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The relationship between water chemistry and surface sediment diatom assemblages in maritime Antarctic lakes

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Abstract: Maritime Antarctic freshwater lakes and their catchments are inherently simple systems in an environment which is characterized by strong seasonality. Such lakes offer excellent opportunities to study the interaction of water chemistry and plant communities. The response of diatom species to environmental gradients was assessed by constructing a diatom and water chemistry dataset from 59 lakes at two locations (Livingston Island, South Shetland Islands and Signy Island, South Orkney Islands). Results indicate that diatom species abundance is predominately related to nutrient and salinity gradients. The dataset will be used to create transfer functions which can be applied to sediment core diatom assemblages to reconstruct historical patterns of lake chemistry.

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Introduction

Diatoms (Bacillariophyceae) are unicellular siliceous algae which are common in water bodies throughout the world. They are commonly reported from the Antarctic where they are abundant in many streams and lakes (Kobayashi 1963, Pankow *et al.* 1987, Oppenheim & Ellis-Evans 1989, Oppenheim & Greenwood 1990). Diatoms are generally well preserved and abundant in lake sediments, their remains can be identified to species level and typically a large number of species are recorded. Diatom remains in dated lake sediment cores have been used extensively in temperate and tropical regions for reconstructing past changes in water chemistry and show great potential for studying environmental change in the Antarctic (Schmidt *et al.* 1990, Björck *et al.* 1991, Wasell & Håkansson 1992).

Diatom species composition is strongly related to lake water chemistry, and there is a well documented literature concerning the response of individual species to pH (Hustedt 1937–1939, Nygaard 1956), salinity (Kolbe 1927, Hustedt 1957) and nutrient (Nygaard 1949, Stockner 1971, 1972) gradients. More recently attempts have been made to quantify these relationships using multivariate statistical methods (e.g. Dixit *et al.* 1991). This approach generally involves the collection of new data in the form of a training, or calibration, dataset, relating a modern lake surface sediment diatom assemblage, which represents an integrated sample of the various living diatom communities in the lake, to contemporary water chemistry. Environmental variables which are strongly related to diatom distribution can be identified, and the relationships quantified. These relationships, or *transfer functions*, can then be applied to fossil diatom assemblages from sediment cores to provide environmental reconstructions of key hydrochemical variables.

Quantitative relationships between diatoms and environmental gradients have been established in many parts of the world. Much research has concentrated on the relationship between diatoms and pH (Gasse & Tekaia 1983, Charles & Whitehead 1986, Birks *et al.* 1990), but datasets have also been constructed more recently to investigate the relationship between diatoms and nutrients (Whitmore 1989, Hall & Smol 1992), and salinity (Fritz *et al.* 1991, Juggins 1992). These studies have recognized the importance of constructing regional datasets reflecting the particular water chemistry and diatom flora of different geographic areas.

Although diatom taxa are broadly cosmopolitan there are a number of unusual and unique forms common in the Antarctic. This, together with a lack of autecological information, makes it necessary to construct a training set specifically for the Antarctic as an essential prerequisite to diatom-based environmental reconstruction. This paper describes the lake-water characteristics of a new 59-lake surface sediment diatom/water chemistry dataset, and presents a preliminary analysis of the response of the diatom species to environmental gradients in the maritime Antarctic.

The study sites

Lakes from two areas of the maritime Antarctic were studied (Fig. 1, Table I), the Byers Peninsula (Livingston Island, South Shetland Islands, 62° 40'S, 61° 00'W) and Signy Island (South Orkney Islands, 60°43'S, 45°38'W). The Byers Peninsula is the largest ice-free area of the South Shetland Islands covering an area of *c.* 50 km^2. The highest part of the Peninsula (Chester Cone) is 193m high, but most of the area consists of a central platform lying between 85 and 100m. Two lower platforms (at 28–50 m and 11–17 m) are situated between the central platform and the coast (John & Sugden 1971). The geology of the area

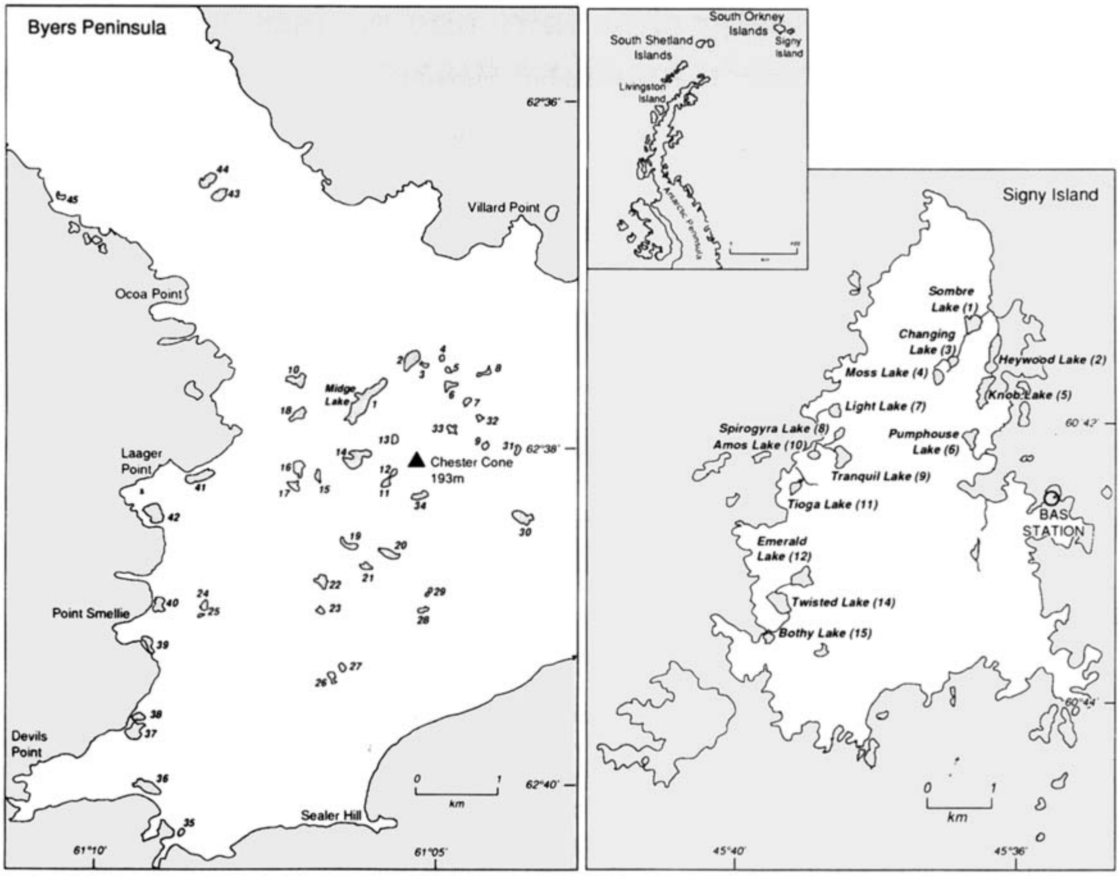

Fig. 1. Location of sample sites on Signy and Livingston islands. Lakes are referred to by number on Livingston Island, and by name and number on Signy Island.

consists of Jurassic–Cretaceous sediments (shales and sandstones) and Upper Jurassic–Lower Cretaceous volcanic rocks (basaltic agglomerates, augite-andesites, volcanic breccias and tuffs) (Hobbs 1968). The Holocene history of the area is summarized by Björck *et al.* (1991). Most of the inland area is not vegetated but scattered clumps of mosses and lichens do occur. The coastal area is somewhat richer and supports two flowering plant species (*Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl.) with a limited development of coastal moss carpets.

Signy Island covers an area of *c.* 20 km^2 and is low lying, with a maximum height of 279m. The terrain is rugged and large areas (32 %) are covered with permanent snow and ice. The geology consists of intensely folded metamorphic sediments, mainly garnetiferous quartz-mica-schists, with some amphibolites and marbles (Matthews & Maling 1967). The ice-free areas of Signy Island are comparatively well vegetated with extensive areas of moss and lichen as well as patches of *C. quitensis* and *D. antarctica* (Smith 1972). Large peat banks have accumulated on Signy Island reflecting greater stability and more acid soils compared to the generally unstable, porous and more alkaline volcanic soils of Livingston Island. Signy Island lakes are, with one exception, in more vegetated catchments than virtually all the Livingston Island lakes which are mainly on the barren central plateau (Fig. 1).

Livingston and Signy Islands share a maritime Antarctic climate which is moister and milder than continental Antarctica. Mean annual air temperatures are sub-zero (-3°C) but mean monthly temperatures exceed 0°C for at least one month in summer. Permafrost is present below an active layer of 0.3–0.7 m (Chambers 1966, John & Sugden 1971).

The Signy Island lakes are glacial in origin and range from oligotrophic clearwater to turbid eutrophic systems (Heywood *et al.* 1979, 1980). The lakes at Signy Island are all relatively shallow (generally <10 m deep) and ice-covered to a depth of 1–1.5 m for 8–12 months each year. The Livingston Island lakes are also shallow (Table I) and appear to have a similar depth of ice cover. However, the greater winter snow accumulation insulates these lakes from early summer air temperatures, and ice-out appears to be several weeks later than the majority of systems at Signy Island. In summer all lakes are ice-free and well mixed by wind.

The major source of nutrients in maritime Antarctic lakes is from bird and seal excreta. Nutrients are thus largely transferred from the much more productive marine ecosystem either directly into lakes by animals or indirectly via runoff from the catchment (Smith 1988). This has become particularly pronounced at Signy Island where, over the past 10 years, the catchments of some lakes have been colonized by large numbers of Antarctic fur seals (*Arctocephalus gazella*), representing the overspill from rapidly expanding populations on subantarctic South Georgia. In some areas the effects of these seals have been profound, with almost complete destruction of catchment moss communities (Smith 1988,1990), enhanced nutrient runoff and

Table I. Physico-chemical results of lakes sampled on Livingston and Signy islands.

Lake code	Altitude (m)	Max depth (m)	pH	Conductivity (μS cm^{-1})	Chl*a* (μg l^{-1})	Phae (μg l^{-1})	NO_3^- (μg l^{-1})	NH_4^+ (μg l^{-1})	TDN (μg l^{-1})	SRP (μg l^{-1})	Cl^- (mg l^{-1})	TP (mg l^{-1})	Na^+ (mg l^{-1})	K^+ (mg l^{-1})	Mg^{2+} (mg l^{-1})	Ca^{2+} (mg l^{-1})	SRS (μg l^{-1})
LN01	89	8.6	6.82	131	0.05	1.26	2.0	6.5	86.0	1.5	21.5	9.0	5.8	0.2	1.9	2.2	1192.7
LN02	88	3.0	6.92	110	0.29	0.41	2.0	1.5	181.0	0.5	15.8	0.5	3.9	0.1	1.4	1.7	1062.3
LN03	85	3.4	7.02	101	0.26	0.46	4.0	1.5	210.0	0.5	15.0	32.0	3.4	0.1	0.7	1.3	1166.4
LN04	99	0.1	6.92	282	0.05	1.24	0.5	5.5	63.0	0.5	36.8	5.0	11.5	0.1	4.4	7.9	1206.0
LN05	90	2.7	7.32	114	0.73	0.71	0.5	1.5	161.0	0.5	20.5	5.0	5.5	0.1	1.1	0.9	573.6
LN06	96	3.7	7.42	91	0.49	0.22	8.0	3.5	442.0	0.5	18.0	3.5	2.8	0.1	1.1	1.0	1034.5
LN07	94	2.6	7.52	93	0.68	1.16	12.0	1.5	178.0	0.5	18.3	2.0	3.1	0.1	1.3	1.4	977.7
LN08	91	1.3	7.62	60	0.34	0.52	23.0	2.5	519.0	0.5	10.5	3.5	1.6	0.1	0.5	0.7	809.4
LN09	102	1.6	7.52	71	0.39	0.22	2.0	11.5	413.0	0.5	13.5	7.5	2.1	0.2	1.0	0.8	1032.9
LN10	39	0.7	7.42	143	1.16	0.60	5.0	0.5	356.0	22.0	21.3	12.0	7.0	0.1	2.9	6.3	799.0
LN11	68	2.3	7.52	70	0.65	0.92	28.0	4.2	202.0	17.5	15.0	1.0	3.3	0.1	1.0	1.0	1217.2
LN12	70	5.3	7.52	77	0.64	0.44	28.0	3.2	500.0	6.5	14.0	0.5	2.9	0.1	1.0	1.0	1354.9
LN13	74	0.2	7.72	67	0.59	1.20	30.0	0.5	68.0	0.5	15.0	3.5	2.1	0.1	1.0	0.7	1005.0
LN14	81	5.4	7.62	78	0.09	0.62	25.0	0.5	392.0	0.5	17.5	1.0	3.3	0.1	1.3	1.6	918.2
LN15	74	1.5	7.42	119	0.95	0.41	21.0	0.5	191.0	0.5	23.5	5.0	7.8	0.1	1.2	2.0	1980.0
LN16	66	7.1	7.52	122	0.37	0.82	30.0	0.5	131.0	0.5	24.3	1.0	6.4	0.2	1.9	2.2	1432.1
LN17	70	3.3	7.62	87	0.47	0.25	9.0	0.5	80.0	0.5	17.3	2.0	3.6	0.1	1.9	1.6	982.2
LN18	36	0.7	7.62	105	0.55	0.22	7.0	0.5	389.0	0.5	17.8	9.0	6.0	0.2	1.6	2.0	1223.0
LN19	87	3.0	7.62	105	0.28	1.77	0.5	1.7	392.0	0.5	15.0	1.0	3.3	0.1	1.4	2.7	1122.0
LN20	93	2.0	7.72	80	0.54	0.62	0.5	6.0	78.0	0.5	11.8	6.5	1.8	0.1	1.0	1.6	856.4
LN21	88	1.5	7.52	105	0.29	0.22	0.5	1.7	31.0	0.5	15.0	3.5	3.3	0.1	1.7	6.1	791.0
LN22	81	4.5	7.62	110	0.91	0.91	0.5	2.0	278.0	0.5	13.5	6.5	2.9	0.1	1.5	3.4	115.1
LN23	85	0.2	7.82	242	0.56	0.55	0.5	6.3	109.0	0.5	39.0	5.0	10.4	0.2	4.3	5.8	1382.8
LN24	58	1.0	7.92	129	1.03	2.96	0.5	2.8	243.0	0.5	17.8	5.0	3.8	0.1	1.8	3.2	1090.5
LN25	58	0.6	8.12	329	1.42	0.69	12.0	22.0	420.0	16.0	45.0	15.6	11.4	0.3	4.8	7.3	1089.8
LN26	72	3.4	6.72	103	0.45	0.38	10.0	3.0	304.0	0.5	9.5	2.0	1.5	0.1	0.8	1.5	605.9
LN27	86	4.3	6.62	113	0.67	0.43	4.0	5.0	90.0	0.5	17.5	3.5	3.7	0.1	1.6	3.4	1006.1
LN28	83	4.8	6.62	107	0.69	0.60	25.0	5.5	56.0	0.5	11.5	2.0	3.0	0.1	1.4	3.7	1139.8
LN29	99	0.1	6.82	80	0.90	0.58	8.0	0.5	57.0	0.5	15.2	1.0	2.7	0.5	1.1	1.9	606.2
LN30	103	3.9	7.22	86	0.80	1.70	5.0	5.5	429.0	7.0	17.3	5.0	3.8	0.5	1.0	0.7	847.0
LN31	83	0.9	7.42	73	0.59	0.61	4.0	1.5	355.0	0.5	13.5	5.0	2.6	0.5	1.9	0.5	1229.7
LN32	80	0.1	6.82	91	2.89	2.18	26.0	2.7	113.0	0.5	14.8	2.0	2.1	0.5	1.2	0.8	1365.3
LN33	83	0.6	6.82	91	0.44	0.76	6.0	5.0	260.0	0.5	16.3	1.0	3.4	0.2	1.1	0.7	1643.7
LN34	92	1.5	6.92	64	0.63	0.44	6.0	5.0	125.0	0.5	11.8	6.5	1.8	0.2	1.1	0.5	764.3
LN35	5	0.5	6.72	303	7.36	4.42	15.0	26.0	540.0	5.0	27.8	16.0	2.0	0.2	2.7	8.6	1284.3
LN36	5	0.4	7.02	278	6.83	2.60	8.0	20.5	370.0	3.5	34.0	19.5	2.0	9.5	4.0	4.8	962.8
LN37	5	0.4	8.02	2960	7.80	2.08	5.0	25.0	383.0	3.7	644.0	42.0	188.0	1.2	34.0	33.6	1260.0
LN38	5	0.4	8.02	425	4.58	1.56	15.0	34.0	798.0	16.0	39.0	20.5	30.0	0.2	4.0	17.2	898.2
LN39	5	0.4	8.02	381	3.83	0.26	6.0	17.5	3311.0	3.5	38.8	160.0	11.0	0.5	3.8	4.4	763.2
LN40	5	0.3	8.92	620	6.29	6.38	6.0	32.0	100.0	24.5	65.0	71.0	14.0	0.5	6.8	12.2	386.0
LN41	5	0.3	7.62	394	2.36	1.89	2.0	18.0	528.0	7.5	40.0	19.5	4.0	0.3	4.5	13.2	850.2
LN42	5	0.3	7.62	425	5.17	0.52	420.0	95.0	1175.0	133.0	25.5	7.5	10.0	0.3	3.5	8.6	749.3
LN43	143	1.5	7.92	71	0.14	0.21	40.0	14.0	190.0	6.5	9.8	3.5	2.2	0.1	0.6	1.2	558.7
LN44	144	1.7	7.62	143	1.69	1.12	50.0	8.5	1358.0	2.5	16.0	3.5	3.7	0.1	1.7	5.5	886.3
LN45	80	2.7	7.52	187	0.62	0.75	23.0	10.5	225.0	4.0	17.3	3.5	7.6	0.1	1.8	2.0	772.6
SG01	10	11.2	6.82	78	3.99	1.74	181.9	12.9	272.5	2.6	25.8	9.0	24.9	1.0	4.6	3.8	169.2
SG02	4	6.4	6.92	134	10.06	5.19	327.0	56.1	614.7	32.1	42.3	122.1	33.2	1.5	5.9	4.0	201.1
SG03	35	5.4	6.82	94	2.43	0.58	146.4	8.5	223.2	3.5	25.3	10.8	23.0	1.0	4.2	3.4	236.6
SG04	48	10.4	6.82	40	1.85	0.77	111.0	5.6	204.0	2.3	23.2	7.8	12.6	1.2	1.4	2.2	137.0
SG05	8	3.5	7.32	62	8.70	6.60	123.3	16.3	328.7	0.9	18.7	33.7	22.8	1.4	3.1	4.1	168.4
SG06	20	4.0	6.92	86	3.02	1.13	63.6	7.1	174.9	3.5	18.4	9.4	13.8	1.2	2.5	4.2	83.7
SG07	35	4.4	6.82	121	9.21	3.57	33.4	11.2	145.9	1.4	44.1	27.6	29.6	2.3	4.7	4.9	122.9
SG08	25	1.5	7.42	60	1.51	1.23	116.2	17.4	209.6	0.3	19.4	11.0	28.8	2.2	4.7	6.2	149.5
SG09	28	8.0	6.92	52	1.53	1.15	80.7	1.8	146.4	0.3	16.7	5.0	16.3	1.0	2.7	3.1	88.8
SG10	8	4.3	8.12	120	4.11	4.28	520.6	214.4	1150.5	205.4	33.9	252.5	36.0	3.4	20.3	9.7	88.8
SG11	35	4.0	7.42	134	4.29	4.06	105.7	53.3	421.8	28.0	20.9	73.9	30.0	1.8	6.1	5.2	127.2
SG12	45	15.0	6.62	67	1.33	0.54	97.3	10.3	187.7	3.2	23.4	7.6	12.3	1.2	2.1	2.4	76.3
SG14	30	4.0	6.82	92	2.43	1.01	65.6	2.5	150.2	2.6	28.7	9.5	17.3	1.5	3.4	4.2	56.2
SG15	4	2.0	6.82	233	1.24	0.42	570.7	94.8	864.7	54.5	44.2	180.6	20.8	1.7	4.1	4.7	191.5

TDN = Total dissolved nitrogen; SRP = Soluble reactive phosphorus; TP = Total phosphorus; SRS = Soluble reactive silicate.

increased organic carbon and nitrogen loadings in the lakes and lake sediments (Ellis-Evans 1990). In contrast, most freshwater Livingston Island lakes are situated inland and receive virtually no animal inputs, although the brackish coastal lakes are heavily influenced by sea spray and in some cases have large animal and bird populations in summer.

The biology of several of the Signy Island lakes has been studied in some detail (Ellis-Evans 1981, 1984, 1985, Hawes 1985, Oppenheim & Ellis-Evans 1989, Oppenheim & Greenwood 1990). In contrast the Livingston Island lakes are extremely poorly studied and little is known of their limnology beyond the work of Hansson (1990), and Hansson & Håkansson (1992).

Methods

Surface sediments and water chemistry were obtained from 45 sites on the Byers Peninsula, Livingston Island, and from 14 sites on Signy Island (Fig. 1). Lakes are referred to by number alone in the case of Livingston Island lakes where official names have not been assigned. Signy lakes are referred to by both number and official name.

Water sampling

At Livingston Island, 2 l water samples were taken in acid-washed plastic bottles from sites near the outflow of each lake and samples were filtered (by GF/F) shortly after collection. Filters were placed in methanol and frozen for subsequent chlorophyll analysis and water samples were either analysed within 24 h of collection (for conductivity, nitrate, ammonium and soluble reactive phosphate) or frozen for later analysis. Separate filtered samples were collected for dissolved reactive silicate analysis and measured within three days. pH was measured *in situ* or immediately on return to the base camp with a hand-held pH meter (Jenway model 3070) and pH electrode (Russell Scientific) designed for low conductivity waters. Temperature and conductivity were measured by a Jenway model 4070 meter and electrode, and oxygen measurements by a YSI model 57 system. Water analysis followed the methods of Mackereth *et al.* (1978) and in all cases produced colour reactions which were measured at the field camp using a Pye Unicam SP6-550 UV\\Vis spectrophotometer.

At Signy Island routine monthly measurements are made on Sombre Lake and Heywood Lake, whilst all the lakes are sampled at three critical periods (early winter, spring and summer open water) each year. The analyses include dissolved oxygen, conductivity and temperature profiles which are measured in the field with YSI probes and meters, and pH, chloride, nitrate, nitrite, ammonia, total dissolved nitrogen, soluble reactive phosphorus, total dissolved phosphorus, total phosphorus and dissolved reactive silicate which are analysed in the laboratory. The latter are measured by the methods described in Mackereth *et al.* (1978) except pH (Corning Delta pH meter and low conductivity water pH electrode).

To enable the comparison with Livingston Island only the summer data from Signy Island were used. These were averaged for the two years previous to the time when the surface sediment sample was obtained, this being augmented by the more detailed information from the routine sampling programme on Sombre and Heywood lakes. Winter conductivity values were used when summer measurements were not available as midwater conductivity changed little throughout the year.

Surface sediment sampling

Sediment cores were collected from the deepest part of each lake with either a gravity type corer (Glew 1989), or a BAS corer (Ellis-Evans 1982), operated from either a small inflatable boat or from the ice. Livingston Island lakes were sampled in 1991 and Signy Island lakes were sampled between 1985 and 1991. The top 0–0.5 cm slice of each core was used for the surface sediment sample.

Diatom analysis

Diatoms were prepared from the surface sediment samples by oxidation using H_2O_2 (Renberg 1990). At least 500 valves per sample were counted on random transects using a Leitz Laborlux S microscope with phase-contrast at 1000x. Diatoms were identified using a range of floras, in particular Hustedt (1927–66), Krasske (1939), LeCohu & Maillard (1983, 1986), Krammer & Lange-Bertalot (1986, 1988) Lange-Bertalot & Krammer (1989), & Schmidt *et al.* (1990). The taxonomic status of certain species is rather preliminary and more complete descriptions will be given elsewhere.

Data analysis

Diatom species were expressed as relative abundances (% total diatoms) and only those present at >1% in any single sample, or with >2 occurrences (79 species) were retained. For multivariate analyses all chemical variables were $\log_{10}$ transformed except for pH. Ordinations were implemented by the computer program CANOCO 3.10 (ter Braak 1987, 1990), with rare species downweighted in all cases. Cluster analysis of the environmental data (unweighted pair-group clustering applied to a standardized Euclidean distance matrix) was performed using the program CLUSTER (H.J.B. Birks unpublished). The program TWINSPAN (Hill 1979) was used for cluster analysis of the diatom data.

Results

Water chemistry

The results of the physico-chemical analyses are shown in Table I. Principal components analysis (PCA) and cluster analysis are used to summarize the major patterns of variation within this data, and these results are presented as a PCA correlation biplot and dendrogram in Fig. 2. In the biplot, variables with high positive correlation generally have small angles between their biplot arrows. Variables with long arrows have high variance, and are generally the more important within the data.

The cluster analysis divides the lakes into four groups. Groups 1 and 2 consist of the inland and coastal Livingston Island lakes respectively. Group 3 contains the Signy Island lakes, and Group 4 contains three outliers, separated on the basis of high nutrient concentrations, in the case of SG10 (Amos Lake), or high conductivities (LN37 and LN40). The first two principal components (λ_1=0.50, λ_2=0.16) account for 66% of the total variance, and effectively capture the main patterns of variation in the environmental data. The first axis is related to indicators of trophic status (total phosphate, orthophosphate, total dissolved nitrogen, chlorophyll *a* and phaeopigments) and associated ions (calcium and magnesium), and contrasts the nutrient poor inland Livingston sites of Group 1, plotted on the left of the diagram, with the nutrient-rich coastal Livingston and Signy sites such as SG10 (Amos Lake), SG02 (Heywood Lake) and LN42.

Axis 2 reflects two gradients. The first running from top right to bottom left is related to salinity and separates the high conductivity coastal Livingston sites of Groups 2 and 4 from the remainder. Some sites, plotted top right, exhibit a very strong marine influence, particularly LN37 which has a conductivity of 2960 μS and associated high sodium and chloride values (Table I). The second is related to dissolved silica, potassium and nitrate and runs from top left to bottom right, separating the generally high nitrate and potassium, low dissolved silica lakes on Signy Island, plotted bottom right, from low nitrate and potassium, high dissolved silica sites on Livingston Island.

Fig. 3 shows scatter plots and correlations of selected variables, and highlights the negative correlation of nutrient-related variables and conductivity with altitude, as a result of the influence of marine birds and mammals at the low altitude coastal sites. There is no strong pH gradient in the data, although pH is weakly correlated with conductivity.

Diatom analysis

TWINSPAN classification was used to group sites on the basis of their diatom assemblages. Three main groups of sites were identified and these are represented in the dendrogram at the top of Fig. 4. Group 1 consists of the Signy Island sites, and is further divided into two. Group 1a contains the coastal, more eutrophic sites, whilst Group 1b contains the inland oligotrophic sites. Group 2 consists of the majority of the Livingston Island sites, and includes all the inland sites plus LN45 which although situated near the coast, is at an altitude of 80 m. Group 3 consists of the low-lying coastal Livingston Island sites.

Fig. 4 also shows the major patterns of diatom distribution and abundance for each group of lakes (a list of diatom codes, names and authorities is given in Appendix 1). Group 1a has high frequencies of *Achnanthes pinnata*, *A. subatomoides*, *A. renei*, *Navicula seminulum*, *Nitzschia perminuta*, *Synedra rumpens* and *A. delicatula*. Group 1b has a higher frequency of *Cymbella minuta* and *A. minutissima*, and a lower frequency of *S. rumpens*. In Group 2 *N. seminulum*, *Fragilaria pinnata*, *Navicula tantula* and *A. metakryophila* are important. Group 2b also has high percentage abundances of *A. renei* and *N. australomediocris*. In Group 3 there are high percentage abundances of *N. perminuta*, *Navicula gregaria* and *Fragilaria construens* var. *binodis*. Group 3a also has high abundances of *Nitzschia paleacea*, *Nitzschia gracilis*, *Nitzschia hamburgiensis* and *Pinnularia* species 1. Whilst Group 3b has high abundances of *Nitzschia frustulum* and *Navicula capitata* var. *hungarica*.

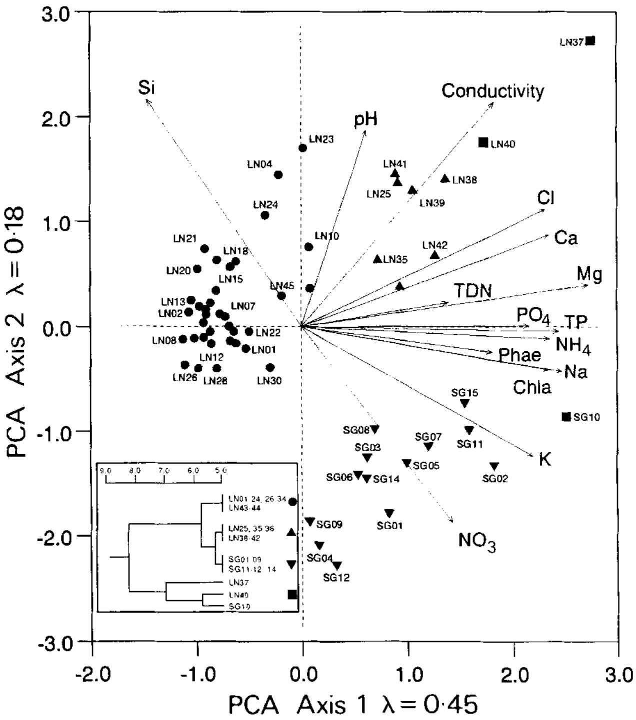

Fig. 2. Principal components analysis (PCA) correlation biplot. Symbols for lake sites are according to the groups defined by cluster analysis, see inset. Sites numbered as in Fig. 1 with the prefix LN to denote Livingston Island samples and SG to denote the Signy Island sites. ● = Group 1; ▲ = Group 2; ▼=Group 3; ■ = Group 4.

The three main groups identified on the basis of their diatom assemblages are broadly similar to the groups identified by water chemistry alone. This suggests that diatom distribution is strongly related to the main gradients in the chemical environment. The relationships between the diatom assemblages and the environmental variables are explored in more detail using canonical correspondence analysis (CCA) (ter Braak 1986) and the results plotted in Fig. 5, together with the site groups defined above. The length of the environmental arrows indicate their relative importance in explaining the variation in the diatom data, and their orientation indicates their correlation with the ordination axes.

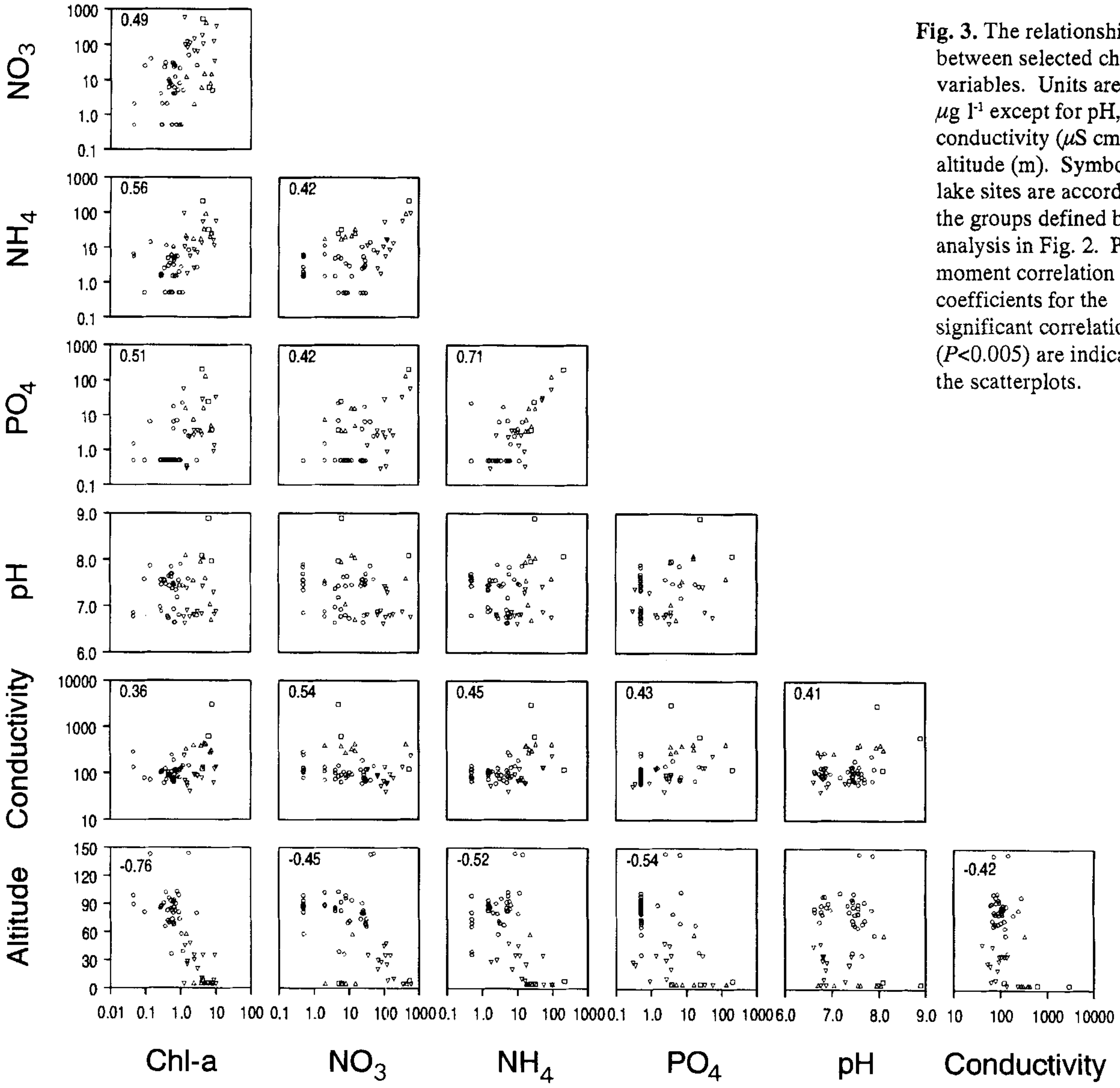

Fig. 3. The relationship between selected chemical variables. Units are log μg l^{-1} except for pH, conductivity (μS cm^{-1}) and altitude (m). Symbols for lake sites are according to the groups defined by cluster analysis in Fig. 2. Product moment correlation coefficients for the significant correlations (P<0.005) are indicated in the scatterplots.

The first two CCA axes (λ_1=0.30, λ_2=0.28) account for 17% of the variance in the weighted averages of the diatom data. Monte Carlo unrestricted permutation tests (99 permutations) of axis 1 and axis 2 (with axis 1 as covariable) indicate that both axes are significant (P < 0.05) (ter Braak 1990). Axis 1 is strongly related to conductivity (inter-set correlation = 0.76), and contrasts the high salinity coastal Livingston sites (Group 3b), and their constituent taxa *Navicula gregaria* (NA023A), *Navicula* species 1 (ZZZ952), *Nitzschia* species 1 (ZZZ957) and *Pinnularia* species 2 (ZZZ947), plotted on the right of axis 1, with the dilute waters found on Signy Island (Group 1b) such as Moss, Emerald and Twisted Lakes. These sites, with their characteristic taxa *Achnanthes minutissima* (AC013A), *Navicula* cf. *difficillima* (ZZZ980), and *Navicula bryophila* (NA045A), are plotted on the left of the diagram.

Axis 2 is strongly related to chlorophyll *a*, ammonium and silicate (inter-set correlations 0.64, 0.65, and -0.72, respectively) and again appears to reflect two gradients. The first, from top right to bottom left is related to trophic status and separates the oligotrophic inland Livingston sites of Group 2, plotted bottom left, from the other sites. Taxa characteristic of the former include *Achnanthes lanceolata* (AC001A), *A. exigua* (AC008A), *Navicula seminulum* (NA005A), *N. tantula* (NA086A), and *Stauroneis* species 1 (ZZZ941). Taxa plotted top right, such as *Fragilaria construens* var. *binodis* and *Nitzschia* species 1 (ZZZ957) are associated with the high conductivity, high nutrient waters of the coastal Livingston sites, while those plotted top centre such as *A. pinnata* (AC040A), *Navicula* species 3 (ZZZ989), *Gomphonema angustatum* var. *productum* (GO003B), *Achnanthes subatomoides* (AC136A) and *Fragilaria construens* var. *venter* (FR002C) are characteristic of the low conductivity, high nutrient sites on Signy Island (Group 1b). The second gradient runs from top left to bottom right and essentially separates Signy from Livingston lakes, and identifies

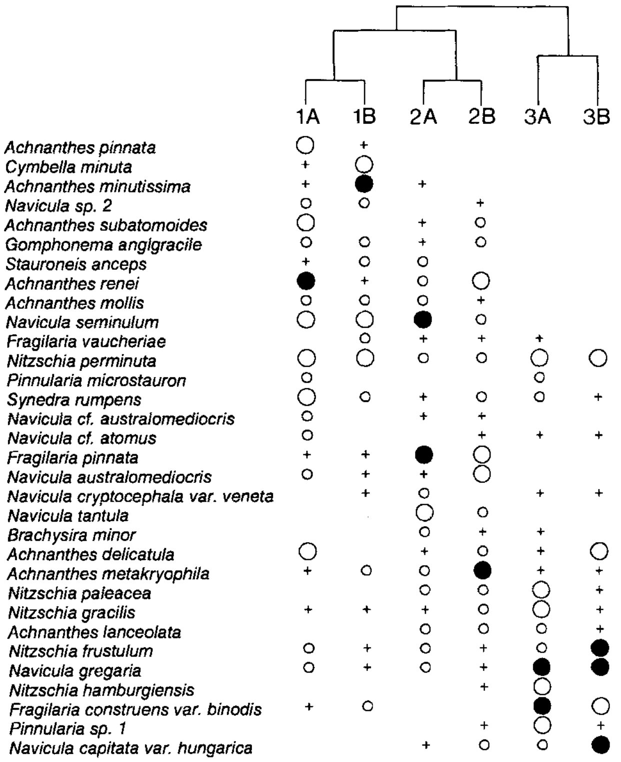

Fig. 4. TWINSPAN results showing groups of sites (top) and associated mean percentage diatom abundances *<2% *2–5% *5–10% *>10% Group 1A = sites SG2, SG5, SG6, SG8, SG10, SG11 and SG15 Group 1B = sites SG1, SG3, SG4, SG7, SG9, SG12 and SG14 Group 2A = sites LN1–7, LN9, LN10, LN14–19, LN21-24, LN27 and LN31 Group 2B = sites LN8, LN11-13, LN20, LN26, LN28–30, LN32–34, LN36 and LN43–45 Group 3A = sites LN35 and LN38–40 Group 3B = sites LN25, LN37, LN41 and LN42

taxa found either exclusively or in greater abundance on Signy Island, plotted in the top left quadrant (e.g. *Achnanthes minutissima* (AC013A), *A. incognita* (AC137A), *Navicula bryophila* (NA045A) and *Cymbella minuta* (CM031A)).

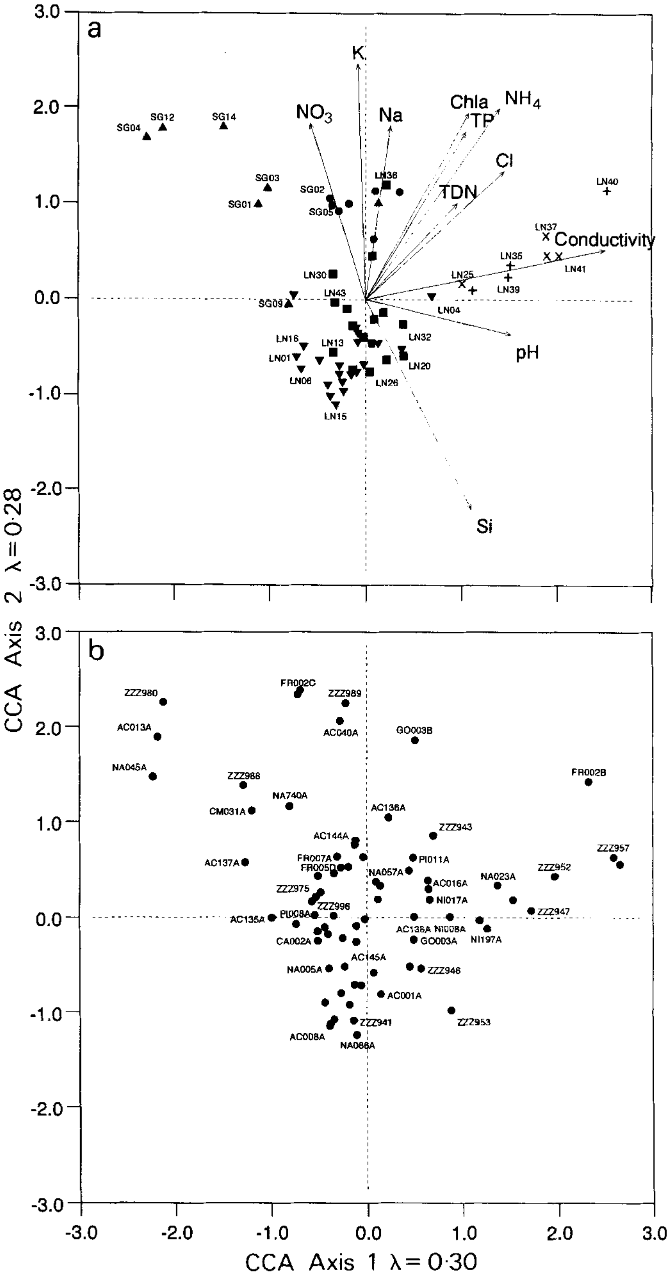

Fig. 5. Canonical correspondence analysis ordination diagram showing the relationship between sites. **a.** environmental gradients and **b.** diatom species. In **a.** sites are grouped according to the TWINSPAN results *1A *1B *2A *2B *3A *3B. A list of diatom codes and their equivalent species is given in Appendix 1.

Discussion

The lakes sampled on Livingston and Signy islands have quite distinct water chemistry, with the former having higher silicate and lower potassium and nitrate values than the Signy Island sites. Silicate is present in large amounts at both sites, being the major rock matrix component. However, tephra deposits may also provide an additional source of silica at Livingston Island (Björck *et al.* 1991) and silicate is probably released more readily at Byers than at Signy due to the higher weathering rate, and is thus present at high concentrations during the ice-free periods. Potassium is very mobile compared to silicate and would be quickly depleted from the weathered surface layers of Byers mineral particles. Slower weathering rates at Signy would result in a slower release rate and thus lower amounts of potassium moving into the water phase, but over a more extended period of time.

Work by Christie (1987) and Hawes (1983) suggests that precipitation, largely in the form of ammonium, is the main source of external nitrogen for oligotrophic systems, and this would quickly be converted to nitrate in soils and lakes. At Signy there are substantial penguin colonies which could potentially enhance this ammonium precipitation component (Christie 1987) whereas lakes on the central plateau of Livingston Island are not close to penguin colonies or even downwind, judging from wind direction data (Ellis-Evans, unpublished).

Due to the limited field period only one water chemistry measurement was made for most Livingston Island lakes, but where additional samples were taken, little variation between samples was noted. In addition, past experience of almost 20 years water sampling at Signy Island suggests that a summer measurement provides a reasonable estimate of the conditions experienced by diatoms in the growing season as the water column of such lakes are well mixed in summer open water conditions. The Livingston and Signy islands sites have comparable water chemistry to other freshwater Antarctic lakes, for example, in the Ablation Point area, Alexander Island (Heywood 1977), in the Vestfold Hills, East Antarctica (Laybourn-Parry & Marchant 1992, Laybourn-Parry *et al.* 1992) and with inland (180 km from the shelf) Antarctic lakes in the Untersee Oasis, East Antarctica (Kaup *et al.* 1988).

Although there are differences in the diatom flora of Livingston Island and Signy Island the range of species found in this study resembles that found in Southern America (Cleve-Euler 1948, Krasske 1939, 1949), the Subantarctic e.g. Kerguelen (Bourelly & Manguin 1949, 1954) and the maritime and continental Antarctic (Pankow *et al.* 1987, Schmidt *et al.* 1990, Björck *et al.* 1991). The flora consists of a mixture of taxa, some of which appear to be endemic to this region, for example *Achnanthes metakryophila*, *Achnanthes renei* and *Navicula australomediocris* and some of which are cosmopolitan, for example, *Navicula seminulum* and *Achnanthes minutissima*.

An unusual feature of the diatom flora is that no typical planktonic diatoms occur on either Livingston or Signy Islands, and although planktonic forms have been reported from Antarctic lakes (eg. Lavrenko 1965, Baker 1967) they are not common. This is in marked contrast to lakes in more temperate areas where diatom assemblages are often dominated by planktonic forms, for example the genera *Stephanodiscus* and *Cyclotella*. The absence of an Antarctic diatom plankton may be related to their lack of morphological or physiological characteristics (eg. high bouyancy capacity or inability to form resting stages) which would enable them to survive prolonged periods of ice cover (Heywood 1978, Guilizzoni *et al.* 1992). In addition, summer open water temperatures are low, for example when compared to Arctic lakes. The shallow nature of some of the lakes is probably not important since even small shallow ponds in temperate areas commonly develop a diatom plankton (eg. Guzkowska & Gasse 1990, H. Bennion pers. comm. 1992).

The patterns of diatom distribution and abundance are clearly related to the main chemical gradients of the lakes. Forward selection and associated Monte Carlo unrestricted permutation tests (99 permutations) of the significance of the environmental variables (ter Braak 1990) suggest that conductivity, potassium, chlorophyll *a*, sodium and ammonium make significant ($P<0.05$) contributions to explaining the variation in the diatom assemblages. Although there is not a planktonic diatom response to trophic status in these lakes, benthic diatoms in Antarctic lakes appear to act similarly to those in lakes in the rest of the world. For example species which are associated with nutrient-rich waters in the Antarctic such as *Fragilaria construens* var. *binodis*, *Achnanthes pinnata*, *Gomphonema angustatum* and *Achnanthes subatomoides* have a total phosphorus optima of >10 $\mu g l^{-1}$ in a Canadian data set (Hall & Smol 1992). Although little is known about the relationships between diatoms and environmental variables in Antarctic lakes, available data do support the results found here. Oppenheim (1990) in a study of 11 Signy Island lakes identified diatom species which were characteristic of proglacial, oligotrophic and mesotrophic lakes. In a further study of two of these lakes (Sombre Lake and Light Lake) redundancy analysis was used to show that the nutrient status was important in determining the epiphytic diatom assemblages (Oppenheim & Greenwood 1990). Hansson & Håkansson (1992) identified diatom species characteristic of nutrient poor and nutrient rich waters. However, their analysis did not include the effect of conductivity which this study has shown to be very important in determining diatom community composition.

This exploratory analysis of the relationship between diatom species and chemistry in the Maritime Antarctic has shown that diatom abundance can be related to environmental variables. The next stage in data analysis will be to calculate the quantitative responses of individual diatom species to nutrient and salinity gradients. This will enable the environmental reconstruction of nutrient and salinity histories of Antarctic lakes using diatoms preserved in lake sediments. It will therefore be possible to test hypotheses concerning lake development or the influence of recent animal populations in determining present day nutrient levels. There is a growing realization that Antarctic lake sediments can be used to reconstruct past environments and past lake conditions (Tatur & De Valle 1986, Mäusbacher *et al.* 1989, Schmidt *et al* 1990, Björck *et al.* 1991), and the use of quantitative relationships between diatoms and water chemistry derived from a maritime Antarctic data set should contribute significantly to future lake reconstruction studies.

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Appendix 1. List of diatom codes, species and authorities.

AC001A	*Achnanthes lanceolata* (Breb. ex Kutz.) Grun. in Cleve & Grun.
AC013A	*Achnanthes minutissima* Kutz.
AC008A	*Achnanthes exigua* Grun.
AC016A	*Achnanthes delicatula* Kutz.
AC040A	*Achnanthes pinnata* Hust.
AC135A	*Achnanthes mollis* Krasske
AC136A	*Achnanthes subatomoides* (Hust.) Lange-Bertalot & Archibald in Krammer & Lange-Bertalot
AC137A	*Achnanthes incognita* Krasske
AC138A	*Achnanthes germainii* Manguin in Bourelly & Manguin
AC144A	*Achnanthes renei* Lange-Bertalot & Schmidt
AC145A	*Achnanthes metakryophila* Lange-Bertalot & Schmidt
BR008A	*Brachysira minor* (Krasske) nov. com.
CA002A	*Caloneis bacillum* (Grun.) Cleve
CM031A	*Cymbella minuta* Hilse ex Rabenh.
FR001A	*Fragilaria* cf. *pinnata*
FR002B	*Fragilaria construens* var *binodis* (Ehr.) Grun.
FR002C	*Fragilaria construens* var *venter* (Ehr.) Grun.
FR005D	*Fragilaria virescens* var *exigua* Grun. in Van Heurck
FR007A	*Fragilaria vaucheriae* (Kutz.) J.B. Petersen
GO003A	*Gomphonema angustatum* (Kutz.) Rabenh.
GO003B	*Gomphonema angustatum* var *productum* Grun. in Van Heurck
NA005A	*Navicula seminulum* Grun.
NA007B	*Navicula cryptocephala* var *veneta* (Kutz.) Rabenh.
NA023A	*Navicula gregaria* Donk.
NA045A	*Navicula bryophila* J.B. Petersen
NA057A	*Navicula elginensis* (Greg.) Ralfs in Pritch.
NA066B	*Navicula capitata* var *hungarica* (Grun.) R. Ross
NA086A	*Navicula tantula* Hust.
NA734A	*Navicula australomediocris* Lange-Bertalot & Schmidt
NA740A	*Navicula bicephala* Hust.
NI005A	*Nitzschia perminuta* (Grun. in Van Heurck) Perag.
NI008A	*Nitzschia frustulum* (Kutz.) Grun. in Cleve & Grun.
NI017A	*Nitzschia gracilis* Hantzsch
NI033A	*Nitzschia paleacea* (Grun. in Cleve & Grun.) Grun. in Van Heurck
NI197A	*Nitzschia hamburgiensis* Lange-Bertalot
PI008A	*Pinnularia divergens* W. Smith
PI011A	*Pinnularia microstauron* (Ehrenb.) Cleve
SY002A	*Synedra rumpens* Kutz.
ZZZ941	*Stauroneis* species 1
ZZZ943	*Navicula* cf *atomus*
ZZZ946	*Pinnularia* species 1
ZZZ947	*Pinnularia* species 2
ZZZ952	*Navicula* species 1
ZZZ953	*Navicula* cf. *pupula*
ZZZ957	*Nitzschia* species 1
ZZZ975	*Amphora* species 1
ZZZ977	*Navicula* cf *australomediocris*
ZZZ980	*Navicula* cf *difficillima*
ZZZ988	*Navicula* species 2
ZZZ989	*Navicula* species 3
ZZZ992	*Gomphonema angustatum/gracile*
ZZZ996	*Stauroneis* species 2