

Research Article

Distribution of diatoms, chironomids and cladocera in surface sediments of thirty mountain lakes in south-eastern Switzerland

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Abstract. Surface sediments from 30 mountain lakes in south-eastern Switzerland (Engadine, Grisons) were analysed for subfossil diatom, chironomid, and cladoceran assemblages. Ordination techniques were used to identify relevant physical and chemical environmental parameters that best explain the distribution of these biota in the studied lakes. Diatom assemblage composition showed a strong relationship with physical (e.g., lake depth, temperature, organic content of surface sediments) and chemical variables (e.g., lake-water pH, alkalinity, silica concentration). The greatest variance in chironomid and cladoceran assemblages is explained by dissolved organic carbon (DOC) content of lake water, temperature, and the organic content of surface sediments, all parameters which

are highly correlated with lake elevation. Increasing lake depth is reflected in diatom and cladoceran assemblages by higher percentages of planktonic species, whereas chironomid assemblages in the deep Engadine lakes are characterised by a high proportion of lotic taxa. In contrast to similar studies in the Northern and Southern Alps, subfossil assemblages in the Engadine mountain lakes showed a strong relationship with DOC, which in these weakly buffered lakes is negatively correlated with altitude. According to our findings, chironomid and cladocera remains have a considerable potential as quantitative palaeotemperature indicators in the Engadine area. This potential is somewhat weaker for diatoms which seem to be more strongly influenced by water chemistry and lake bathymetry.

Key words. Diatoms; chironomids; cladocera; mountain lakes; water chemistry; Engadine.

Introduction

Alpine and arctic lakes are increasingly affected by changing climatic and environmental conditions (Douglas et al., 1994; Saros et al., 2003; Smol et al., 2005).

As a direct consequence of the global warming trend, an increase in lake-water temperatures and reduction of ice-cover duration is occurring, as both lake-water temperatures and the spring ice break-up dates are related to ambient air temperatures (Livingstone, 1997; Livingstone and Lotter, 1998). Furthermore, these lakes are influenced by indirect effects of increasing temperature, such as reduced snow cover in the catchment, increasing weathering rates, and increasing erosion (Sommaruga-

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Wögrath et al., 1997). Moreover, airborne pollution (e.g., Wolfe et al., 2001) and other human-induced changes such as altered land-use patterns may be superimposed on climatic changes (Heiri and Lotter, 2003). In their combination, it is expected that these factors will exert a considerable influence on the physical and chemical structure of alpine and arctic lake ecosystems, and will act as substantial stressors to aquatic biota in these regions (Hinder et al., 1999; Rautio et al., 2000). However, due to the remote location of many arctic and alpine lakes and associated logistic constraints, it is often difficult to document biotic and abiotic changes on a regular monitoring basis (e.g., Battarbee et al., 2002).

Palaeolimnological techniques offer the unique opportunity to assess the lake response to historical environmental change and impacts of human activity (Anderson and Battarbee, 1994; Smol, 2002). Both abiotic and biotic proxy-indicators of past environmental conditions are preserved in lake sediments and can be analysed to reconstruct past climatic variability (Lotter et al., 1997; Bigler et al., 2002), chemical conditions (Renberg et al., 1993; Lotter, 1998; Lotter et al., 1998) and biotic assemblages in lakes (Uutula and Smol, 1996; Heiri et al., 2003). The interpretation of fossil assemblages, however, requires detailed knowledge on the modern occurrence of organisms and the relation of environmental gradients related to that distribution. A lack of ecological understanding of aquatic biota may cause considerable difficulties when interpreting fossil records in alpine and arctic areas. These alpine and arctic environments are those most important to understand, because they are particularly sensitive to global change (IPCC, 2001). There is a clear need for information on how climate changes have affected these regions in the past and on how alpine and arctic ecosystems are responding to changing environments.

The Engadine is an alpine valley situated in the eastern Swiss Alps, that has been the focus of a number of palaeoenvironmental studies to reconstruct the history of human-induced nutrient enrichment (Züllig, 1982; Ariztegui and Dobson, 1996; Ariztegui et al., 1996; Lotter, 2001), glacial activity (e.g., Leemann and Niessen, 1994; Maisch et al., 2000), vegetation history (e.g., Gobet et al., 2003; Gobet, 2004) and to examine the relationships between sedimentation processes and climate (Ohlendorf et al., 1997). However, these studies were carried out in the large lakes situated at the bottom of the Engadine Valley, whereas alpine lakes around the treeline ecotone, which have been shown to be well suited for organism-based environmental reconstruction (Lotter and Bigler, 2000; Hausmann et al., 2002; Lotter et al., 2002; Heiri et al., 2003) remain largely unexplored. A first step to explore these lakes as palaeolimnological archives is to investigate their limnological characteristics and the distribution of lacustrine biota. Whereas such extensive survey

data of small alpine lakes are available in the northern and southern Swiss Alps (Lotter et al., 1997; Lotter et al., 1998; Marchetto, 1998; Müller et al., 1998), they are largely missing from the eastern and central parts of the Swiss Alps.

In the following, we present a survey of lacustrine biota in the Engadine area. Subfossil assemblages of chironomids, cladocerans and diatoms in the surface sediment of 30 lakes ranging in elevation from 962 to 2815 m a.s.l. were analysed to assess the taxonomic composition of extant assemblages in subalpine and alpine lakes and to assess the distribution of these organisms with respect to major limnological and climatic parameters, which have been reported to have a strong influence on aquatic biota in the Swiss Alps (Lotter et al., 1997; Lotter et al., 1998). The study of subfossil material, however, puts some constraints on the achievable taxonomic resolution of the analyses. Nevertheless, fossil assemblages in surface sediment samples have the advantage of integrating biotic remains from the entire lake basin and over a number of years (Frey, 1988). They therefore provide a more comprehensive picture of the extant lacustrine flora and fauna than would otherwise be attainable except by intensive monitoring programs. Furthermore, surface sediment assemblages are directly comparable with the fossil record, an obvious advantage if the modern distribution of aquatic organisms is to be used to interpret palaeolimnological records. We concentrate on diatoms, chironomids and cladocerans as all of these organisms are diverse (Stoermer and Smol, 1999; Korhola and Rautio, 2001; Brooks, 2003), sensitive to limnological and climatic conditions (Lotter et al., 1997; Lotter et al., 1998) and represent different compartments of lake ecosystems (Frey, 1988). Furthermore, the remains of these organisms preserve well and remain identifiable in lake sediments and they are therefore valuable indicators of past environmental change (Battarbee et al., 2001; Korhola et al., 2001; Walker, 2001).

Study area and sites

We sampled 30 lakes in south-eastern Switzerland (Grisons). Most of them are located in the Upper Engadine, and a few sites are in the Lower Engadine (TAR-10, and NAR-11) and the Poschiavo (VIO-14, SAO-15, and POS-25, Fig. 1). The climate in the Engadine is influenced by air masses both from the south (i.e., the Mediterranean Sea) and the north (i.e., the North Atlantic Ocean, Urfer et al., 1979). The sites cover broad gradients in temperature and precipitation, as well as catchment vegetation types: some are located within the larch (*Larix decidua*) and stone pine (*Pinus cembra*) dominated forests, whereas others are well above tree line and vegetation is sparse in the watershed (Table 1). The sampled lakes show considerable differences in lake morphology (e.g., maximum lake depth) and catchment

size. In general the large, deep lakes (>30 m) are located in the valley bottom at lower altitudes (STM-21, POS-25, SIL-28, CHS-29, and CHN-30, see Table 1). The bedrock composition in the Upper Engadine consists predominantly of granite and gneiss, with locally present calcareous intrusions lead to neutral (pH ~7) lake-water conditions in most lakes (Table 1).

Methods

Sampling and laboratory procedures

All lakes were sampled during August 2002, except SIL-28, CHS-29 and CHN-30, which were sampled in November 2002. At each lake, we collected two one-litre water samples, the first at 1-m water depth and the second *c.* 1–3 m above the sediment surface, or, for deep lakes, well below the thermocline (Table 1). The water samples were stored at 4°C in glass bottles until analysis. A WTW Multi-line P4 (lakes #1–15) and EUTECH pH-Scan2 (lakes #16–30) pH meter was used for pH, and a WTW 330 LF conductivity meter for in situ measurements of conductivity and temperature. For both pH and conductivity, equipment was calibrated at each lake prior to measurements.

Further water chemistry analyses were carried out in the laboratories of the Swiss Federal Institute for Environmental Science and Technology (Eawag), Dübendorf. Alkalinity was measured by titration with strong acid to pH 4.3. Dissolved organic carbon (DOC) concentration was determined by thermal oxidation by a Shimadzu TOC-500 analyzer. Phosphate was determined photometrically with the molybdenum blue method, nitrate with the salicylic acid method, and silica (Si) with the molybdosilicate method (DEW, 1996). Total phosphorous (TP) and total nitrogen (TN) were measured in unfiltered samples, after acidic digestion in an autoclave for 2 h at 120°C using $K_2S_2O_8$. The detection limits for DOC, TP and TN were 0.5 mg C L^{-1} , $5 \text{ } \mu\text{g P L}^{-1}$ and 0.5 mg N L^{-1} , respectively.

We used July air temperature (July T) Climate Normals (1961–1990) from the Swiss Meteorological Institute (MeteoSwiss) corrected to sea level. For each lake site the average July T was calculated as the weighted mean of the three closest meteorological stations weighted by the inverse distance between lake and meteorological station. All values were corrected for altitude applying a lapse rate of $0.6^\circ\text{C } 100\text{m}^{-1}$ (Livingstone et al., 1999) before calculating the weighted average. In the Alps, air temperature and surface water temperature in lakes are closely correlated during the summer months (Livingstone et al., 1998; Livingstone et al., 1999), and mean air temperature can be estimated with a reasonably high accuracy even for remote alpine lakes during the summer months based on the available network of mete-

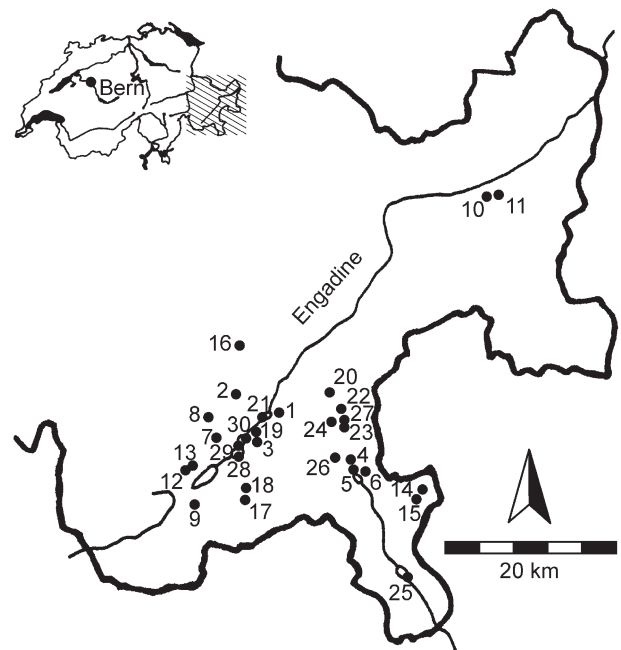


Figure 1. Map of the study area showing the location of the sampled lakes. The lakes are numbered according to Table 1.

orological stations. Hence, summer air temperature is probably a more robust approximation of summer water temperature at our study sites than the spot measurements taken during fieldwork.

Surface sediments were obtained in the deepest part of the lake basins using a modified 80 mm diameter Kajak-corer (Renberg, 1991). Samples of 0–1, 1–2, and 2–3 cm sediment depth were stored in NASCO whirl-paks and kept cool and dark until analysis. The organic content in the surface sediments was estimated using loss-on-ignition (LOI) and expressed as the percent weight loss after combustion at 550°C for 4 h (Dean, 1974; Heiri et al., 2001).

Diatom preparation followed standard procedures involving treatment with H_2O_2 (30%) and HCl (10%), followed by heating for >7 h at 70°C (Battarbee, 1986). After rinsing the samples with distilled water until pH was neutral, they were dried onto coverslips and permanently mounted using Naphrax mounting medium. Enumeration of diatoms (>500 frustules per sample) was done using a Leica DMR microscope at 1000× magnification with phase contrast optics. Diatom taxonomy largely followed Krammer and Lange-Bertalot (1986–1991).

After deflocculation at room temperature in KOH (10%) for 2 h, chironomid samples were sieved (100 μm mesh size) and chironomid remains were separated from other remains under a stereo-microscope (40× magnification). Chironomid head capsules were mounted in Euparal mounting medium after dehydration and identified using a microscope at 100×–400× magnification. Identification

Table 1. Major environmental variables characterizing the sampled lakes. G-Nitrate was below the detection limit (<0.5 mg N L⁻¹) in all lakes, except in the epilimnion sample of CAV-9 (0.6 mg N L⁻¹).

Code	Lake Name	Sampling Date (DD.MM.)	Altitude (m)	Coordinates Switzerland		July T (°C)	LOI 550 °C (%)	Max. Lake Depth (m)	Secchi Depth (m)	Sample Depth (m)	Water T (°C)		Conductivity (µS cm ⁻¹)		pH		DOC (mg C L ⁻¹)		G-Phosphate (µg P L ⁻¹)		Alkalinity (mmol L ⁻¹)		Silica (mg H ₄ SiO ₄ L ⁻¹)	
				X	Y						Epi	Hypo	Epi	Hypo	Epi	Hypo	Epi	Hypo	Epi	Hypo	Epi	Hypo	Epi	Hypo
STA-1	Lej da Staz	06.08.	1809	786500	152300	10.22	45	4.7	3.2	3.5	17.3	n.a.	132	n.a.	7.3	n.a.	5.5	3.8	16.1	15.3	1.17	1.19	9.2	8.7
JUL-2	Julterpass-See	06.08.	2280	775800	149100	7.66	12	3.5	Bottom	2.5	13.5	n.a.	86	n.a.	7.8	n.a.	1.4	1.5	8.8	10.4	0.79	0.79	8.7	9.1
NAL-3	Lej Nair	06.08.	1864	782800	149400	10.06	30	6.0	5.0	4.5	15.7	n.a.	59	n.a.	6.8	n.a.	2.3	2.3	8.9	11.3	0.64	0.64	10.3	9.6
NIR-4	Lej Nair	07.08.	2223	797500	143800	9.59	18	11.4	8.5	8.5	12.8	n.a.	31	n.a.	6.7	n.a.	1.5	1.4	14.4	12.3	0.37	0.35	10.0	9.5
PIT-5	Lej Pitschen	07.08.	2220	797200	144000	9.54	37	5.0	Bottom	3.5	11.7	n.a.	33	n.a.	6.9	n.a.	1.6	1.6	14.4	14.4	0.47	0.47	6.5	7.5
CRU-6	Lagh da la Cruseta	07.08.	2307	798800	143300	9.26	15	11.2	7.5	8.0	13.2	n.a.	44	n.a.	7.0	n.a.	1.1	1.1	14.1	20.0	0.49	0.50	5.7	6.5
TSP-7	Lej de la Tscheppa	08.08.	2616	777700	147000	5.73	8	27.0	11.0	17.0	10.2	6.6	35	40	6.9	n.a.	0.7	0.9	7.6	11.1	0.44	0.46	9.2	9.5
SUV-8	Lej Suvretta	08.08.	2602	778800	153200	5.61	20	8.0	Bottom	5.0	10.1	10.1	94	92	7.0	n.a.	0.7	0.8	8.2	10.5	0.56	0.59	7.0	9.2
CAV-9	Lagh da Cavloc	09.08.	1907	774400	139000	9.89	22	17.0	12.5	13.0	13.7	6.8	43	45	6.8	6.6	1.4	1.3	8.6	12.9	0.51	0.55	16.1	8.5
TAR-10	Lai da Tarasp	12.08.	1404	815500	184500	13.54	23	4.9	4.8	3.5	15.1	14.9	256	258	7.3	7.5	2.7	2.8	10.5	11.5	2.83	2.88	10.6	10.5
NAR-11	Lai Nair	12.08.	1544	816500	184500	12.71	54	5.1	3.5	2.0	14.9	14.7	301	301	7.5	7.3	3.4	3.4	8.2	8.3	3.40	3.39	9.0	9.6
LUN-12	Lagh dai Lunghein	13.08.	2484	771900	143200	6.43	10	20.5	12.0	15.0	7.1	6.2	249	396	7.3	7.1	0.6	0.6	5.6	5.5	0.85	0.94	6.2	7.4
LNA-13	Lej Nair	13.08.	2456	773300	144300	6.62	12	10.9	9.0	7.5	8.6	8.3	42	43	7.0	7.3	0.9	0.8	8.3	6.5	0.44	0.43	4.6	4.6
VIO-14	Lagh da Val Viola	14.08.	2159	807600	142800	9.32	26	13.2	Bottom	9.5	9.5	9.3	45	45	6.4	6.3	0.7	0.9	5.3	<5.0	0.28	0.27	6.6	6.3
SAO-15	Lagh da Saoseo	14.08.	2028	806700	142100	10.16	19	17.0	Bottom	12.0	6.9	5.3	59	60	6.9	6.9	0.6	0.5	<5.0	5.5	0.27	0.27	5.7	5.9
PAL-16	Lai da Palpuogna	25.08.	1918	779900	161600	9.62	9	20.4	14.5	16.0	8.3	6.2	555	631	8.4	8.4	0.6	0.7	<5.0	<5.0	1.65	1.74	10.4	10.9
ALV-17	Lej Alv	26.08.	2639	781900	140200	5.46	3	10.2	8.0	8.0	8.9	9.0	60	60	8.0	8.3	0.5	<0.5	<5.0	<5.0	0.51	0.48	9.7	6.8
SGR-18	Lej Sgrischus	26.08.	2618	781700	141300	5.59	4	6.4	6.0	4.0	11.1	11.0	84	84	8.5	8.6	0.6	0.6	30.4	12.1	0.70	0.71	8.0	10.1
MAR-19	Lej Marsch	26.08.	1810	782800	149800	10.38	21	5.5	Bottom	4.0	23.2	22.7	59	59	7.5	7.5	2.3	2.4	11.1	13.7	0.64	0.63	8.2	7.6
MUR-20	Lej Muragl	27.08.	2713	791900	153800	5.18	10	6.0	Bottom	4.0	8.7	8.7	72	73	7.6	7.3	0.7	0.6	<5.0	<5.0	0.38	0.40	5.6	5.5
STM-21	Lej da San Murezzan	27.08.	1768	784800	152000	10.51	11	44.0	7.5	20.0	14.4	11.5	125	141	7.6	6.8	0.9	0.9	12.4	15.9	0.89	0.93	6.5	4.7
PRÜ-22	Lej da Prùna	28.08.	2815	794600	150500	4.98	16	17.5	Bottom	13.0	8.2	7.9	59	59	6.8	6.6	<0.5	<0.5	46.3	6.3	0.22	0.21	8.2	7.7
PIS-23	Lej da la Pischla Süd	28.08.	2770	795100	149800	5.34	18	14.4	11.5	10.0	9.5	9.4	124	129	7.6	7.1	<0.5	n.a.	11.7	n.a.	0.43	n.a.	6.3	n.a.
LAN-24	Lej Languard	28.08.	2594	793100	150200	6.21	8	9.2	8.0	7.0	10.4	9.5	57	58	7.7	7.6	0.6	0.8	39.3	12.4	0.45	0.45	5.5	4.1
POS-25	Lago di Poschiavo	29.08.	962	804500	129000	16.37	6	85.0	11.0	20.0	15.2	11.7	129	134	7.8	7.7	0.7	0.8	10.6	24.2	0.94	0.93	9.0	6.8
DIA-26	Lej da Diavolezza	29.08.	2573	794800	144200	7.10	5	14.8	4.5	11.0	8.5	5.0	58	60	8.2	7.4	0.5	<0.5	18.7	34.5	0.49	0.50	5.3	5.0
PIN-27	Lej da la Pischla Nord	28.08.	2770	794850	150150	5.29	10	10.4	Bottom	n.a.	8.3	n.a.	32	n.a.	6.4	n.a.	<0.5	n.a.	8.5	n.a.	0.21	n.a.	9.4	n.a.
SIL-28	Lej da Silvaplana	11.09.	1791	781000	147000	10.61	3	77.0	9.0	40.0	12.7	6.4	107	122	7.8	7.8	1.1	1.1	8.2	8.4	0.93	1.05	3.8	5.4
CHS-29	Lej da Champfèr Süd	11.09.	1791	781500	148600	10.55	8	16.0	9.0	10.0	12.6	12.1	113	114	7.8	8.0	1.1	1.1	8.2	10.6	0.93	0.88	2.4	2.4
CHN-30	Lej da Champfèr Nord	11.09.	1791	781800	149300	10.53	15	36.0	11.0	10.0	13.2	13.0	111	112	8.3	8.3	1.0	2.0	7.3	8.6	0.87	0.90	2.2	2.2

was largely based on mentum characteristics described in Hofmann (1971), Wiederholm (1983) and Schmid (1993). *Thienemannimyia*-type includes Tanypodinae head capsules with a ventral and dorsal pore arrangement similar to *Conchapelopia*, *Rheopelopia*, *Telopelopia* and *Thienemannimyia* in Rieradevall and Brooks (2001). *Zavrelimyia* A features a pore arrangement on the head capsule as described by Heiri (2001). Tanytarsini head capsules were split into different categories following Heiri (2004) (for *Tanytarsus* I-III, *Micropsectra*, *Cladotanytarsus*), Heiri (2001) (for *Paratanytarsus* and *Tanytarsus* IV-VI) and Hofmann (1971) (for *Tanytarsus lugens*-type).

Cladoceran samples were prepared using standard methods (Frey, 1986; Prazakova and Fott, 1994; Korhola et al., 2001). Sediment was deflocculated using 10% KOH and heated (approximately 70–80°C) for 0.5 h and subsequently sieved using 40 µm mesh size. Aliquots of the residue were examined using a microscope at 100× and 200× magnification and identified according to Frey (1958; 1959), Korinek (1971) and Flössner (2000). The minimum number of exuviae of a given species in the samples was estimated based on the most abundant cladoceran skeletal fragment in the samples (Frey, 1986).

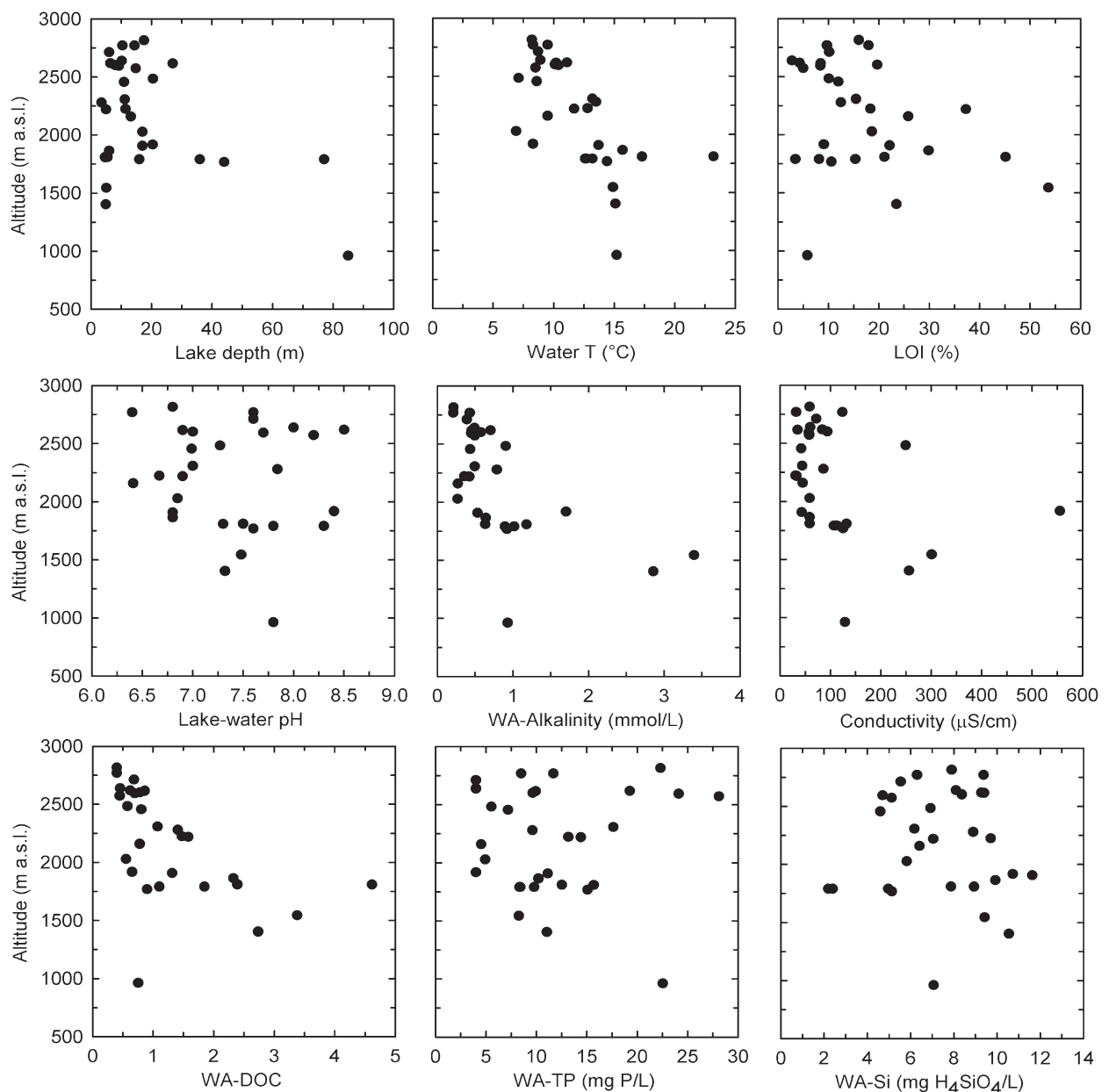


Figure 2. Major environmental variables in relation to the altitude of the study lakes.

Numerical analyses

Diatom, chironomid and cladoceran taxa (Figs. 3–5) recorded in less than three lakes were excluded for numerical analyses. The percentage biological data were square root transformed prior to numerical analyses in order to stabilise their variances. To assess whether to apply linear- or unimodal-based numerical techniques (ter Braak, 1986), we analysed each biological data set by Detrended Correspondence Analysis (DCA, Hill and Gauch, 1980), choosing the options detrending-by-segments, non-linear rescaling and downweighting of rare taxa (Fig. 6). As all analysed biological data sets have compositional gradient lengths of more than two standard deviation units, we used unimodal based species-response models (ter Braak and Prentice, 1988; Birks, 1995), i.e., Canonical Correspondence Analysis (CCA, ter Braak, 1986).

A series of partial CCAs was carried out with each environmental parameter as sole constraining variable to assess its explanatory power. For this purpose, we averaged the two water samples collected in each lake by applying a weighted averaging (WA) procedure for conductivity, DOC, TP, alkalinity, and silica as described by Lotter et al. (1998). For pH, we used measurements from 1 m water depth, as the application of WA procedure is not appropriate for parameters on a logarithmic scale. For parameters showing a skewed distribution in the 30 lake data set (i.e., LOI, water depth, conductivity, DOC, TP, alkalinity), log-transformation was applied before further numerical analysis. A TP dummy variable was created taking into account the differences of TP concentrations in epilimnion and hypolimnion, related to the minimum within the data set. The numerical treatments resulted in

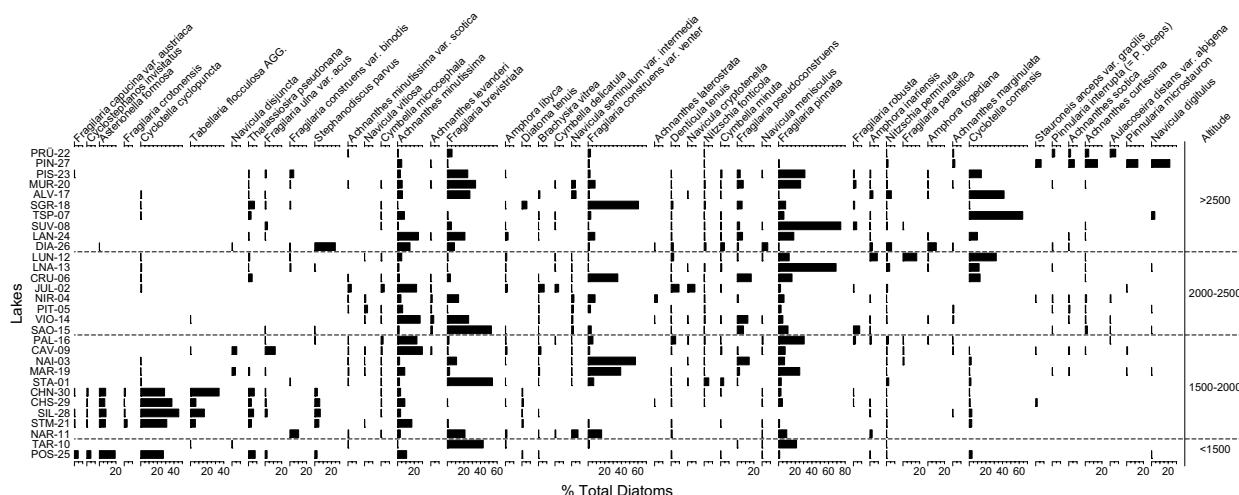


Figure 3. Distribution of most abundant diatoms in surface sediments of the sampled lakes along the altitudinal gradient. The lakes are abbreviated according to Table 1.

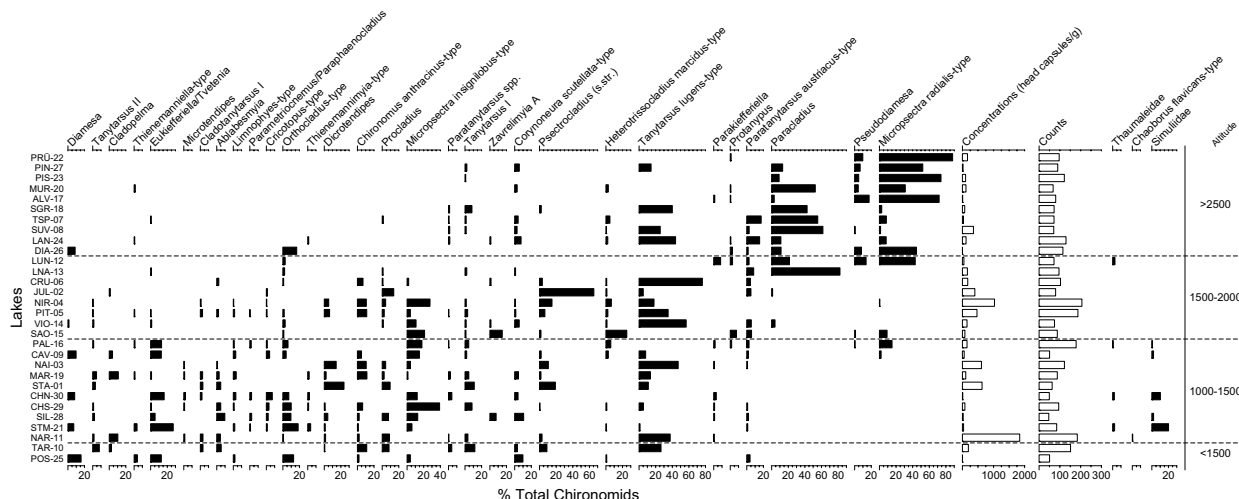


Figure 4. Distribution of most abundant chironomids in surface sediments of the sampled lakes along the altitudinal gradient. The lakes are abbreviated according to Table 1.

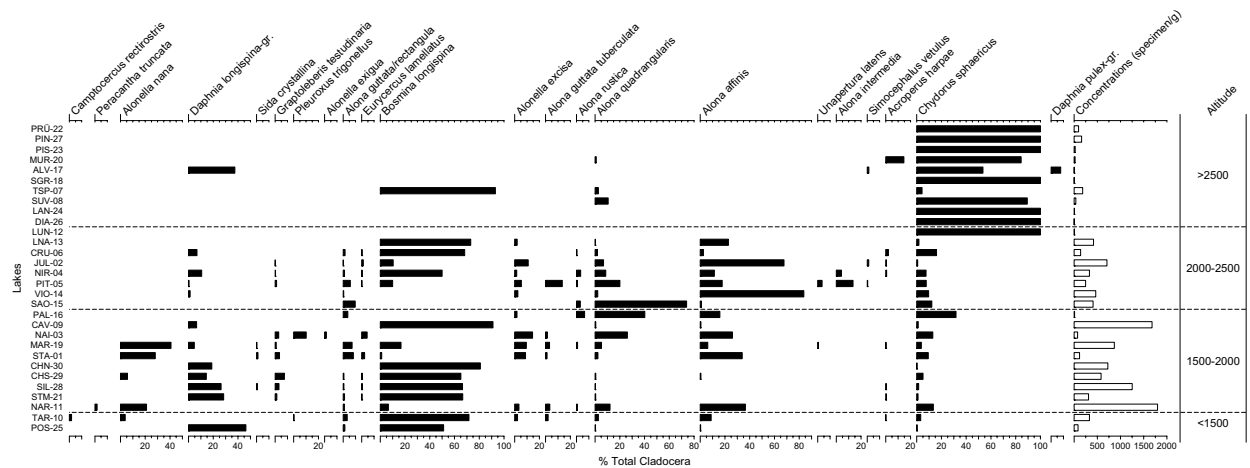


Figure 5. Distribution of most abundant Cladocera in surface sediments of the sampled lakes along the altitudinal gradient. The lakes are abbreviated according to Table 1.

an extension of the number of environmental variables from initially 13 to 29 (Table 1). All 29 environmental variables were initially included in the partial CCAs. The percentage variance explained by each variable was calculated (Table 2) and the statistical significance assessed by Monte Carlo permutation tests involving 999 unrestricted permutations (ter Braak, 1990; Lotter et al., 1997). Subsequently, the environmental data set was reduced to the most powerful variables explaining the highest amount of variance in the three biological data sets (Table 2), i.e. July T, LOI, log-Depth, Water T, log 1m-Conductivity, 1m-pH, logWA-DOC, logWA-TP, logWA-alkalinity and WA-Si.

The reduced environmental data set including ten variables and the biological data set including all 30 lakes were used in CCA (Fig. 7). In addition to this direct gradient analysis, we applied a TWINSpan classification (Hill, 1979) with two division levels to all biological data sets, which resulted in four groups of lakes for each biological data set.

Results

Environmental data and water chemistry

Several environmental variables reflecting lake water chemistry and lake physical properties are related to climatic parameters such as summer and winter temperatures, which in the Alps are closely correlated to elevation (Schär et al., 1998) (Table 1). As expected, the measured water temperatures decreased with increasing altitude (Fig. 2), in agreement with a previous survey of the relationship between air and water temperature in the northern Swiss Alps (Livingstone et al., 1999). DOC, LOI, and alkalinity also show a clear relationship with altitude. In high-elevation lakes, values for DOC, LOI

and alkalinity were low. In contrast, these parameters were more variable at lower elevation. No clear relationship between TP, silica, pH, and conductivity and elevation was observed (Fig. 2).

The differences between chemical properties of surface waters (1m; epilimnion) and bottom waters (sampled a few meters above sediment surface; hypolimnion) are negligible for several chemical variables (i.e., pH, alkalinity, DOC, conductivity). Some lakes showed a distinct thermal stratification (e.g., TSP-7, CAV-9, POS-25, DIA-26 and SIL-28), which particularly affected the TP concentrations, leading to higher TP-concentrations in the bottom water (Table 2). However, three lakes (SGR-18, PRÜ-22 and LAN-24) showed high TP concentrations in the bottom waters without any distinct thermal stratification. The silica concentrations were in general very similar between surface and bottom waters, except in CAV-9, where a considerably higher value was recorded in the surface water sample (Table 2). The chemical differences in epilimnion and hypolimnion within some lakes illustrate the need for a weighted average approach (see methods) to obtain an appropriate value for each chemical parameter in each lake.

In contrast to TP-concentrations, the measured TN-concentrations were low ($<0.5 \text{ mg N L}^{-1}$) in all lakes except CAV-9 (0.6 mg N L^{-1}), indicating that the lakes could be nitrogen-limited during the sampled period (Maberly et al., 2002; Camacho et al., 2003). Nitrogen concentrations in high altitude lakes are generally rather low in Central Europe, but may show considerable seasonal differences (Müller et al., 1998). This low nitrogen concentration in high altitude lakes is a result of relatively low agricultural land-use in their catchment, but is also affected by higher runoff in high-elevation catchments due to increasing precipitation (Müller et al., 1998).

Table 2. Percentage variance explained by each environmental variable in constrained correspondence analyses (CCA) using one single environmental variable at a time. The significance is indicated based on 999 unrestricted Monte Carlo permutations ($p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$). The full data set includes all 30 lakes; for the reduced data set the deep lakes (i.e., STM-21, POS-25, SIL-28, CHS-29, and CHN-30) were excluded. Bold displayed variables are used for CCA (Fig. 7).

Variable	Diatoms		Chironomids		Cladocera	
	Full	Reduced	full	reduced	Full	Reduced
	Variance explained (%)					
Altitude	7.8**	5.8	15.2***	18.4***	15.9***	18.7***
July T at sea level	5.7*	6.8*	3.2	4.0	2.9	3.3
July T	6.8**	5.8	15.1***	19.1***	15.5***	18.2***
LOI	6.3*	5.1	10.9***	14.0***	12.7**	13.1***
log-LOI	7.0**	5.5	10.3**	14.4***	13.6***	15.2***
Depth	13.2***	4.9	10.8***	12.4***	12.2***	8.3*
log-Depth	12.6***	5.4	12.8***	14.4***	13.7***	10.0*
Secchi	3.8	5.0	9.9***	12.8***	6.9*	7.8*
Water T	4.9	5.5	14.2***	17.8***	12.9***	14.0***
1m-Conductivity	3.6	4.9	3.9	5.9	2.6	3.4
log1m-Conductivity	6.1*	6.9*	3.8	4.7	2.0	4.4
WA-Conductivity	3.7	4.9	3.9	5.9	2.4	3.2
logWA-Conductivity	6.2*	6.9*	3.7	4.7	1.9	4.2
1m-pH	8.2***	7.0**	3.4	3.5	3.0	4.0
1m-DOC	4.3	4.9	13.6***	17.2***	12.7***	14.5***
log1m-DOC	4.7	6.1	17.2***	21.4***	16.3***	18.7***
WA-DOC	4.2	5.2	15.2***	18.9***	13.9***	16.1***
logWA-DOC	4.9	6.4*	18.2***	22.4***	17.4***	19.9***
1m-TP	4.2	5.0	2.6	2.7	6.0	6.0
log1m-TP	3.6	4.7	2.7	3.4	3.7	4.3
WA-TP	3.4	4.4	2.6	2.9	3.1	4.2
logWA-TP	3.4	4.1	3.4	4.6	3.4	4.2
dummy-TP	5.4	5.5	4.9	4.3	8.0*	6.9
1m-Alkalinity	4.5	5.5	6.8*	8.6*	5.0	5.7
log1m-Alkalinity	7.4**	7.8**	7.9**	9.3**	5.6	6.2
WA-Alkalinity	4.4	5.5	6.8*	8.6*	4.9	5.7
logWA-Alkalinity	7.4**	7.8**	8.0**	9.4**	5.5	6.2
1m-Si	6.0*	4.7	3.9	7.6*	2.2	5.0
WA-Si	7.9***	4.2	5.0	7.8*	4.8	4.1

Diatoms

A total of 202 diatom taxa were recorded in the surface sediments of the 30 sampled lakes. The distribution of the most abundant taxa is presented along the altitudinal gradient (Fig. 3). Some taxa (e.g., *Cyclotella comensis*) show distinct abundance patterns in relation to elevation and climate related variables, whereas others (e.g., *Achnanthes minutissima*, *Fragilaria* spp.) do not. Strong differences in diatom assemblages were recorded between deep (>30m water depth) and shallow lakes (3–15 m). In shallow lakes, surface sediments were dominated by periphytic diatoms, whereas in the deeper lakes located at the bottom of the valleys (STM-21, POS-25, SIL-28, CHS-29, CHN-30), planktonic taxa such as *Cyclotella cyclopuncta*, *Asterionella formosa* and *Tabellaria flocculosa* dominated the assemblages.

A DCA of all taxa present in at least 3 lakes revealed a compositional gradient of 3.39 standard deviations units along the first axis, indicating that unimodal-based numerical methods are appropriate to analyse the data. The first DCA axis showed a relatively high eigenvalue ($\lambda = 0.49$) and separated the five lakes located at lower elevations from the rest of the lakes, whereas the second DCA axis was considerably weaker ($\lambda = 0.17$) and did not show a clear separation of the sampled lakes (Fig. 6A). We calculated a series of partial CCAs using one single constraining environmental variable at a time. For the full lake-set, water depth was identified as the strongest variable explaining 12.6% of the variance within the diatom data set (Table 2). Other statistically significant environmental variables were lake-water pH (8.2%) silica (7.9%), altitude (7.8%), alkalinity (7.4%), mean July

air temperature (6.8%), LOI (6.3%) and conductivity (6.1%). After excluding the five deepest lakes from the data set (STM-21, POS-25, SIL-28, CHS-29, and CHN-30), the explanatory power of lake depth decreased considerably and explained only 5.4% (statistically not significant) of the variance (Table 2). Based on the partial CCA, the set of environmental variables was reduced, by selecting for each parameter the numerical treatment (untransformed/log-transformed, 1 m measurement/WA of measurements) which explained the highest amount of variance in the diatom data set (Table 2).

The relationship between the reduced set of environmental variables and the diatom distribution was assessed by means of CCA. Lake depth was the strongest environmental variable associated with CCA-axis 1 (eigenvalue $\lambda = 0.45$) (Fig. 7A), which was negatively correlated with LOI of surface sediment and the silica content of lake-water (Fig. 7A). The second axis ($\lambda = 0.17$) is mainly related to water chemistry variables, such as conductivity, alkalinity, lake-water pH, and TP. The CCA biplot illustrates the secondary gradient within the diatom data set, and suggests that both physical (e.g., lake depth, climate, LOI) and chemical (e.g., alkalinity, conductivity, pH, TP) variables have a strong influence on diatom distribution patterns.

The diatom classification based on TWINSpan separated at the first level the five deep lower-elevation lakes (STM-21, POS-25, SIL-28, CHS-29, CHN-30) from the other samples, mainly because these deep lakes all contained the planktonic diatom species *Cyclostephanos invisitatus* (Fig. 7A). At the second level of separation, the remaining 25 lake-set was split based on water chemistry conditions. One group contained four lakes with relatively low lake-water pH (NIR-4, PIT-5, PRÜ-22, PIN-27), where the diatom species *Achnanthes scotica* and *Achnanthes subatomoides* were found. In the large remaining lake-subset ($n = 21$), relatively high pH values were recorded, and diatom assemblages contained species such as *Amphora libyca*, *Cymbella minuta*, *Denticula tenuis* and *Cyclotella comensis*. The second division within the five deep lakes grouped the two samples from the interconnected lake-basins of Lej da Champfèr (CHN-29, CHS-30) together, based on the occurrence of *Fragilaria robusta*. Overall, the TWINSpan classification supported the results obtained by ordination methods. Lake depth seems to be the major environmental gradient explaining variations in the diatom flora. The secondary gradient seems to be related mainly to water chemistry (pH) and climate (July T).

Chironomids

A total of 62 different chironomid taxa were identified in the surficial sediments of the sampled lakes. The chironomid assemblages show distinct changes with elevation (Fig. 4). Taxa such as *Eukiefferiella/Tvetenia*, *Microten-*

dipes, and *Thienemannimyia*-type are found predominantly in lakes below 2000 m a.s.l. A strong shift in assemblage composition is apparent at ca. 2300 m a.s.l. A number of common chironomid taxa such as *Microprosetra insignilobus*-type, *Psectrocladius* (s. str.), and *Procladius*

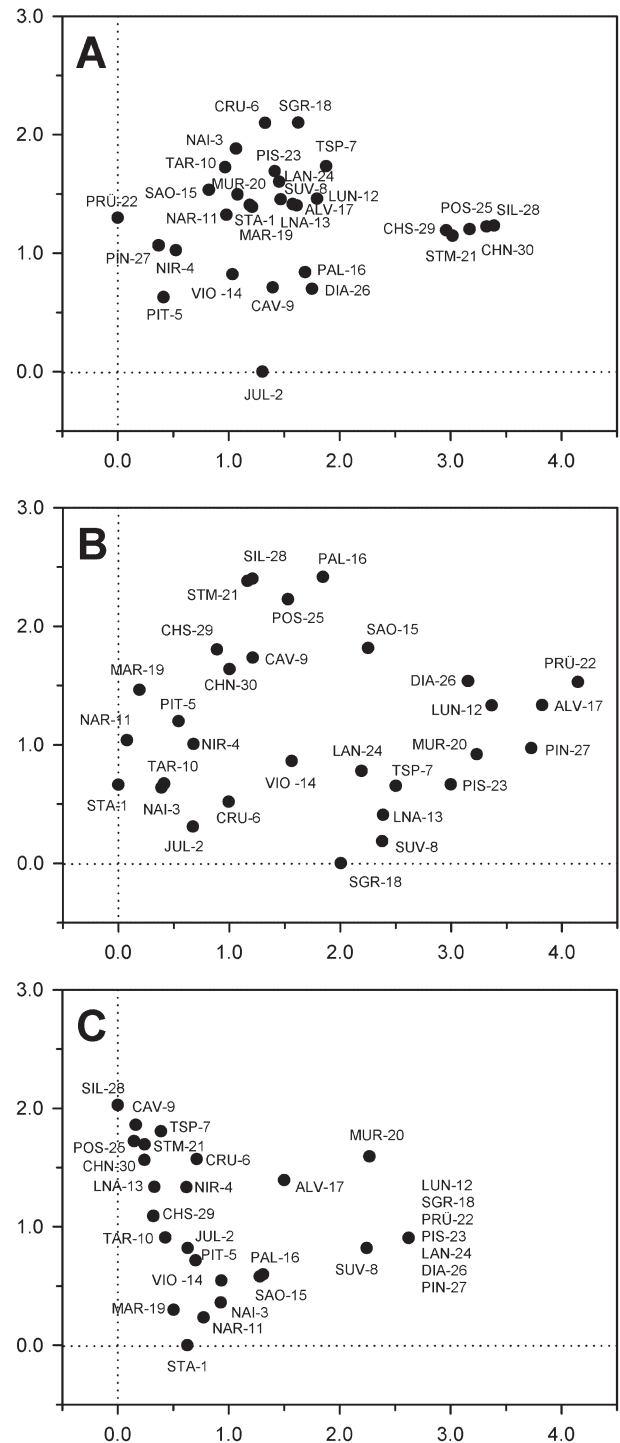


Figure 6. Detrended Correspondence Analysis (DCA) plot including site scores for (A) diatoms, (B) chironomids and (C) Cladocera. Seven lakes in panel (C) have identical scores due to a uniform fauna.

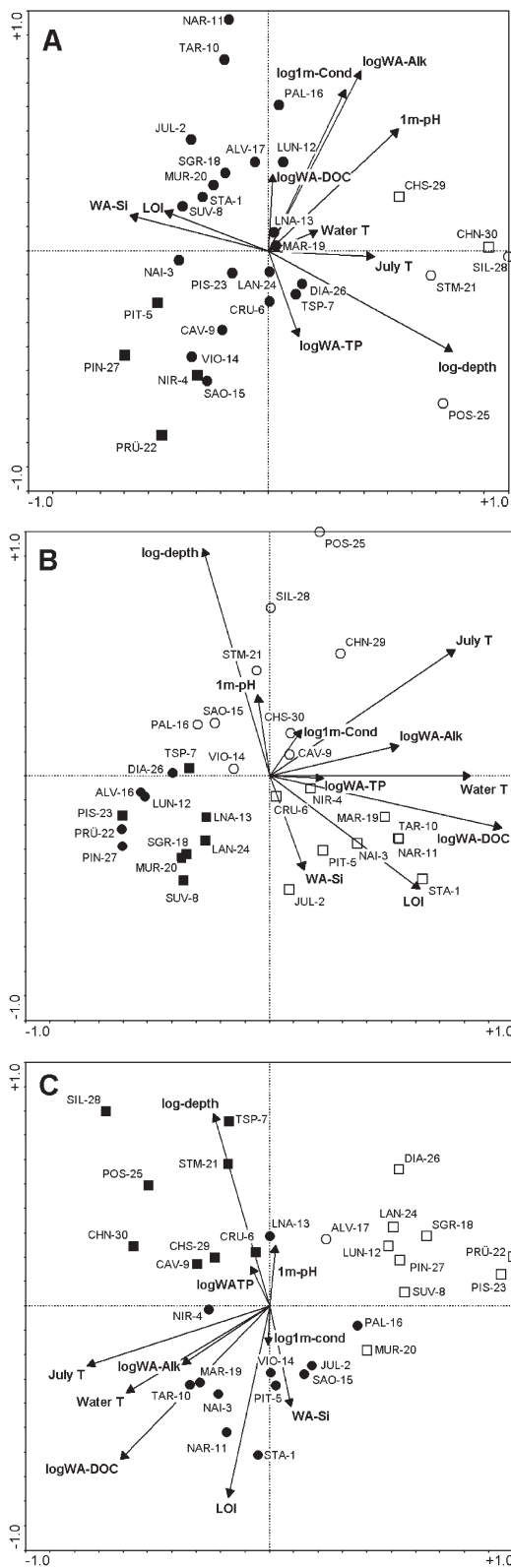


Figure 7. Canonical Correspondence Analysis (CCA) ordination biplot with site scores and major environmental variables (see Table 2) for (A) diatoms (B) chironomids and (C) Cladocera. Lake symbols are chosen according to TWINSpan divisions. The first division separated open from full symbols, the second divisions separated circles from squares.

are largely restricted to lakes below this elevation, and are replaced by taxa such as *Paracladius*, *Pseudodiamesa*, and *Micropsectra radialis*-type in high-altitude lakes. Only a few chironomid taxa occur over the entire altitudinal gradient, e.g. *Corynoneura scutellata*-type, *Heterotrissocladus marcidus*-type or *Tanytarsus lugens*-type.

A DCA of the chironomid assemblages indicates a gradient length of 4.14 SD units along the first axis (Fig. 6B), therefore indicating that unimodal based numerical methods are appropriate. The first axis separates high-altitude lakes such as PRÜ-22, ALV-17 and PIN 27 from lakes at lower elevations (e.g. STA-1, NAR-11, MAR-19) and is significantly stronger than the second DCA-axis ($\lambda_1 = 0.62$, $\lambda_2 = 0.22$). The second axis seems to be largely separating deep lakes (e.g. STM-21, SIL-28, POS-25) from the remainder.

Partial CCAs of the full 30-lake data set using a single constraining variable indicate that DOC is the strongest environmental variable explaining 18.2% of the total variance in the chironomid assemblages (Table 2), closely followed by July air temperature (15.1%) and water temperature (14.2%). Additional statistically significant variables were maximum water depth (12.2%), LOI (10.9%), and conductivity (8.0%). If the five deep, low-elevation lakes were excluded from the analysis all these parameters explained a distinctly higher proportion of variance in the chironomid assemblages, and the silica concentration became a statistically significant variable (Table 2).

The number of environmental parameters was reduced by selecting the weighting scheme for the water samples and the transformation that explained the most variance in the partial CCAs (Table 2). A CCA calculated using this reduced environmental data set and the chironomid assemblages of all 30 lakes resulted in a first CCA axis ($\lambda_1 = 0.54$) separating high altitude lakes from lakes at lower elevation (Fig. 7B) and hence also closely related to water temperature, July air temperature and DOC. The second axis ($\lambda_2 = 0.36$) separates the deep, low-altitude lakes from the remaining samples.

At the first level of division, TWINSpan of the chironomid assemblages splits the 30-lake dataset into two groups of similar size. The first group is characterized by the presence of *Micropsectra radialis*-type and at least moderate abundances (>2%) of *Paracladius*, and contains 12 high-altitude lakes (2450–2815 m a.s.l.) with very low DOC concentrations (0.4–0.9 mg C L⁻¹). The second group of 18 lakes is typically characterized by *Micropsectra insignilobus*-type and includes lakes at lower altitudes (960–2310 m a.s.l.) with higher DOC levels (0.55–4.61 mg C L⁻¹). At the second level of division the high altitude lakes are split into a group of seven lakes characterized by the presence of *Corynoneura scutellata*-type and a group of five lakes characterized by high abundances (>5%) of *Pseudodiamesa*, with no clear dif-

ferentiation of the two groups in relation to the measured environmental variables. The second division of the lower altitude lakes results in a group of deeper (13–85 m maximum depth), colder lakes (7–15 °C surface water temperature) with lower DOC concentrations (0.6–1.9 mg C L⁻¹) and a group of shallower (4–11 m), warmer lakes (12–23 °C water temperature) with somewhat elevated DOC concentrations (1.1–4.6 mg C L⁻¹). The group of deeper lakes is characterized by abundances >2% of *Orthocladius*-type and the shallower lakes by the presence of *Procladius*. TWINSpan confirms the results of the CCA by indicating that the chironomid assemblages have the strongest relationship with parameters reflecting climate and elevation (July air temperature, altitude, DOC), whereas a clear relationship between chironomid assemblages and lake depth is apparent in lower altitude lakes.

Cladocera

A total of 22 cladoceran taxa were identified in the sampled lakes. As in the other two indicator groups the analysed subfossil assemblages show a distinct change and decrease with altitude (Fig. 5). High-elevation lakes typically feature a high abundance of *Chydorus sphaericus* remains in their surface sediments and a very low diversity of cladoceran assemblages. Lakes below ca. 2500 m a.s.l. are characterized by more diverse cladoceran assemblages including taxa typical for littoral habitats, such as the chydorids *Alona quadrangularis*, *Alona affinis*, and planktonic taxa such as *Bosmina longispina* and *Daphnia longispina*-group. Of the identified cladocerans only a few are restricted to lakes at lower elevations and of these only *Alonella nana* occurs in more than one lake. A distinctly lower cladoceran concentration was found in high altitude lakes dominated by chydorids (Fig. 5).

A DCA with the 30-lake dataset reveals a first axis with a gradient length of 2.62 standard deviation units, indicating that unimodal-based numerical methods are appropriate for further analysis. The eigenvalue of the first DCA axis ($\lambda_1 = 0.55$) is more than three times higher than for the second ($\lambda_2 = 0.17$). The first DCA axis separates high-altitude lakes with a high proportion of *Chydorus sphaericus* from the remaining samples, whereas the second axis largely separates samples based on the proportion of the planktonic taxa *Daphnia longispina*-gr. and *Bosmina longispina*.

Partial CCAs of the full 30-lake data set indicate that DOC explains the highest amount of variance in the cladoceran assemblages (17.4%), closely followed by altitude (15.9%), July T (15.5%), water T (12.9%) and LOI (12.7%) (Table 2). All of these environmental variables are significant if assessed by a Monte Carlo permutation test. If the deep, low-elevation lakes are eliminated from the analyses the explanatory power of all of these parameters except lake depth shows a distinct increase (Table 2).

A CCA calculated with a reduced environmental dataset (i.e. with a single value per environmental variable) produces a first CCA axis ($\lambda_1 = 0.46$) strongly related to July T, water T, and partially to DOC (Fig. 7C). This axis separates high altitude *C. sphaericus*-dominated lakes from others. The second axis ($\lambda_2 = 0.34$) is strongly related to maximum water depth and LOI, partially related to DOC, and separates the deep, low-elevation lakes and TSP-7 from the remaining lower altitude sites.

The first division of a TWINSpan classification of cladoceran assemblages separates 10 high-elevation lakes (>2484 m a.s.l.) from the remaining samples. These lakes are characterized by a high relative abundances (>40%) of *C. sphaericus* and low DOC concentrations (0.4–0.8 mg C L⁻¹). A single lake (ALV-17) is separated from this group at the second level of division based on the presence of *Simocephalus vetulus*. The second first division group encompasses lakes over a range of altitudes (962–2616 m a.s.l.) with higher DOC concentrations (0.6–5.5 mg C L⁻¹). At the second-level of TWINSpan division this group is split into eight comparatively deeper lakes (max. lake depth 11–85 m) and 12 comparatively shallower lakes (3.5–20 m) based on the occurrence of high abundances of *B. longispina* (>20%) in the deeper lakes and of the presence of *Allonella excisa* in the shallower lakes.

Discussion

Biological subfossils in lake sediments contain valuable information about climatic and environmental conditions prevailing during the lifetime of those organisms. However, to interpret subfossil diatom, chironomid and cladoceran assemblages, detailed ecological knowledge about distribution, optima and tolerance of these biota is required. Unfortunately, such information is still fragmentary (Lotter et al., 1997) and often restricted to local calibration data sets encompassing lakes from a limited geographical area. In the Alps, calibration sets are available for diatoms from the northern and southern Swiss Alps (Lotter et al., 1997; Lotter et al., 1998), the Austrian Alps (Wunsam et al., 1995; Schmidt et al., 2004) and the Italian Alps (Marchetto and Schmidt, 1993). For chironomids and cladocerans a surface sediment data set from the northern and southern Swiss Alps has been developed (Lotter et al., 1997; Lotter et al., 1998; Heiri et al., 2003). However, information on the distribution of subfossil diatoms, chironomids and cladocerans in the surface sediments of lakes from the Central Swiss Alps is still lacking. Due to bedrock geology of the catchment of these lakes, the buffering capacity of their waters tends to be low. Consequently, different water chemistry conditions (with respect to, e.g., pH, conductivity, DOC) than in the northern and southern Alps can be expected. Therefore, it

is questionable whether aquatic biota show the same distribution patterns in relation to morphometric, physical and chemical parameters in central Alpine lakes as in hardwater lakes on calcareous bedrock.

The lakes in the Engadine area have been selected to encompass a large altitudinal gradient and include those from high alpine vegetation zones, across the treeline ecotone, to subalpine coniferous forests. In our study lakes, the distribution of diatom, chironomid and cladoceran taxa with respect to elevation is similar to that of the northern and southern Swiss Alps (Lotter et al., 1997; Heiri, 2001). High-elevation diatom assemblages are dominated by species previously reported from alpine lakes in the Alps, such as small *Fragilaria* taxa (e.g., *F. pinnata*, *F. pseudoconstruens*, *F. brevistriata*) and *Achnanthes minutissima* (Fig. 3). At lower altitudes these species are replaced by planktonic taxa more typical of deep lakes, such as *Cyclotella cyclopuncta*, *Asterionella formosa*, and *Tabellaria flocculosa*. Chironomid assemblages at high altitudes are dominated by cold stenothermous taxa, e.g., *Micropsectra radialis*-type and *Pseudodiamesa* (Fig. 4). These taxa are replaced in warmer, lower elevation lakes by chironomids with a broader altitudinal distribution in the Alps, such as *Tanytarsus lugens*-type and *Psectrocladius sordidellus*-type, or in the warmest lakes by taxa such as *Micropsectra insignilobus*-type, *Dicrotendipes*, *Ablabesmyia*, *Procladius* and *Cladopelma*. Similar to the northern and southern Alps, high altitude cladoceran assemblages show a very low diversity and often contain *Chydorus sphaericus* as the only cladoceran species (Fig. 5). At elevations below ca. 2500 m a.s.l. other chydorids become more abundant and planktonic cladocerans such as *Bosmina longispina* and *Daphnia longispina*-group can form a large proportion of the cladoceran assemblages in the sediments.

Considering the large altitudinal range of our study lakes, it is not unexpected that altitude and correlated environmental parameters such as July T, water T, DOC, and LOI explained a high proportion of variance in the biological proxy data sets (Table 2). This finding is in agreement with previously published surface sediment data sets from the northern and southern Swiss Alps, where summer temperature explained 6.3%, 6.3%, 21.4% and 9.5% of the variance in subfossil diatom, benthic cladoceran, planktonic cladoceran and chironomid assemblages, respectively (Lotter et al., 1997). Similarly, summer air or water temperature has been identified as important environmental factors in subarctic lakes of northern Europe for diatom (Weckström et al., 1997; Rosén et al., 2000; Bigler and Hall, 2002), cladoceran (Korhola et al., 2000) and chironomid assemblages (Olander et al., 1999; Korhola et al., 2000; Brooks and Birks, 2001; Larocque et al., 2001). Diatoms and cladocerans are not directly exposed to air temperatures during their life-cycle and chironomids only during their

very short adult stage (days to several weeks at most, Oliver, 1971).

It may therefore seem unexpected that July air temperature explains more variance in our subfossil assemblages than the water temperature measurements taken during field work. However, since water temperature can fluctuate significantly both within the diurnal cycle as well as within a given month, single spot measurements provide only a poor approximation of monthly mean water temperature values (Livingstone et al., 1999). This may explain the strong relationship between assemblages of all three organism-groups and mean July air temperature in our data set.

The sampled lakes in the Engadine range from 3.5 to 85 m in maximum depth. Water depth explains a significant proportion of variance in subfossil assemblages of all three studied organism-groups (Table 2). It has been shown that the proportion of benthic and littoral diatom taxa in sediments from a large, deep lake (Lage Maggiore, N. Italy) in the southern Alps is low (Marchetto et al., 2004), and similarly, diatom assemblages in deep Engadine lakes (>30 m) consist predominantly of planktonic taxa (Fig. 8A). Lake depth affects diatom assemblage composition mainly through habitat properties and substrate availability (Lotter et al., 2000). Therefore, lake depth is an important explanatory variable for diatom assemblages in surficial lake sediments from the northern and southern Swiss Alps (Lotter et al., 1997), Scandinavia (Bigler et al., 2002) and Alaska (Gregory-Eaves et al., 1999).

Subfossil cladoceran assemblages include both planktonic and benthic taxa. True planktonic taxa in the studied Engadine lakes are *Daphnia longispina*-group, *D. pulex*-group, and *Bosmina longispina*. *Chydorus sphaericus* can become planktonic during phases of high productivity (Frey 1988). However, in the meso- and oligotrophic lakes studied during this survey this species, like other chydorid species, most likely forms part of the meiobenthos. In the Engadine, *B. longispina* is common in lakes below ca. 2500 m a.s.l. and present in a single high altitude lake (TSP-07; Fig. 5). The abundance of this taxon shows no clear relationship with water depth. *D. pulex*-group remains have been found in a single high-altitude lake (ALV-17). In contrast to *B. longispina*, the abundance of *D. longispina*-group remains shows a clear relationship with lake depth. With a single exception (ALV-17), high percentages (>18%) of *D. longispina*-group are restricted to lakes with a water depth of 36 m or more. The ratio between truly planktonic species and the remaining cladocerans is strongly related to water depth (Fig. 8C), with deeper lakes (>20 m depth) featuring very high percentages of planktonic cladocerans. In shallower lakes a clear relationship between the proportion of planktonic species and water depth is apparent in lakes where *Daphnia* or *Bosmina* are present. However, in a

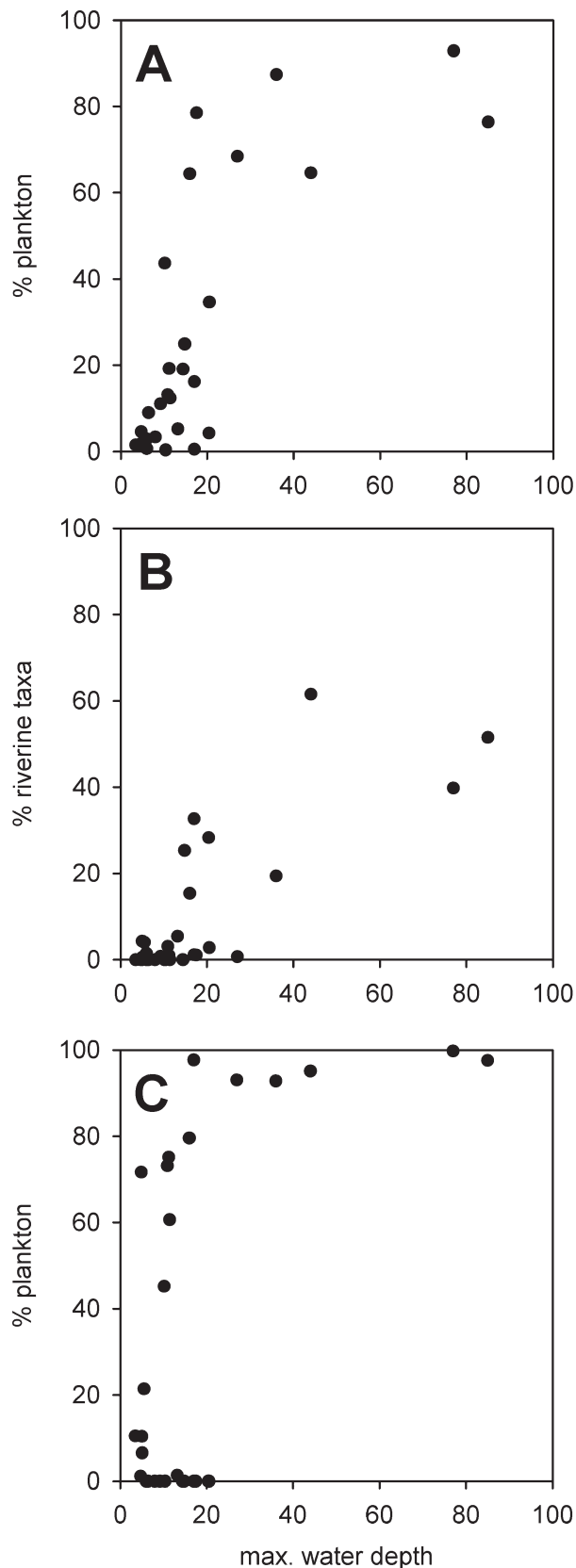


Figure 8. Percentages of planktonic diatoms (A), running water chironomids (B) and planktonic cladocerans (C) in subfossil assemblages in the surface sediments of the 30 study lakes.

number of shallow lakes true planktonic taxa are absent from the cladoceran assemblages. The distribution of planktonic cladocerans in surface sediments is in agreement with other studies which indicate a strong relationship between the proportion of planktonic cladocerans in fossil assemblages and lake depth (e.g., Frey, 1988; Korhola et al., 2000; Jeppesen et al., 2001). Planktonic cladocerans in alpine lakes are also strongly affected by the presence of fish. For example, Manca and Armiraglio (2002) report that *Daphnia* remains are largely absent in alpine lakes in northern Italy where fish had been regularly introduced. Comprehensive data on the presence of fish are not available for lakes in the Engadine region, but introduction of salmonids is common practice in lakes in the Swiss Alps (e.g., Barbieri et al., 1999). Therefore, the absence of planktonic cladocerans in many of the shallower lakes in our data set may be related to fish predation.

In contrast to cladocerans and diatoms, chironomids do not include true planktonic taxa, although the first instar larvae of some lacustrine species temporarily enter the water column for dispersal. Nevertheless, a statistically significant relationship between chironomid assemblages and water depth has been observed in the Engadine lakes (Table 2). Studies of the distribution of living chironomid larvae indicate that a number of species show a preference for either deep lakes and hypolimnetic environments, or shallower lakes and littoral environments (e.g., Brundin, 1949; Gerstmeier, 1989; Rieradevall et al., 1999). Surprisingly, subfossil chironomid assemblages in the deepest lakes in our data set show an increased relative abundance of taxa typical of stream habitats rather than of taxa typical for deep lakes. The percentage of chironomids typical of running water ranges between 6 and 27% in lakes shallower than 6 m but rises to 14 to 85% in lakes deeper than 15 m (Fig. 8B). Furthermore, deeper lakes such as STM-21, SIL-28, CHN-30, CAV-9 and PAL-16 contain a high proportion of subfossils belonging to Simuliidae and Thaumaleidae, aquatic insects restricted to running water habitats (Currie and Walker 1992; Wagner 1997) (Fig. 4). In general, the chironomid assemblages in the deepest parts of lake basins are composed of species living in the lake center, and those transported into deeper parts originating from the margins of the lake and its tributaries (Hofmann, 1971; Frey, 1988; Heiri, 2004). Furthermore, low oxygen conditions in the bottom waters, as reported from at least one lake in our data set (STM-21, Züllig, 1995), and food limitation in the hypolimnion can become an important factor restricting the occurrence of benthic animals (Wetzel, 2001). Thus, the high proportion of running water chironomid remains in the deepest study lakes could be explained by a reduced abundance of chironomid larvae living in the hypolimnion in combination with a preferential deposition of running water chironomid remains. Available evi-

dence therefore indicates that the strong relationship between lake depth and chironomid assemblages in our data set is influenced to a large extent by taphonomic processes (i.e. transport of chironomid remains from stream habitats to the lake center).

Diatom assemblages in our data set show a significant relationship with lake-water pH, alkalinity and silica. Again, these chemical variables have previously been reported as influencing subfossil assemblage composition, for example in the northern and southern Swiss Alps (Lotter et al., 1997; Lotter et al., 1998), the Austrian Alps (Wunsam et al., 1995; Schmidt et al., 2004), or in Scandinavia (Weckström et al., 1997; Rosén et al., 2000; Bigler et al., 2002). Even though lake-water pH (and alkalinity) is probably the strongest variable controlling diatom assemblage composition by affecting many chemical and biochemical processes, there is still no detailed physiological understanding on how pH influences competition between diatom taxa (Battarbee et al., 2001). Silica is important both in regulating the size of phytoplankton crop and the species composition, but usually phosphorus and nitrogen are the most important nutrients regulating diatom assemblage composition (Battarbee et al., 2001). In our data set, the phosphorus gradient is rather short and nitrogen concentrations are (except in CAV-09) below detection limit, thus giving silica a more important role in explaining the diatom assemblage composition in the numerical analysis.

For chironomids and cladocerans in the Alpine region, the high explanatory power of DOC is, in contrast to temperature or lake depth, unexpected. In Scandinavian humic lakes, where the concentration of DOC is often related to altitude (Karlsson et al., 2001; Larocque et al., 2001), DOC has been reported as a major environmental variable influencing chironomid assemblage composition. However, in the Alpine region DOC concentrations are generally substantially lower than in Scandinavian brownwater lakes. Furthermore, chironomid assemblages in our data set are not dominated by taxa typical for humic lakes such as *Zalutschia zalutschicola*, or *Heterotanytarsus apicalis*. The zooplankton of humic lakes typically features a high abundance of *Chaoborus flavicans* (Diptera: Chaoboridae). However, only a single *C. flavicans*-type mandible was found in one of the Engadine lakes with comparatively high DOC concentrations (NAR-11; Fig. 4). In lakes in the northern and southern Swiss Alps, DOC concentrations explain only 4.8%, 15.6% and 6.9% of the variance in subfossil benthic cladoceran, planktonic cladoceran and chironomid assemblages, respectively (Lotter et al., 1997). This contrasts with 17.4–22.4% of the total variance explained by DOC in the cladoceran and chironomid assemblages analysed in the Engadine area (Table 2). In our study lakes DOC is highly negatively correlated with altitude ($r = -0.69$) in lakes higher than 1400 m a.s.l. This relationship

is stronger than the correlation between DOC and altitude in lakes in the northern and southern Alps in a similar altitudinal range ($r = -0.38$) (Lotter et al., 1998). It is therefore possible that the strong relationship between chironomid and cladoceran assemblages and DOC in the Engadine lakes is actually a consequence of the strong influence of temperature on the studied lake ecosystems rather than an effect of the different DOC concentrations. However, lakes in the Engadine feature distinctly higher DOC values at the lower end of this altitudinal range than lakes on calcareous bedrock in the northern and southern Alps (Fig. 9). A number of key parameters for lake ecosystems such as light penetration and oxygen concentrations can be strongly influenced by DOC concentrations, leading to distinct zoobenthos and zooplankton assemblages in humic lakes (e.g., Brundin, 1949; Nyman et al., 2005). It may therefore also be possible that the elevated DOC concentrations in some of the studied lakes in the Engadine area had a distinct influence on chironomid and cladocerans assemblages independent of temperature.

LOI also explains a significant proportion of the variance in the chironomid and cladoceran assemblages (Table 2). The organic matter content of sediments, usually assessed as LOI, has been reported as a strong explanatory variable in surface sediment cladoceran and chironomid assemblages in Fennoscandia (Korhola et al., 2000; Larocque et al. 2001). However, in these data sets, as in the Engadine lakes, LOI is correlated with summer temperature. Next to the correlation with summer temperature ($r = 0.35$) LOI also shows a negative correlation with water depth in our study lakes ($r = -0.39$), with the coolest and deepest lakes containing sediments with a very low organic matter content and warm, shallow lakes featuring a wide range of LOI values (Table 1). Furthermore, LOI is highly correlated with DOC ($r = 0.77$). Since at least chironomid larvae can inhabit lake sediments themselves and a number of chironomids and cladocerans are detritus feeders (Pinder, 1986; Korhola et al., 2001) the organic matter content of lake sediments may have a distinct impact on chironomid and cladoceran populations. However, for both organism-groups summer temperature, DOC, and water depth explain a higher proportion of the variance. Therefore, the apparent relationship between chironomid and cladoceran assemblages and LOI may be influenced to a considerable extent by the effects of temperature, DOC, and water depth.

In contrast to a number of studies relating the distribution of surface sediment assemblages of diatoms, chironomids, and cladocerans to lake nutrient conditions (e.g., Bennion et al., 1996; Brodersen et al., 1998; Lotter et al., 1998; Brooks et al., 2001), TP values in the studied lakes did not explain a significant proportion of variance for any of the studied organisms. This is likely a consequence of the comparatively short phosphorus gradient encompassed by our study lakes, which do not include

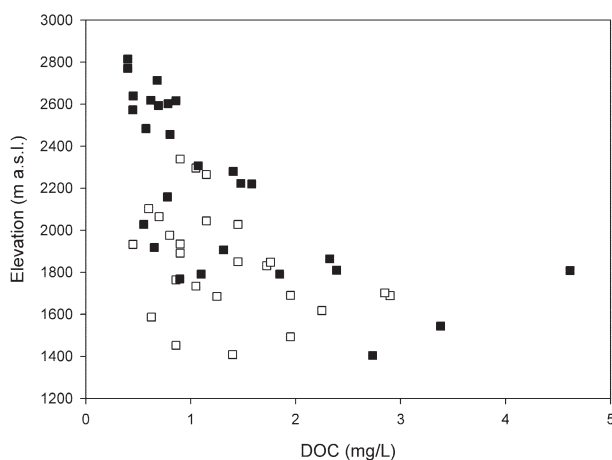


Figure 9. DOC concentrations in lakes in the Engadine region (solid squares) and in the northern and southern Swiss Alps (open squares; Lotter et al., 1998) plotted versus altitude. Only lakes above 1400 m a.s.l. are shown.

strongly eutrophic and hypertrophic lakes. Furthermore, the strong gradients in elevation and lake depth may have further obscured any relationship between the fossil assemblages and lake nutrient conditions.

Conclusions

We studied the relationship between subfossil diatom, chironomid, and cladoceran assemblages in the surface sediments of 30 lakes in the Engadine area, SE Switzerland, and major physical and chemical parameters. Our aim was to identify relevant environmental parameters for biota in these lakes in order to compare them with existing calibration data sets on different bedrock or in different geographical regions. Strong, statistically significant relationships have been identified between diatom assemblages and water depth, pH, and the silica content of lake water, whereas weaker relationships were observed between diatoms and alkalinity, July air temperature, and the organic content of lake sediments. Chironomid and cladoceran assemblages show a strong relationship with parameters correlated with altitude in the Engadine lakes such as the DOC content of lake water, July air temperature, water temperature, and the organic content of lake sediments. Furthermore a strong relationship exists with water depth for both organism-groups.

The distribution of diatom, chironomid, and cladoceran assemblages with altitude is similar in the Engadine region as in the northern and southern Alps, although in the poorly buffered waters of south-eastern Switzerland this relationship may be reinforced by the strong correlation between the DOC content of the lakes and elevation. Increasing lake depth is reflected in diatom and cladoceran assemblages by a higher proportion of remains origi-

nating from planktonic taxa. In contrast, chironomid assemblages in the deep Engadine lakes were characterized by high abundances of running water taxa.

The strength of the relationship between the different environmental parameters and the subfossil assemblages indicate that parameters related with altitude and temperature exert the strongest influence on the composition of subfossil chironomid and cladoceran assemblages in the Engadine area. This suggests that, as in alpine lakes on calcareous bedrock (Lotter et al., 1997; Heiri and Lotter 2005), fossil assemblages of these organisms have considerable potential as palaeotemperature indicators. In contrast, the relationship of diatoms to elevation is considerably weaker in the Engadine, and assemblages are also strongly influenced by water depth and water chemistry variables such as pH and silica concentrations.

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