrophic clear-water lakes; dystrophic brown-water lakes (bog lakes); and polluted lakes. He also found that the oligotrophic lakes had the highest number of cladoceran species, whereas *Alona rectangula* and *Chydorus sphaericus* preferred nutrient-enriched lakes. A similar study in North American lakes was carried out by Synerholm (1979). The ecological groups of chydorids established by Whiteside (1970) have been confirmed for lakes in northern Germany (Hofmann, 1996) and were used in palaeoecological studies to explain long-term changes in the littoral zone (Hofmann, 1986a, submitted; Korhola, 1990).

The use of *Bosmina* taxa as trophic indicators is affected by the strong predominance of *Bosmina longirostris* in the data-set. It was present in 61 lakes and made up more than 80% of the planktonic remains in 39 lakes and more than 50% in 50 lakes, while the oligotrophic *B. longispina* is represented by only four occurrences which were restricted to altitudes above 1690 m a.s.l. *B. longirostris* is indicative of eutrophic conditions only when it occurs alone or together with other eutrophic species (such as *B. coregoni*). It is not generally excluded from oligotrophic waters, where it may occur together with *B. longispina* (Frey, 1988). *B. longirostris* is over represented in the data-set due to the exclusion of large water bodies. The indicative potential of the *Bosmina* taxa is also limited as they include two forms of uncertain taxonomic status and unknown ecological preferences, namely *Bosmina* sp. A (‘long mucro’) and *Bosmina* sp. B (‘short mucro’), found in 18 and 19 lakes, respectively. The major part (86%) of these occurrences originates from sites below 700 m altitude.

Chironomids

Chironomids have traditionally been used to classify lakes according to their hypolimnetic oxygen levels (Brundin, 1956; Sæther, 1979; Hofmann, 1986b, 1988) which are related to trophic state and basin morphometry. However, food availability is likely also to be important, particularly in defining the lower trophic limit of species (Wiederholm, 1984; Lindegaard, 1995). Taxa of the *Tanytarsus lugens*-community (Brundin, 1956) are indicative of well-oxygenated conditions, whereas *Chironomus* taxa indicate oxygen-poor situations. Accordingly, Walker (1995) predicted an increase in *Chironomus* spp. with eutrophication. Jonasson (1969) states that amongst chironomids

C. anthracinus is best adapted to low oxygen, but as it does not feed at low oxygen concentrations, this will result in a slow or negligible growth of their larvae. Sæther (1979) attributed many chironomids to specific trophic states and Wiederholm (1980) found a good correlation between TP/mean lake depth and a benthic quality index using seven chironomid indicator taxa. Recently, in connection with diatom and geochemical analyses, Walker et al. (1993) used chironomids to reconstruct eutrophication-related changes in a Canadian lake.

Quantitative inference models have related the distribution of chironomids primarily to climatic variables such as summer surface-water or air temperatures (e.g. Walker et al., 1991; Lotter et al., 1997a; Olander et al., 1997). Furthermore, they are also useful as palaeosalinity indicators (Walker et al., 1995), and a model has been developed for inferring hypolimnetic O_2 conditions (Quinlan et al., in press).

The concentration of chironomid remains in the surficial profundal sediments of the investigated lakes is highly dependent on the hypolimnetic oxygen content (Schmäh, 1993). Eutrophic and hypertrophic lakes with hypolimnetic oxygen depletion have either no head capsules or very low head-capsule concentrations in their sediments, a phenomenon well known in the chironomid literature (e.g. Wiederholm & Eriksson, 1979; Kansanen, 1985; Walker et al., 1993). The profundal assemblages are often dominated by taxa washed in from the littoral zone (Schmäh, 1993). There is therefore a strong indirect influence of trophic state on deepwater chironomid assemblages via the availability of oxygen (Hofmann, 1988). Profundal oxygen concentrations are also, in part, a function of basin morphometry. The *Tanytarsus lugens*-community can thus persist in the profundal zone of large, deep lakes better than in shallower lakes of similar productivity (Sæther, 1980). The hypolimnion of large, deep lakes is likely to exhibit less oxygen depletion.

Succession from a *Tanytarsus lugens*-community to a *Chironomus* assemblage in the profundal zone as a response to eutrophication has been observed in several studies from different temperate regions (e.g. Hofmann, 1971; Wiederholm & Eriksson, 1979; Warwick, 1980; Günther, 1983; Kansanen, 1985). Habitat structure and ecological conditions in the littoral zone are more variable and complex than in the profundal region. Therefore, it is difficult to detect clear relationships between the trophic state of a lake and the structure of its littoral chironomid community (Bayerisches Landesamt für Wasserwirtschaft, 1993).

Chrysophytes

Despite some recent advances in cyst identification, such as the introduction of a standardized terminology (Cronberg & Sandgren, 1986) and the publication of an atlas of chrysophycean cysts (Duff et al., 1995), cyst taxonomy is based on morphotype description. A number of morphotypes, in particular those lacking specific ornamentation, may be produced by several species. Moreover, the same species can produce different types of cysts according to sexual or asexual cyst formation, genetic differences, or environmental conditions (e.g., Sandgren, 1981, 1983). These factors as well as the fact that only a few cyst morphotypes have been linked to the taxa that produce them hamper the use of chrysophyte cysts for palaeolimnological inferences.

Although in recent years chrysophytes have mainly been used in palaeolimnology to study lake acidification (e.g., Duff & Smol, 1991; Cumming et al., 1991; Rybak et al., 1991; Marchetto & Lami, 1994; Facher & Schmidt, 1996), or changes in salinity (e.g. Cumming et al., 1993), they have for a long time been recognized as important potential indicators of environmental conditions, such as trophic status (for reviews, see Cronberg, 1986; Smol, 1995). To avoid problems arising from morphological classification of chrysophycean cysts, Smol (1985) proposed the use of a ratio between chrysophyte cysts and diatom valves (C/D) to trace past changes in lake trophic status. Chrysophytes are generally considered indicators of cool, nutrient-poor waters (Rosen, 1981; Sandgren, 1988). Nevertheless, chrysophyte cysts have not always to be considered oligotrophic indicators. In Frains Lake (Michigan), Carney (1982) and Carney & Sandgren (1983) found a decline in the C/D ratio and an increase in cyst accumulation rate in relation to lake eutrophication, when the diatom flora shifted from *Cyclotella* to *Stephanodiscus* dominance. In a sediment study Zeeb et al. (1994) found that chrysophyte cysts responded without lag to experimental lake eutrophication, whereas diatoms and chrysophyte scales showed a lag of 2–3 years. They, therefore, concluded that cysts track short-term changes in water chemistry.

In the lakes considered in the present study, the C/D ratios are significantly related (Kendall test, $p<0.01$) to altitude and, negatively, to temperature, alkalinity, conductivity, and total nitrogen concentration. However, these relations are too weak to be used for reliable palaeoenvironmental reconstructions (Lotter et al., in press). The relationship between C/D and temperature was only significant when a parametric model was used with the original data or after logarithmic transformation. The cyst assemblages are generally dominated by unornamented cysts, either with or without collar. Most of these types were grouped into counting units because they often cannot be attributed to a species. Moreover, several chrysophytes may produce the same cyst types. As a consequence their distribution covers the whole TP gradient (collective categories 49–120; 146–156; 53–152–198–234) or is limited to lakes with TP concentrations below 50 μg l^{-1} (type 29 and collective categories 50–51–52–110; 1–148; 127; 183). Also distributed along the whole TP gradient are the types 76 and 171 (large cysts ornamented with spines and indentation), the collective category 158–164 (cysts ornamented with verrucae), and, surprisingly, the collective category 33–222 (small cysts with short ridges), which is reported as most common in deep oligotrophic lakes (Duff et al., 1995). Small cysts with long spines (collective category 114–115–218), which are considered typical for productive lakes, are restricted in our training-set to lakes with TP concentrations between 10 and 50 μg l^{-1}. This range represents the lower part of the TP gradient in our data-set, but is higher than the TP levels where most chrysophytes generally develop. Common cysts with defined preferences for characteristic trophic levels are types 88, 133, and 205 (restricted to lakes with TP concentrations of 10–20 μg l^{-1}), 153 (found in lakes with TP concentrations of 20–50 μg l^{-1}), and the types 41, 58–118, 116, 180, 189, and 214 (in lakes with TP concentrations higher than 50 μg l^{-1}).

In our surface-sediment training-set, the quantitative relationship between chrysophyte cyst assemblages and TP concentration is rather poor. This may be related to the small number of lakes with cysts in sufficient quantity to obtain reliable counts, and to the resulting short TP gradient that is biased towards mesotrophic to eutrophic lakes. Surprisingly, out of the 37 lakes with a high enough C/D ratio none are oligotrophic (0–10 μg TP l^{-1}) according to OCDE (1982) standards, but are mesotrophic (10–35 μg TP l^{-1}) (56.8%) or eutrophic (40.5%). On the other hand, out of the 41 lakes having a very low C/D ratio, only 2.6% are oligotrophic. The low cyst numbers in the modern training-set of this study may indicate that these lakes are already too enriched in nutrients for chrysophytes to be competitive.

Finally, the data-set presented here comprises both high mountain and lower altitude lakes, and may include some additional and unmeasured environmental gradients, such as the stability of thermal stratification, the length of the growing season (Smol, 1985), and the availability of organic material for phagotrophy (Sanders et al., 1985), all of which may be important variables for the development of the chrysophyte flora.

General discussion

Phosphorus has been identified as one of the limiting elements for phytoplankton biomass. TP values in lakes show a distinct annual cyclicity (Gibson et al., 1996). In contrast to other studies (e.g. Bennion, 1994; Anderson & Odgaard, 1994), the lakes in our modern surface sediment training-set show their highest TP concentrations during the circulation period which generally takes place during early spring. We have taken these values as the basis for our inference models because they are the maximum values available for the spring diatom growth (Lund, 1969) that may represent a substantial part of the phytoplankton biomass.

Although there are distinct changes in the composition of the investigated aquatic organisms along the sampled TP gradient, their relationship to TP is weaker than it is to temperature (Lotter et al., 1997a). According to the gradient lengths of the second, unconstrained axes, TP is a strong gradient for diatoms, whereas it is weaker for benthic cladocera and chironomids (Table 2), and is very weak for planktonic cladocera and chrysophytes. For these biota, there are clearly secondary gradients that are more important than TP, such as temperature, conductivity, alkalinity, or DOC (see Table 1, and Lotter et al., 1997a, Table 2). This is also evident in the relatively high number of benthic cladocera and, particularly, of chironomid taxa that show no statistically significant relationship to TP (Table 2).

The residuals of the diatom, benthic cladocera, and chironomid WA-PLS inference models for TP all show an over-estimation at the low end and an under-estimation at the high end of the gradient (Figures 3, 5, 7). The reasons for this bias are discussed by Lotter et al. (1997a). This inherent bias in WA-PLS based models has consequences for TP reconstructions: very low TP values will be over-estimated, whereas very high TP concentrations may be under-estimated. There is also considerable scatter in the middle part of the TP gradient (Figures 3, 5, 7) that may be related to the interannual variability in the TP data (e.g. Catalan & Fee, 1994). The low end as well as the very high end of the TP gradient includes very few sites in our training-set. By extending the training-set to include more oligotrophic and hypertrophic lakes, both ends

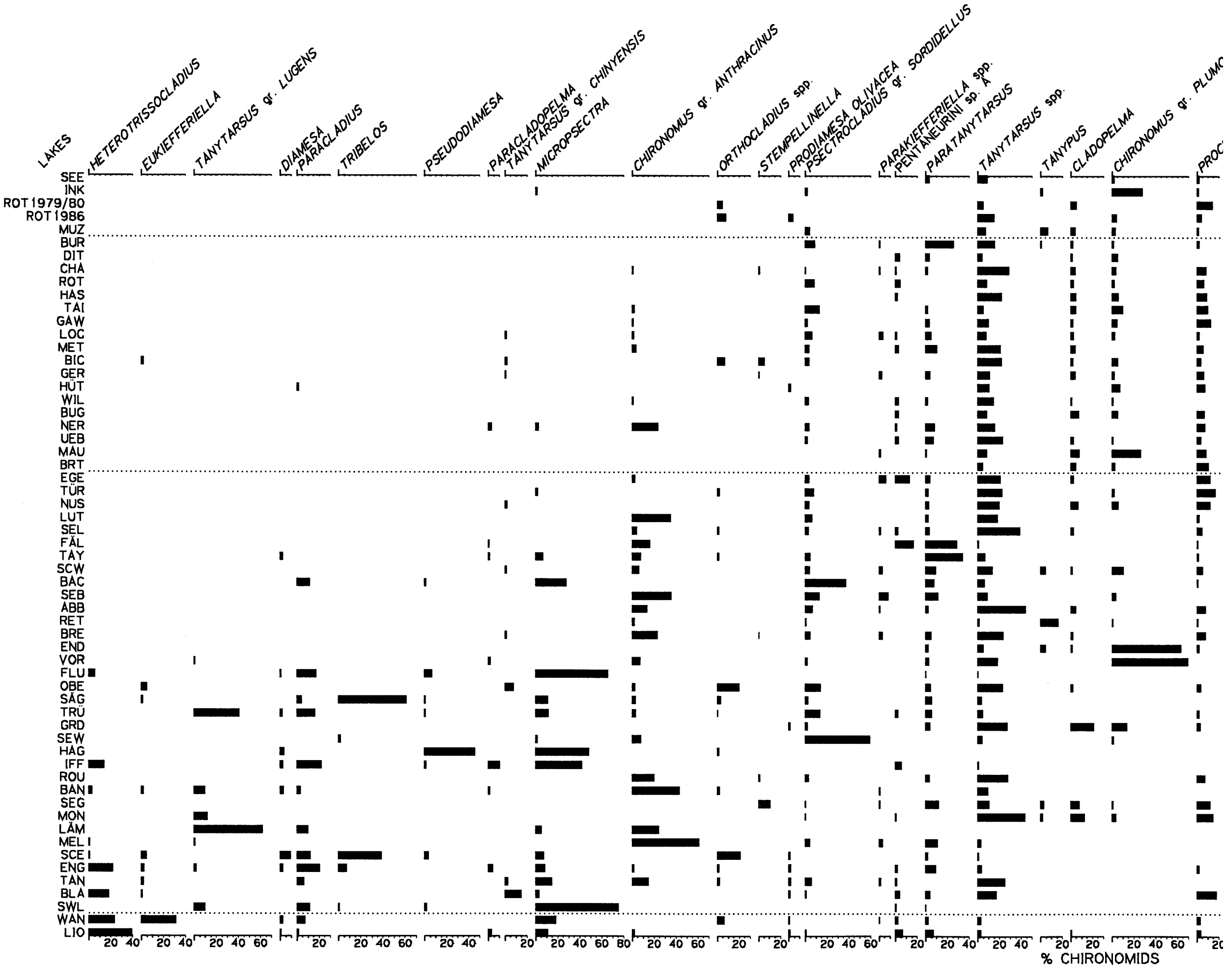

Figure 6. Distribution of chironomids along the TP gradient. Only selected taxa are shown. Classification of trophic status is according to OCDE (1982).

of the gradient would have a stronger basis and the model might potentially predict more reliable values at the extreme ends of the gradient.

The RMSEP of all the different models are very small due to the $\log_{10}$ transformation of the TP values. After back transformation the errors range between 1.55 (diatoms) and 1.91 μg TP l^{-1} (benthic cladocera). Given the high annual and interannual variability in epilimnetic TP concentrations, these errors as well as any sample-specific reconstruction errors are serious underestimates of the total variability in epilimnetic TP concentrations. However, WA-PLS models presented here are solely for mean TP for the circulation period.

Conclusions

The surface-sediment assemblages used in this study show strong relationships between TP concentrations during the circulation period and diatoms and, to a lesser degree, benthic cladocera and chironomids. These relationships permit the use of these biota in TP inference models. The majority of the taxa occurring in at least 20% of the samples in the individual training-sets have statistically significant relationships to TP (78.1% diatoms; 72.2% benthic cladocera; 58.6% chironomids). Planktonic cladocera and chrysophytes show

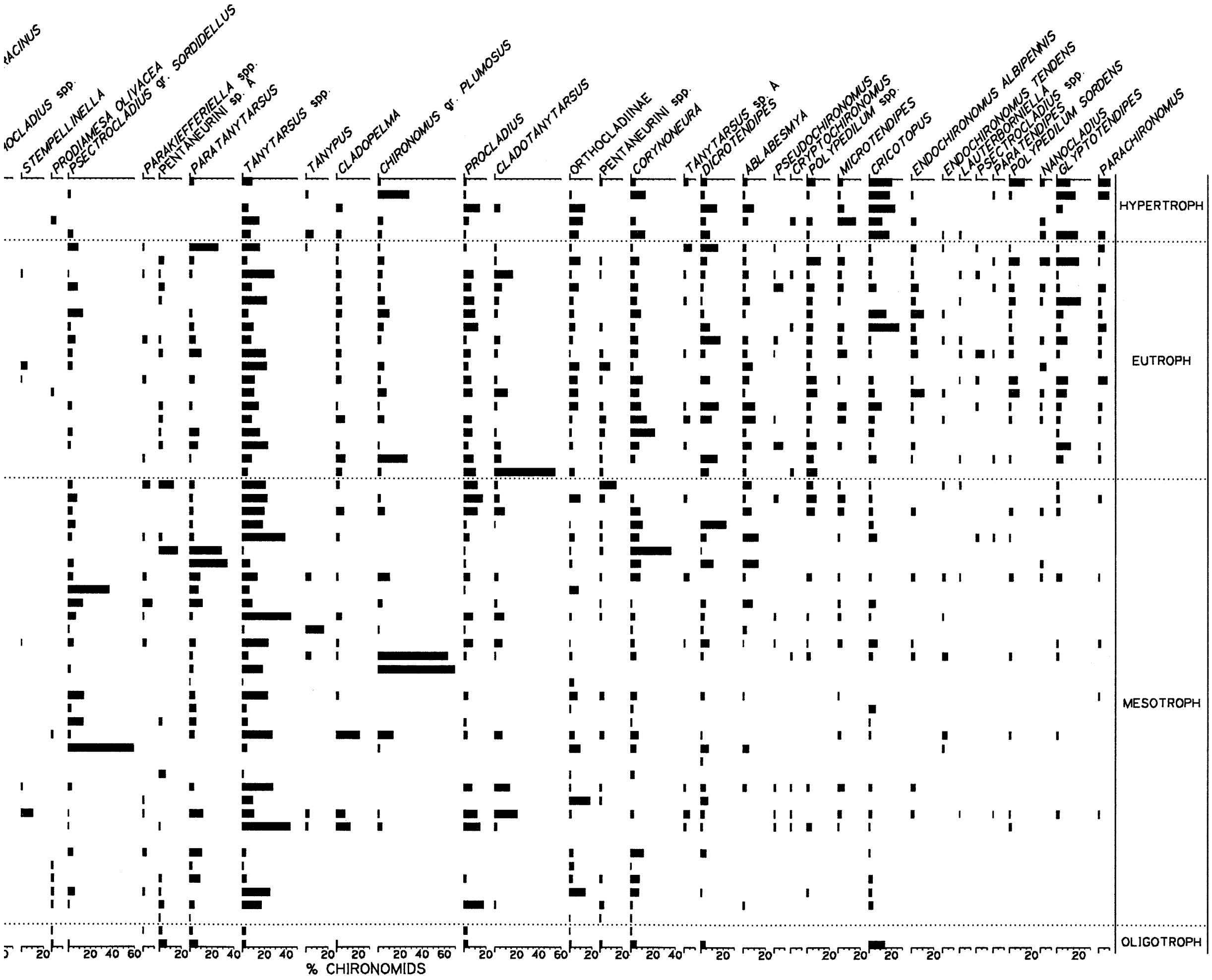

Figure 6. Continued

a very weak relationship to TP and have, therefore, not been used for developing TP inference models.

The diatom – TP inference model shows the highest predictive power, as has also been shown in several other investigations. Multy-proxy approaches using a combination of independent biota-inferred TP reconstructions may provide a more reliable estimation of past trophic lake status than the traditionally used indicator species or single biota approach.

According to our results TP, which may be regarded as a summary variable for trophic status, is a less important variable for explaining, in a statistical sense, the abundance of different taxa than the climatic variables in our data-set (Lotter et al., 1997a). This may well be related to the fact that climate is a major driving agent for aquatic ecosystems which is itself significantly influencing lake productivity and trophic status.

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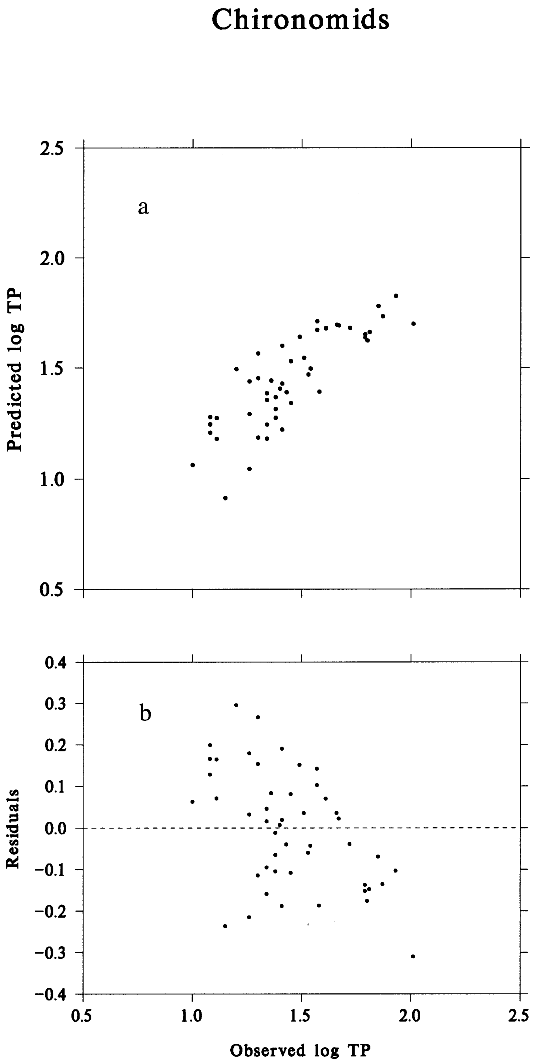

Figure 7. Chironomid – $\log_{10}$TP training-set: (a) plot of predicted $\log_{10}$TP against observed $\log_{10}$TP based on a 2-component WA-PLS model, and (b) plot of residuals (predicted – observed) against observed $\log_{10}$TP.

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References

Agbeti, M. D., 1992. Relationship between diatom assemblages and trophic variables: a comparison of old and new approaches. Can. J. Fish. aquat. Sci. 49: 1171–1175.

Agbeti, M. & M. Dickman, 1989. Use of lake fossil diatom assemblages to determine historical changes in trophic status. Can. J. Fish. aquat. Sci. 46: 1013–1021.

Anderson, N. J., 1993. Natural versus anthropogenic change in lakes: the role of the sediment record. Trends in Ecology and Evolution 8: 356–361.

Anderson, N. J., 1995. Naturally eutrophic lakes: reality, myth or myopia? Trends in Ecology and Evolution 10: 137–138.

Anderson, N. J. & B. V. Odgaard, 1994. Recent palaeolimnology of three shallow Danish lakes. Hydrobiologia 275/276: 411–422.

Anderson, N. J. & B. Rippey, 1994. Monitoring lake recovery from point-source eutrophication: the use of diatom-inferred epilimnetic total phosphorus and sediment chemistry. Freshwat. Biol. 32: 625–639.

Anderson, N. J., B. Rippey & C. E. Gibson, 1993. A comparison of sedimentary and diatom-inferred phosphorus profiles: implications for defining pre-disturbance nutrient conditions. Hydrobiologia 253: 357–366.

Bayerisches Landesamt für Wasserwirtschaft (ed.), 1993. Biologische Trophieindikation im Litoral von Seen. Materialien 31: 1–173.

Bennion, H., 1994. A diatom-phosphorus transfer function for shallow, eutrophic ponds in southeast England. Hydrobiologia 275/276: 391–410.

Bennion, H., S. Wunsam & R. Schmidt, 1995. The validation of diatom-phosphorus transfer functions: an example from Mondsee, Austria. Freshwat. Biol. 34: 271–283.

Bennion, H., T. E. H. Allott, D. T. Monteith, C. A. Duigan, E. Y. Haworth, N. J. Anderson & S. Juggins, 1996a. The Anglesey lakes, Wales, UK: changes in trophic status of three standing waters as inferred from diatom transfer functions and their implications for conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 6: 81–92.

Bennion, H., S. Juggins & N. J. Anderson, 1996b. 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. H., 1980. Plant macrofossils in Quaternary lake sediments. Archiv für Hydrobiologie Beiheft, 15: 1–60.

Birks, H. J. B., 1994. The importance of pollen and diatom taxonomic precision in quantitative palaeoenvironmental reconstructions. Rev. 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. Technical Guide 5, Quat. Res. Assoc., Cambridge: 161–254.

Bos, D. G., 1996. Cladocera and anostraca as paleolimnological indicators of lake-water conductivity. M. Sci. Thesis, Queen's University, Kingston: 73 pp.

Bos, D. G., B. F. Cumming, C. E. Watters & J. P. Smol, 1996. The relationship between zooplankton, conductivity and lake-water ionic composition in 111 lakes from the Interior Plateau of British Columbia, Canada. Int. J. Salt Lake Res. 5: 1–15.

Boucherle, M. M. & H. Züllig, 1983. Cladoceran remains as evidence of change in trophic state in three Swiss lakes. Hydrobiologia 103: 141–146.

Bradbury, J. P., 1975. Diatom stratigraphy and human settlement in Minnesota. Geol. Soc. Am. Spec. 171: 1–69.

Brenner, M. & M. W. Binford, 1988. Relationship between concentration of sedimentary variables and trophic state in Florida lakes. Can. J. Fish. aquat. Sci. 45: 294–300.

Brooks, J. L. & S. I. Dodson, 1965. Predation, body size, and composition of plankton. Science 150: 28–35.

Brundin, L., 1956. Die bodenfaunistischen Seetypen und ihre Anwendung auf die Südhalbkugel. Rep. Inst. Freshwat. Res. Drottningholm 37: 186–235.

Carney, H. J., 1982. Algal dynamics and trophic interactions in the recent history of Frains Lake, Michigan. Ecology 63: 1814–1826.

Carney, H. J. & C. D. Sandgren, 1983. Chrysophycean cysts: indicators of eutrophication in the recent sediments of Frains Lake, Michigan, USA. Hydrobiologia 101: 195–202.

Catalan, J. & E. J. Fee, 1994. Interannual variability in limnic ecosystems: origin, patterns, and predictability. In Margalef, R. (ed.), Limnology now: a paradigm of planetary problems. Elsevier Science B.V. 81–97.

Christie, C. E. & J. P. Smol, 1993. Diatom assemblages as indicators of lake trophic status in southeastern Ontario lakes. J. Phycol. 29: 575–586.

Crisman, T. L. & D. R. Whitehead, 1978. Paleolimnological studies on small New England (USA) ponds. Part II. Cladoceran community response to trophic oscillations. Pol. Arch. Hydrobiol. 25: 75–86.

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.

Cronberg, G. & C. D. Sandgren. 1986. A proposal for the development of standardized nomenclature and terminology for chrysophycean statospores. In Kristiansen, J. & R. A. Andersen (eds), Chrysophytes: aspects and problems, Cambridge University Press, Cambridge: 317–328.

Cumming, B. F., J. P. Smol & H. J. B. Birks, 1991. The relationship between sedimentary chrysophyte scales (Chrysophyceae and Synurophyceae) and limnological characteristics in 25 Norwegian lakes. Nord. J. Bot., 11: 231–242.

Cumming, B. F., S. E. Wilson & J. P. Smol. 1993. Paleolimnological potential of chrysophyte cysts and scales, and sponge spicules as indicators of lake salinity. Int. J. Salt Lake Res. 2: 87–92.

De Wolf, H., 1982. Method of coding of ecological data from diatoms for computer utilization. Med. Rijks Geol. Dienst 36: 95–98.

Dixit, S. S. & J. P. Smol, 1994. Diatoms as indicators in the environmental monitoring and assessment program-surface waters (EMAP-SW). Environmental Monitoring and Ass. 31: 275–306.

Duff, K. E. & J. P. Smol. 1991. Morphological description and stratigraphic distributions of the chrysophycean stomatocysts from a recently acidified lake (Adirondack Park, N.Y.). J. Paleolim. 5: 73–113.

Duff, K. E., B. A. Zeeb & J. P. Smol, 1995. Atlas of Chrysophycean cysts. Kluwer Academic Press, Dordrecht, The Netherlands, 189 pp.

Engstrom, D. R., E. B. Swain & J. C. Kingston, 1985. A palaeolimnological record of human disturbance from Harvey's Lake, Vermont: geochemistry, pigments and diatoms. Freshwat. Biol. 15: 261–288.

Facher, E. & R. Schmidt, 1996. A siliceous chrysophycean cyst-based pH transfer function for Central European lakes. J. Paleolim. 16: 275–321.

Forsberg, C. & S.-O. Ryding, 1980. Eutrophication parameters and trophic indices in 30 Swedish waste-receiving lakes. Arch. Hydrobiol. 89: 189–207.

Frey, D. G., 1969. Evidence for eutrophication from remains of organisms in sediments. In Eutrophication: Causes, consequences, correctives. Academy of Natural Sciences, Washington D.C.: 594–613.

Frey, D. G., 1988. Littoral and offshore communities of diatoms, cladocerans and dipterous larvae, and their interpretation in paleolimnology. J. Paleolim. 1: 179–191.

Fritz, S. C., J. C. Kingston & D. R. Engstrom, 1993. Quantitative trophic reconstruction from sedimentary diatom assemblages: a cautionary tale. Freshwat. Biol. 30: 1–23.

Gibson, C. E., R. H. Foy & A. E. Bailey-Watts, 1996. An analysis of the total phosphorus cycle in some temperate lakes: the response to enrichment. Freshwat. Biol. 35: 525–532.

Günther, J., 1983. Development of Grossensee (Holstein, Germany): variations in trophic status from the analysis of subfossil microfauna. Hydrobiologia 103: 231–234.

Håkanson, L., 1992. Considerations on representative water quality data. Int. Revue ges. Hydrobiol., 77: 497–505.

Hall, R. I. & J. P. Smol, 1992. A weighted-averaging regression and calibration model for inferring total phosphorus concentration from diatoms in British Columbia (Canada) lakes. Freshwat. Biol. 27: 417–434.

Hall, R. I. & J. P. Smol, 1996. Paleolimnological assessment of long-term water-quality changes in south-central Ontario lakes affected by cottage development and acidification. Can. J. Fish. aquat. Sci. 53: 1–17.

Harmsworth, R. V. & M. C. Whiteside, 1968. Relation of cladoceran remains in lake sediments to primary productivity of lakes. Ecology 49: 998–1000.

Hill, M. O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427–432.

Hofmann, G., 1994. Aufwuchs-Diatomeen in Seen und ihre Eignung als Indikatoren der Trophie. Bibliotheca Diatomologica 30: 1–241.

Hofmann, W., 1971. Die postglaziale Entwicklung der Chironomiden- und *Chaoborus*-Fauna (Dipt.) des Schöhsees. Arch. Hydrobiol. 40: 1–74.

Hofmann, W., 1986a. Developmental history of the Großer Plöner See and the Schöhsee (north Germany): cladoceran analysis, with special reference to eutrophication. Arch. Hydrobiol. 74: 259–287.

Hofmann, W., 1986b. 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 145: 315–321.

Hofmann, W., 1988. The significance of chironomid analysis (Insecta: Diptera) for paleolimnological research. Palaeogeogr., Palaeoclimatol., Palaeoecol. 62: 501–509.

Hofmann, W., 1990. Sukzession der Cladoceren- und Chironomidenfauna im Spät- und Postglazial als Reaktion auf Änderungen des Trophiegrades im Untersee (Kern US 8707). Ber. Röm.-German. Kommission 71: 286–292.

Hofmann, W., 1996. Empirical relationships between cladoceran fauna and trophic state in thirteen northern German lakes: analysis of surficial sediments. Hydrobiologia 318: 195–201.

Hofmann, W. Late-Glacial/Holocene succession of the chironomid and cladoceran fauna of Soppensee (Central Switzerland). J. Paleolim. submitted.

Huisman, J., H. Olff & L. F. M. Fresco, 1993. A hierarchical set of models for species response models. J. Veg. Sci. 4: 37–46.

Jeppesen, E., E. A. Madsen, J. P. Jensen & N. J. Anderson, 1996. Reconstructing the past density of planktivorous fish and trophic structure from sedimentary zooplankton fossils: a surface sediment calibration data set from shallow lakes. Freshwat. Biol. 36: 115–127.

Jonasson, P. M., 1969. Bottom fauna and eutrophication. Eutrophication: causes, consequences and correctives. National Academy of Sciences, Washington D.C.: 274–305.

Kansanen, P. H., 1985. Assessment of pollution history from recent sediments in Lake Vanajavesi, southern Finland. II. Changes in the Chironomidae, Chaoboridae and Ceratopogonidae (Diptera) fauna. Ann. Zool. Fenn. 22: 57–90.

Keating, K. I., 1978. Blue-green algal inhibition of diatom growth: transition from mesotrophic to eutrophic community structure. Science 199: 971–973.

Kerfoot, W. C., 1978. Combat between copepods and their prey: *Cyclops, Epischura* and *Bosmina*. Limnol. Oceanogr. 23: 1098–1103.

Kilham, P., S. S. Kilham & R. E. Hecky, 1986. Hypothesized resource relationship among African planktonic diatoms. Limnol. Oceanogr. 31: 1169–1181.

Kilham, S. S., E. C. Theriot & S. C. Fritz, 1996. Linking planktonic diatoms and climate in the large lakes of the Yellowstone ecosystem using resource theory. Limnol. Oceanogr. 41: 1052–1062.

Kolkwitz, R., 1950. Ökologie der Saprobien. Über die Beziehungen der Wasserorganismen zur Umwelt. Schriftenreihe Verein für Wasser-, Boden- und Lufthygiene 4: 64 pp.

Korhola, A., 1990. Paleolimnology and hydroseral development of the Kotasuo bog, southern Finland, with special reference to the Cladocera. Ann. Acad. Sci. Fenn. Ser. A 155: 1–40.

Krause-Dellin, D. & C. Steinberg, 1986. Cladocera remains as indicators of lake acidification. Hydrobiologia 143: 129–134.

Krause, W., 1981. Characeen als Bioindikatoren für den Gewässerzustand. Limnologica 13: 399–418.

Lange-Bertalot, H., 1978. Diatomeen-Differentialarten anstelle von Leitformen: Ein geeignetes Kriterium der Gewässerbelastung. Arch. Hydrobiol. 51: 393–427.

Lange-Bertalot, H., 1979. Pollution tolerance of diatoms as a criterion for water quality estimation. Nova Hedwigia Beiheft 64: 285–304.

Likens, G. E., 1972. Eutrophication and aquatic ecosystems. In Likens, G. E. (ed.), Nutrients and eutrophication: the limiting-nutrient controversy. ASLO, Lawrence, Kansas: 3–13.

Lindegaard, C., 1995. Classification of water-bodies and pollution. In Armitage, P. D., P. S. Cranston & L. C. V. Pinder (eds), The Chironomidae: Biology and ecology of non-biting midges. Chapman & Hall, London. 385–404.

Lotter, A., 1988. Paläoökologische und paläolimnologische Studie des Rotsees bei Luzern. Pollen-, grossrest-, diatomeen- und sedimentanalytische Untersuchungen. Diss. Bot. 124: 1–187.

Lotter, A. F., 1989. Subfossil and modern diatom plankton and the paleolimnology of Rotsee (Switzerland) since 1850. Aquat. Sci. 51: 338–350.

Lotter, A. F. The recent eutrophication of Baldeggersee (Switzerland) as assessed by fossil diatom assemblages. The Holocene, in press.

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

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

Lowe, R., 1974. Environmental requirements and pollution tolerances of freshwater diatoms. EPA-67014-74-005, US EPA.

Lund, J. W. G., 1969. Phytoplankton. Eutrophication: causes, consequences, correctives. National Academy of Sciences, Washington D.C.: 306–330.

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

Marchetto, A. & A. Lami, 1994. Reconstruction of pH by chrysophycean scales in some lakes of the southern Alps. Hydrobiologia 274: 83–90.

Müller, B., A. F. Lotter, M. Sturm & A. Ammann, The influence of catchment and geographic location on the water and sediment composition of 68 small circumalpine lakes. Aquatic Sciences, in press.

Nygaard, G., 1956. Ancient and recent flora of diatoms and Chrysophycea in Lake Gribsø. Folia Limnologica Scandinavica 8: 50–62.

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

Olander, H., A. Korhola & T. Blom, 1997. Surface sediment Chironomidae (Insecta: Diptera) distributions along an ecotonal transect in subarctic Fennoscandia: developing a tool for palaeotemperature reconstructions. J. Paleolim. 18: 45–59.

Prentice, I. C., 1980. Multidimensional scaling as a research tool in Quaternary palynology: a review of theory and methods. Rev. Palaeobot. Palynol. 31: 71–104.

Quinlan, R., J. P. Smol & R. I. Hall, Quantitative inferences of past hypolimnetic anoxia in south-central Ontario lakes using fossil midges (Diptera: Chironomidae). Can. J. Fish. aquat. Sci., in press.

Rast, W. & M. Holland, 1988. Eutrophication of lakes and reservoirs: a framework for making management decisions. Ambio 17: 2–12.

Reavie, E. D., R. I. Hall & J. P. Smol, 1995. An expanded weighted-averaging model for phosphorus concentrations from diatom assemblages in eutrophic British Columbia (Canada) lakes. J. Paleolim. 14: 49–67.

Rippey, B. & N. J. Anderson, 1996. Reconstruction of lake phosphorus loading and dynamics using the sedimentary record. Envir. Sci. Technol. 30: 1786–1788.

Rosen, G., 1981. Phytoplankton indicators and their relations to certain chemical and physical factors. Limnologica 13: 263–290.

Rybak, M., I. Rybak & K. Nicholls. 1991. Sedimentary chrysophycean cyst assemblages as paleoindicators in acid sensitive lakes. J. Paleolim. 5: 19–72.

Sæther, O. A., 1979. Chironomid communities as water quality indicators. Holarctic Ecology, 2: 65–74.

Sæther, O. A., 1980. The influence of eutrophication on deep lake benthic invertebrate communities. Prog. Water Technol. 12: 161–180.

Salden, N., 1978. Beitrag zur Ökologie der Diatomeen (Bacillariophyceae) des Süsswassers. Dechenia Beihefte 22: 1–238.

Sanders, R. W., K. G. Porter & R. J. McDomough. 1985. Bacterivory by ciliates, microflagellates and mixotrophic algae: factors influencing particle ingestion. EOS, 66: 1314.

Sandgren, C. D., 1981. Characteristics of sexual and asexual resting cyst (statospore) formation in *Dinobryon cylindricum* Imhof (Chrysophyceae, Chrysophicota). Protistologica 16: 259–276.

Sandgren, C. D., 1983. Morphological variability in populations of chrysophycean resting cysts. I. Genetic (interclonal) and encystment temperature effects on morphology. J. Phycol. 19: 64–70.

Sandgren, C. D., 1988. The ecology of chrysophyte flagellates: their growth and perennation strategies as freshwater phytoplankton. In Sandgren, C. D. (ed.), Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press, Cambridge: 9–104.

Schelske, C. L., D. J. Conley, E. F. Stoermer, T. L. Newberry & C. D. Campbell, 1986. Biogenic silica and phosphorus accumulation in sediments as indices of eutrophication in the Laurentian Great Lakes. Hydrobiologia 143: 79–86.

Schindler, D. W., 1987. Detecting ecosystem response to anthropogenic stress. Can. J. Fish. aquat. Sci. 44: 6–25.

Schmäh, A., 1993. Variation among fossil chironomid assemblages in surficial sediments of Bodensee-Untersee (SW-Germany): implications for paleolimnological interpretation. J. Paleolim. 9: 99–108.

Smol, J. P., 1985. The ratio of diatom frustules to chrysophycean statospores: a useful paleolimnological index. Hydrobiologia 123: 199–208.

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.

Stenson, J. A. E., 1976. Significance of predator influence on composition of *Bosmina* spp. populations. Limnol. Oceanogr. 21: 814–822.

Stockner, J. G., 1971. Preliminary characterization of lakes in the Experimental Lakes Area, Northwestern Ontario, using diatom occurrences in sediments. J. Fish. Res. Bd Canada 28: 265–275.

Stockner, J. G. & W. W. Benson, 1967. The succession of diatom assemblages in the recent sediments of Lake Washington. Limnol. Oceanogr. 12: 513–532.

Synerholm, C. C., 1979. The chydorid cladocera fauna from surface lake sediments in Minnesota and North Dakota. Arch. Hydrobiol. 86: 137–151.

Tarapchak, S. J. & C. Nalewajko, 1986. Synopsis: phosphorus – plankton dynamics symposium. Can. J. Fish. aquat. Sci. 43: 416–419.

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

ter Braak, C. J. F., 1990. Update notes: CANOCO version 3.10. Agricultural Mathematics Group, Wageningen.

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., S. Juggins, H. J. B. Birks & H. van der Voet, 1993. Weighted averaging partial least squares regression (WA-PLS): definition and comparison with other methods for species-environment calibration. In Patil, G. P. & C. R. Rao (eds), Multivariate Environmental Statistics. Elsevier: 525–560.

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.

Tilman, D., R. Kiesling, R. Sterner, S. S. Kilham & F. A. Johnson, 1986. Green, bluegreen and diatom algae: taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. Arch. Hydrobiol. 106: 473–485.

van Dam, H., A. Mertens & J. Sinkeldam, 1994. A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. Neth. J. aquat. Ecol. 28: 117–133.

Vollenweider, R. W., 1950. Ökologische Untersuchungen von planktischen Algen auf experimenteller Grundlage. Schweiz. Z. Hydrol. 12: 193–262.

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, London: 405–422.

Walker, I. R., J. P. Smol, D. R. Engstrom & H. J. B. Birks, 1991. An assessment of Chironomidae as quantitative indicators of past climatic change. Can. J. Fish. aquat. Sci. 48: 975–987.

Walker, I. R., E. D. Reavie, S. Palmer & R. N. Nordin, 1993. A palaeoenvironmental assessment of human impact on Wood Lake, Okanagan Valley, British Columbia, Canada. Quat. Int. 20: 51–70.

Walker, I. R., S. E. Wilson & J. P. Smol, 1995. Chironomidae (Diptera): quantitative palaeosalinity indicators for lakes of western Canada. Can. J. Fish. aquat. Sci. 52: 950–960.

Warwick, W. F., 1980. Paleolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. Can. Bull. Fish. aquat. Sci. 206: 1–117.

Whitmore, T. J., 1989. Florida diatom assemblages as indicators of trophic state and pH. Limnol. Oceanogr. 34: 882–895.

Whiteside, M. C., 1969. Chydorid (Cladocera) remains in surficial sediments of Danish lakes and their significance to paleolimnological interpretations. Mitt. Int. Ver. Limnol. 17: 193–201.

Whiteside, M. C., 1970. Danish chydorid cladocera: modern ecology and core studies. Ecological Monographs 40: 79–118.

Whiteside, M. C., 1983. The mythical concept of eutrophication. Hydrobiologia 103: 107–111.

Wiederholm, T., 1980. Use of benthos in lake monitoring. J. Wat. Pollut. Control Federation 52: 537–547.

Wiederholm, T., 1984. Responses of aquatic insects to environmental pollution. In Resh, V. H. & D. M. Rosenberg (eds), The Ecology of Aquatic Insects. Praeger, New York: 508–557.

Wiederholm, T. & L. Eriksson, 1979. Subfossil chironomids as evidence of eutrophication in Ekoln Bay, central Sweden. Hydrobiologia 62: 195–208.

Wunsam, S. & R. Schmidt, 1995. A diatom-phosphorus transfer function for alpine and pre-alpine lakes. Mem. Ist. ital. Idrobiol. 53: 85–99.

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.

Zaret, T. M. & W. C. Kerfoot, 1975. Fish predation on *Bosmina longirostris*: body-size selection *versus* visibility selection. Ecology: 232–237.

Zeeb, B. A., C. E. Christie, J. P. Smol, D. L. Findlay, H. J. Kling & H. J. B. Birks, 1994. Response of diatom and chrysophyte assemblages in Lake 227 sediments to experimental eutrophication. Can. J. Fish. aquat. Sci. 51: 2300–2311.

Züllig, H., 1981. On the use of carotenoid stratigraphy in lake sediments for detecting past developments of phytoplankton. Limnol. Oceanogr. 26: 970–976.

Züllig, H., 1989. Role of carotenoids in lake sediments for reconstructing trophic history during the late Quaternary. J. Paleolim. 2: 23–40.