Diatom species–environment relationships and inference models from Isachsen, Ellef Ringnes Island, Canadian High Arctic

Dermot Antoniades[1,*], Marianne S.V. Douglas[1] & John P. Smol[2]
[1]*Department of Geology, University of Toronto, Earth Sciences Centre, 22 Russell St., Toronto, ON, Canada, M5S 3B1*
[2]*PEARL, Department of Biology, Queen's University, Kingston ON, Canada, K7L 3N6*
(**Author for correspondence: Tel.: + 1-416-978-0665, Fax: + 1-416-978-3938, E-mail: dermot.antoniades@utoronto.ca*)

Abstract

Surface sediment diatom assemblages were examined from 26 freshwater sites near Isachsen (78° 47′ N, 103° 32′ W), Ellef Ringnes Island, a region of diverse and atypical water chemistry for high arctic sites. One hundred and sixty eight diatom taxa were identified from these samples, over 50% of which had not previously been recorded in the Canadian High Arctic. Variations in diatom assemblages were related to changes in measured environmental variables using multivariate techniques. Canonical correspondence analysis (CCA) indicated that five variables contributed significantly to explaining patterns of diatom variation (i.e., COND, DIC, Mn, TPF, TPU). The first CCA axis ($\lambda = 0.44$) was primarily controlled by conductivity-related variables, while CCA axis 2 ($\lambda = 0.21$) was related to particulate concentrations. Diatom-based inference models were generated for the reconstruction of conductivity (RMSEP$_{jack}$ = 0.32, r^2_{jack} = 0.76) and pH (RMSEP$_{jack}$ = 0.40, r^2_{jack} = 0.69). The strengths of these models indicate that it will be possible to reliably infer past trends in conductivity and pH from diatom assemblages preserved in dated sediment cores from the Isachsen region.

Introduction

Characterized by extremes of low temperature, low precipitation, and by prolonged periods of high and low solar radiation, the Canadian High Arctic is recognized as a critical reference area for the detection of global environmental change. Previous work indicates that the Arctic has been disproportionately affected by recent climatic change (Overpeck et al., 1997). With expected future warming of the region, the biota of high arctic limnological systems may be greatly affected by changes in hydrological regimes, longer annual ice-free periods, and increases in incident UV radiation, to name but a few (Rouse et al., 1997).

The lack of long-term instrumental climate records in the Canadian High Arctic limits our ability to evaluate changes in climate. Paleolimnological proxy records, using algal bioindicators such as diatoms, can be invaluable in replacing these missing climate records (Smol & Cumming, 2000). Diatoms are sensitive recorders of change in their environments, and are a major component of the periphyton of high arctic freshwaters (Douglas & Smol, 1999). However, in order to reliably infer environmental conditions from diatom assemblages, the ecological characteristics of diatom assemblages must be explored in new geographic regions by constructing surface sediment calibration sets (Smol, 2002).

Until recently, comparatively little such limnological or paleolimnological research had been completed in the Canadian High Arctic. Over the last decade, however, several limnological studies

have increased our understanding of the physical, chemical, and biological conditions across this diverse region. Studies concerned with diatom autecology are available from Ellesmere Island (Douglas & Smol, 1993, 1995), Bathurst Island (Lim et al., 2001a,c), and Victoria Island (Michelutti et al., 2003a). In addition, descriptive treatments of diatom biostratigraphic records have been published from Ellesmere Island (Douglas et al., 1994; Doubleday et al., 1995; Wolfe, 2000; Smith, 2002), Devon Island (Wolfe & King, 1999), and Cornwallis Island (Michelutti et al., 2003b). Comparable studies have also been completed in the Canadian Subarctic (Rühland et al., 2003) as well as other arctic regions (e.g., Andreev & Klimanov, 2000; Finney et al., 2002; Sorvari et al., 2002; Jones & Birks, 2004). However, the Arctic encompasses large gradients of limnology, geology, and climate. Therefore, considerable additional research is necessary in order to fully understand diatom biogeography and autecology across the Canadian High Arctic.

Ellef Ringnes Island (Fig. 1) is subject to the coldest and cloudiest summer climate in the Canadian High Arctic (Maxwell, 1981). As such, its freshwaters may be among the last in the High Arctic to show the effects of recent climate change. If paleolimnological studies in the Isachsen region reveal a significant degree of biotic change in response to climate warming, this may indicate that there are no remaining high arctic regions that have not been similarly altered. In addition, the freshwaters of the Isachsen region are characterized by tremendous ranges of limnological variables not seen elsewhere in regional studies from the High Arctic (Antoniades et al., 2003a). In contrast to their diverse limnological characteristics, the sites of this study have essentially identical
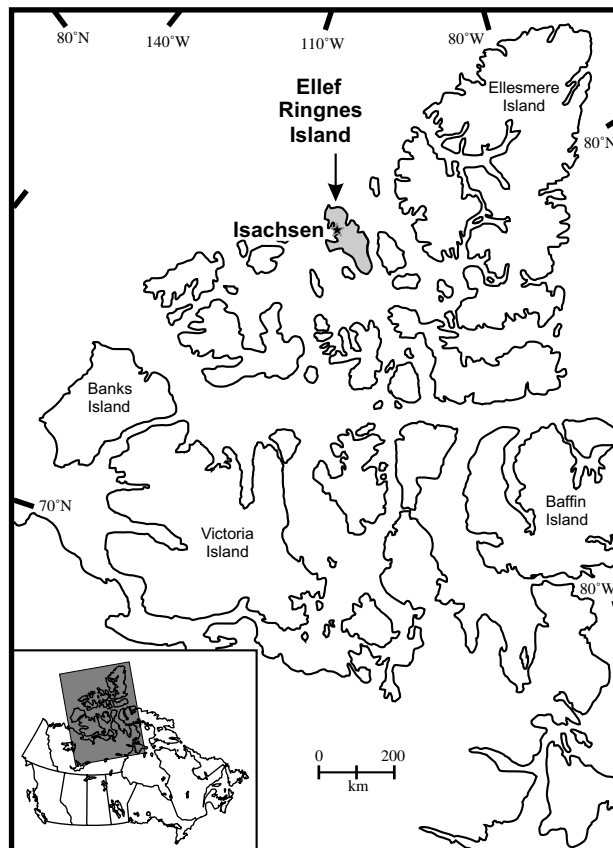

Figure 1. Location map of Isachsen and Ellef Ringnes Island in the Canadian High Arctic Archipelago. (modified from Antoniades et al., 2003a).

climates due to their restricted geographical range (i.e., ~15 km radius). As such, they provide a unique opportunity to evaluate the effects of large water chemistry variations on high arctic diatom assemblages in the absence of climate variation.

This study has the following objectives: (1) to expand the spatial and limnological range of high arctic diatom autecological information by relating differences in limnological variables to patterns of diatom community change from Isachsen, Ellef Ringnes Island; (2) to examine the roles of water chemistry and climate in driving differences in regional diatom assemblages; (3) to compare the taxonomic and autecological characteristics of the Isachsen region with previously published studies from the Canadian High Arctic; and (4) to develop transfer functions for the reconstruction of environmental change from diatom stratigraphic records.

Methods and materials

Site location and description

Isachsen (78° 47′ N, 103° 32′ W) is situated on the west coast of Ellef Ringnes Island, and served as an Environment Canada weather station from April 1948 until its closure in September 1978. A cold, desert climate prevails on Ellef Ringnes Island, and the Isachsen region has the coldest, cloudiest, foggiest summers in the High Arctic (Maxwell, 1981). Average annual precipitation is 102 mm/year, and daily mean temperatures range from −36.4 °C in February to 3.3 °C in July (annual mean = −19.0 °C); (Maxwell, 1982). The growing season is typically less than 1 month long, and the extreme climate and poorly formed soils preclude any significant terrestrial vegetative growth. Less than 10% of the soil surface is vegetated, and growth is restricted mainly to herbaceous plants and mosses (Edlund & Alt, 1989; Nahir, 1996).

Sample preparation and enumeration

Samples were collected for water chemistry and diatom analysis at 26 sites in close proximity (i.e., within 15 km) to the Isachsen weather station (78° 47′ N, 103° 32′ W) between July 21 and 31, 1996 (Fig. 2). Sites were selected in order to encompass the maximum available range of limnological and biological diversity. Of these, 24
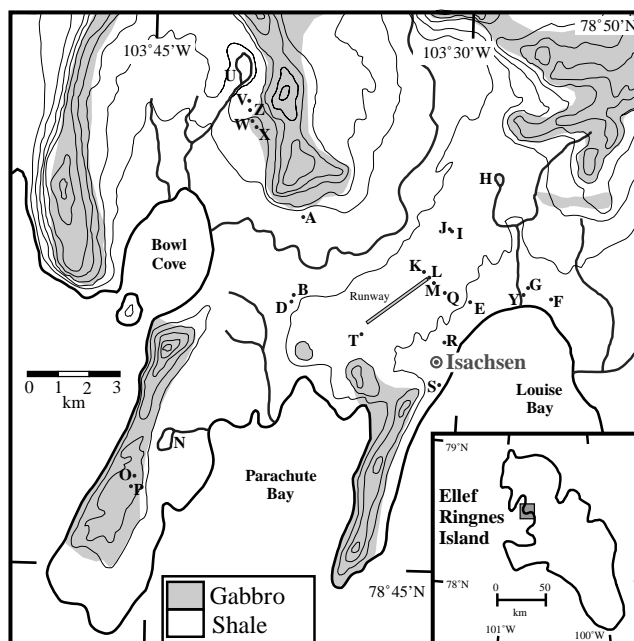

Figure 2. Map of location of Isachsen sample sites. Latitude and longitudes of each site are in Antoniades et al. (2003a). Contour interval = 30.5 m.

were considered ponds (i.e., <2 m depth), one site was a lake (i.e., I-U), and one site was a stream (i.e., I-C). Diameter was estimated visually in the field for small sites, while the diameter of larger sites was calculated from 1:50,000 NTS maps 69 F/12 and 69 F/13. Surface sediment samples were collected from each site using identical procedures used in our previous high arctic surveys (e.g., Lim et al., 2001a), with the exception of three sites (i.e., I-C, I-W, I-Z) where no sediment was present. In these cases, an epilithic sample was substituted.

Diatom samples were prepared using standard techniques (e.g., Pienitz & Smol, 1993) that are briefly described here. Ten milliliters of dilute HCl were added to remove carbonates from the sample, after which the samples were placed in a hot water bath at 100 °C for 1 h to accelerate the reaction. After allowing 24 h for settling, the supernatant was aspirated from the slurries, which were then rinsed with distilled water. This washing procedure was repeated until the slurries reached neutral pH. Subsequently, 10 ml of 1:1 H_2SO_4:HNO_3 were added to the samples in 2 ml increments. The samples were left at room temperature for 24 h, after which they were placed in a hot water bath at 100 °C for a minimum of 1 h to complete the reaction. A washing procedure similar to that following the addition of HCl was followed to return the samples to neutral pH. The slurries were then placed on cover slips and mounted on glass microscope slides in Naphrax® mounting medium (refractive index = 1.74).

Diatom samples were identified and enumerated using a Leica DMRB microscope equipped with Nomarski DIC optics under oil immersion at 1000× magnification. Typically, a minimum of 500 valves per sample was counted to the species or subspecies level. However, in three samples with unusually low concentrations of diatoms relative to siliciclastic particles, only 300 valves were counted (i.e., I-A, I-J, I-M). Taxonomic determinations were based primarily on Foged (1981), Germain (1981), Krammer & Lange-Bertalot (1986–1991) and Krammer (1992).

Water chemistry measurements were carried out both in the field and in subsequent laboratory analysis at the National Water Research Institute (NWRI) in Burlington, Ontario, according to standard protocols (Environment Canada, 1994). The water chemistry of the freshwaters surround-

ing the Isachsen weather station was distinct (Antoniades et al., 2003a) from those reported in other high arctic limnological surveys (e.g., Douglas et al., 1994; Hamilton et al., 2001; Lim et al., 2001b; Michelutti et al., 2002a, b; Antoniades et al., 2003b). The ranges of many measured limnological variables from Isachsen exceeded those found across the entire Canadian High Arctic, with both maxima and minima falling outside of previously identified high arctic ranges. However, median values (Table 1) indicated that, relative to most Canadian High Arctic regions, sites were typically moderately electrolyte rich (specific conductivity (COND) 228 μS/cm), mesotrophic (total phosphorus (TP) 16.9 μg/l), and weakly acidic (pH 6.8). The acidic ponds of the Isachsen region were in stark contrast with the strongly alkaline waters typical of most Canadian High Arctic sites.

The majority of the sites were located within short distances of the Arctic Ocean; however, inputs from marine aerosols were not the main factor controlling ionic concentrations, as specific conductivity was not correlated with distance from the sea or with elevation (Antoniades et al., 2003a). In sites located on shale, variability in conductivity values was related to soil development and to leachate inputs from localized acid sulfate soils, whereas sites on exposed gabbroic bedrock had extremely low solute concentrations (Fig. 2; Foscolos & Kodama, 1981; Antoniades et al., 2003a). A detailed analysis of spatial trends in the physical and chemical limnological characteristics of our sites, as well as further details on Isachsen's climate, geology, and soils, are presented in Antoniades et al. (2003a).

Statistical analysis

The Isachsen diatom and water chemistry datasets were analyzed using several multivariate techniques. Prior to the ordinations, the species and water chemistry datasets were analyzed separately to screen for outliers, defined as sites whose site scores exceeded the 95% confidence interval of the mean principal components analysis (PCA) scores (Birks et al., 1990). In subsequent analyses, the extreme characteristics of water chemistry outliers obscured species–environment trends present in the majority of sites. As such, the environmental

Table 1. Summary of Isachsen water chemistry

Variable	Mean	Median	Std. dev.	Max	Min
SO_4	303.2	131.0	456.3	2100	2.1
Cl	47.4	7.3	133.4	667	0.33
DIC	6.2	2.4	10.0	45.9	0.9
SiO_2	1.42	1.18	1.20	4.05	0.01
Na	71.6	17.0	143.0	546	0.5
Ca	49.0	21.3	63.9	264	1.2
Mg	35.6	12.4	59.0	273	0.5
K	4.3	2.1	5.90	24.7	0.2
Ag	0.001	0.001	0.000	0.001	< 0.001
Al	0.40	0.18	0.55	2.55	0.01
Ba	0.0164	0.0139	0.0119	0.0538	0.0009
Be	0.0003	0.0003	0.0000	0.0003	< 0.0002
Cd	0.001	0.001	0.000	0.001	< 0.001
Co	0.005	0.002	0.008	0.026	< 0.001
Cr	0.002	0.001	0.001	0.005	< 0.001
Cu	0.002	0.001	0.002	0.008	< 0.001
Fe	0.680	0.216	1.362	6.420	0.058
Li	0.049	0.025	0.073	0.341	0.001
Mn	0.2052	0.0180	0.5787	2.7900	0.0018
Mo	<0.001	< 0.001	0	< 0.001	< 0.001
Ni	0.009	0.004	0.012	0.040	< 0.002
Pb	0.005	0.005	0.000	0.005	< 0.005
Sr	0.1261	0.0707	0.1621	0.7170	0.0034
V	0.002	0.002	0.002	0.006	< 0.001
Zn	0.006	0.003	0.007	0.026	0.001
TKN	0.148	0.147	0.087	0.453	0.040
NO_2	0.003	0.002	0.001	0.004	< 0.002
NO_3NO_2	0.035	0.015	0.033	0.091	< 0.010
NH_3	0.031	0.009	0.067	0.250	< 0.005
PN	0.130	0.062	0.201	0.981	0.015
TN	0.295	0.232	0.285	1.525	0.074
POC	1.325	0.609	2.050	9.890	0.256
DOC	2.1	1.9	1.0	4.6	0.9
TPU (μg/l)	41.9	16.9	0.1	256.9	4.5
TPF (μg/l)	6.1	6.3	0.0	17.6	3.0
SRP (μg/l)	0.5	0.4	0.0	2.4	< 0.2
CHLA (μg/l)	1.5	1.2	1.6	5.3	< 0.1
T (°C)	3.0	3.0	1.3	5.5	0.0
pH	6.8	6.8	0.7	7.9	5.1
Cond (μS/cm)	405	228	504	2130	10
Depth (m)	0.99	0.30	2.93	15	0.25
Diam (m)	70	27	111	460	3
ELEV (m)	38	43	21	69	6

See text for abbreviations. Units are mg/l unless otherwise noted.

dataset was transformed to reduce the influence of these extreme sites. Log(x) transformation was required to normalize distributions of aluminum (Al), chlorophyll-a (Chla), chloride (Cl), specific conductivity (COND), copper (Cu), site diameter (Diam), dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), iron (Fe), potassium (K), lithium (Li), magnesium (Mg), manganese (Mn), sodium (Na), particulate organic carbon (POC), particulate organic nitrogen (PON), sulfate (SO_4), strontium (Sr), total phosphorus (TPU), total dissolved phosphorus (TPF) and total nitrogen (TN), log($x + 1$) transformation for calcium (Ca), log($x + 0.5$) transformation was required to normalize depth, and square root transformation for barium (Ba), elevation (Elev), silica (SiO_2), and total Kjeldahl nitrogen (TKN). The species dataset was also square root transformed to reduce the influence of dominant taxa.

The overall community structure and gradient lengths of the species data were investigated using detrended correspondence analysis (DCA), while canonical correspondence analysis (CCA) was used to explore species–environment relationships in the datasets (Jongman et al., 1995). Highly correlated environmental variables were removed from the dataset prior to CCA, as well as those that were below detection limits at a majority of sites, reducing the environmental dataset to 14 variables (i.e., Al, Ba, Chla, COND, Diam, DIC, DOC, Elev, Mn, NH_3, pH, TN, TPF, and TPU). Detrended canonical correspondence analysis (DCCA) constrained to single environmental variables was used to investigate the explanatory potential of each variable individually, and the DCCA gradient length was used to determine whether linear or unimodal techniques were appropriate for subsequent calibration steps (Birks, 1995). All DCA, CCA, and DCCA analyses were performed using the computer program CANOCO version 4.0 (ter Braak, 1998), during which the significances of all axes were tested using 999 unrestricted Monte Carlo permutations.

The strengths and weaknesses of different modeling approaches were evaluated by constructing several models for each variable selected for reconstruction. Weighted averaging (WA), partial least squares (PLS), and weighted-averaging partial least squares (WA-PLS) calibration steps were carried using the programs WACALIB version 3.5 (Line et al., 1994), WAPLS version 1.2 (Juggins & ter Braak, 2000), and C^2 version 1.3 (Juggins, 2003). In addition, the degree to which individual species–environment relationships conformed to the model assumptions was assessed using Huisman–Olff–Fresco methods (Huisman et al., 1993) with the computer program HOF version 2.3 (Oksanen, 1998).

Results and discussion

Initial PCA analysis indicated that two sites were considered outliers according to their water chemistry (i.e., I-N, I-Q), while one site (I-T) was an outlier by its species composition. However, to merit exclusion, a site must be considered an outlier according to both species and water chemistry (H.J.B. Birks, pers. comm.), and so all sites were included in further analyses.

Diatom species–environment relationships

Isachsen diatom communities were distinct from those found elsewhere in the Canadian High Arctic. A total of 168 diatom taxa from 24 genera were identified from our 26 sites (Table 2). Despite homogenous climate across our restricted study area, diatom assemblages showed huge between-site variability, suggesting that the role of water chemistry outweighed that of climate in determining diatom species compositions. Due to the shallow nature of the majority of the sites, diatom assemblages were overwhelmingly dominated by small, benthic taxa, primarily from the genera *Navicula*, *Nitzschia*, *Pinnularia*, and *Achnanthes*.

DCA indicated that the gradient length of the species data exceeded two standard deviations (i.e., 3.38), thus unimodal methods were deemed appropriate for subsequent analyses (Birks, 1995). CCA with forward selection indicated that there were five variables significantly ($p \leq 0.05$) related to the diatom dataset (i.e., COND, DIC, Mn, TPF, and TPU). The first four axes of a CCA constrained to these five variables were significant and explained 31.0% of the measured variance in the diatom data. On the CCA biplot (Fig. 3), the lengths of the arrows represent the relative importance of different variables in explaining diatom distributions, while the angle of arrows

Table 2. List of taxa, with number of occurrences, Hill's N2, and COND and pH optima

Taxon #	Taxon Name	# Occur.	Hill's N2	Max. abun. (%)	Cond WA opt. (μS/cm)	pH WA opt.	pH resp. model
2	*Achnanthes broenlundensis* Foged	1	1.00	0.5	19	6.5	
3	*A. chlidanos* Hohn and Hellerman	1	1.00	0.6	89	7.8	
4	*A. delicatula* Kützing	1	1.00	0.9	17	6.9	
6	*A. flexella* Kützing	2	1.68	2.3	251	6.5	
7	*A. helvetica* Hustedt	9	6.68	11.5	28	6.8	UM
10	*A. kryophila* Petersen	7	6.49	1.3	92	7.0	NR
12	*A. laevis* Oestrup	2	1.92	1.5	278	7.0	
13	*A. marginulata* Grunow in Cleve and Grunow	14	8.09	32.4	56	6.6	UM
14	*A. minutissima* Kützing	4	3.26	5.6	171	6.4	UM
18	*A. petersenii* Hustedt	9	6.24	14.0	120	6.9	NR
20	*A. rossii* Hustedt	1	1.00	1.8	32	6.8	
21	*A. rupestris* Krasske	1	1.00	24.4	603	6.4	
23	*A. subatomoides* Hustedt	1	1.00	0.5	19	6.5	
24	*A. ventralis* Krasske	6	5.79	1.1	25	6.9	UM
28	*Achnanthes* sp. I1	3	2.72	1.8	124	6.1	SD
30	*Amphipleura rutilans* (Trentepohl) Cleve	6	4.81	12.3	775	7.5	SI
32	*Amphora inariensis* Krammer	1	1.00	0.6	89	7.8	
34	*A. pediculus* (Kützing) Grunow ex Schmidt	1	1.00	1.1	32	6.8	
35	*A. spitzbergensis* VanLandingham	10	8.52	6.8	330	7.2	NR
37	*Aulacoseira alpigena* (Grunow in Van Heurck) Krammer	1	1.00	4.8	10	6.7	
38	*Aulacoseira* sp. I1	13	12.28	1.3	235	7.0	NR
40	*Caloneis aerophila* Bock	19	12.42	47.6	91	6.6	SD
41	*C. arctica* (Krasske) Lange-Bertalot	2	1.68	1.2	26	7.3	
43	*C. clevei* (Lagerstedt) Cleve	1	1.00	0.4	891	7.0	
46	*C. silicula* (Ehrenberg) Cleve	6	5.59	1.2	175	6.7	NR
49	*Caloneis* sp. I2	15	9.62	22.4	371	7.2	NR
50	*C. subclevei* Krammer	9	8.56	1.3	85	6.5	NR
54	*Cyclotella pseudostelligera* Hustedt	1	1.00	2.9	32	6.8	
55	*Cylindrotheca gracilis* (Brebisson) Grunow in Van Heurck	5	4.49	1.5	336	7.1	NR
58	*Cymbella angustata* (W. Smith) Cleve	2	2.00	0.4	18	6.8	
59	*C. arctica* (Lagerstedt) Schmidt	2	1.69	1.1	23	6.8	
65	*C. cuspidata* Kützing	1	1.00	0.5	32	6.8	
66	*C. descripta* (Hustedt) Krammer and Lange-Bertalot	2	2.00	0.4	46	6.8	
69	*C. falaisensis* (Grunow) Krammer and Lange-Bertalot	1	1.00	0.6	49	7.1	
74	*C. lapponica* Grunow	6	5.18	2.3	29	6.7	UM
75	*C. latens* Krasske	6	4.75	4.3	71	6.8	UM
77	*C. microcephala* Grunow in Van Heurck	2	2.00	0.4	213	7.2	
78	*C. minuta* Hilse in Rabenhorst	4	3.35	2.6	45	7.2	NR
79	*C. obscura* Krasske	1	1.00	0.7	32	6.8	
82	*C. silesiaca* Bleisch in Rabenhorst	3	2.62	2.1	48	7.1	NR

Table 2. (Continued)

Taxon #	Taxon Name	# Occur.	Hill's N2	Max. abun. (%)	Cond WA opt. (μS/cm)	pH WA opt.	pH resp. model
100	*Denticula kuetzingii* Grunow	2	2.00	0.4	23	6.9	
101	*D. subtilis* Grunow	2	1.31	29.9	1886	7.9	
102	*Diadesmis contenta* (Grunow) Mann	2	1.73	7.8	21	6.9	
103	*D. gallica* W.Smith	10	5.81	21.0	36	6.7	UM
104	*D. paracontenta* Lange-Bertalot and Werum	20	14.05	37.5	176	6.9	NR
105	*D. perpusilla* (Grunow) Mann	11	6.42	26.7	64	6.6	SU
106	*Diatoma anceps* (Ehrenberg) Kirchner	1	1.00	2.1	295	6.7	
108	*D. tenuis* Agardh	9	8.02	4.2	530	7.1	NR
114	*Eunotia arcus* Ehrenberg	1	1.00	1.3	49	7.1	
116	*E. boreotenuis* Lange-Bertalot and Nörpel-Schempp	3	2.71	2.4	18	6.7	UM
118	*E. monodon* Ehrenberg	2	2.00	0.7	13	6.8	
119	*Eunotia* sp. I1	2	1.98	1.1	25	6.7	
120	*E. praerupta* Ehrenberg	4	3.54	2.3	24	6.5	NR
121	*E. pseudopectinalis* Hustedt	2	1.90	0.9	13	6.6	
122	*E. rhyncocephala* Hustedt	2	1.83	2.6	62	7.4	
124	*Fragilaria capucina* Desmazières	3	2.89	8.6	44	6.7	UM
128	*Fragilaria pinnata* Ehrenberg	3	2.30	11.4	18	6.7	UM
129	*Fragilaria vaucheriae* (Kützing) Petersen	8	6.25	13.5	28	6.9	NR
130	*Frustulia rhomboides* (Ehrenberg) De Toni	1	1.00	0.7	19	6.5	
133	*Gomphonema angustatum* Agardh	2	2.00	0.6	160	7.3	
134	*G. clavatulum* Ehrenberg	2	2.00	0.6	150	7.4	
141	*G. parvulum* (Kützing) Kützing	1	1.00	2.9	32	6.8	
145	*Hannaea arcus* (Ehrenberg) Patrick	4	3.89	1.0	77	7.2	NR
146	*Hantzschia amphioxys* (Ehrenberg) Grunow	2	1.82	1.3	62	7.4	
147	*Meridion circulare* (Greville) Agardh	2	1.96	2.3	176	7.2	
148	*Navicula atomus* var. *permitis* (Hustedt) Lange-Bertalot	1	1.00	1.3	89	7.8	
149	*N. bacillum* Ehrenberg	1	1.00	0.4	295	6.7	
151	*N. bryophila* (Petersen) Lange-Bertalot	1	1.00	0.3	49	7.1	
152	*N. angustata* Grunow	1	1.00	0.4	17	6.9	
156	*N. cincta* (Ehrenberg) Ralfs	13	10.86	9.5	451	7.3	UM
158	*N. cocconeiformis* Gregory ex Greville	5	4.32	1.8	44	6.6	SU
159	*N. cryptocephala* Kützing	9	7.63	5.4	35	7.0	NR
161	*N. elginensis* (Gregory) Ralfs	1	1.00	0.6	89	7.8	
163	*N. farta* Hustedt	1	1.00	0.6	123	7.1	
166	*N. gandrupii* Krasske	23	17.10	54.6	249	6.9	NR
167	*N. genustriata* Hustedt	1	1.00	0.6	89	7.8	
168	*N. gerloffii* Schimanski	8	6.91	5.1	51	6.8	NR
169	*N. gibbula* Cleve	6	5.46	2.6	65	7.1	NR
170	*N. globulifera* Hustedt	7	6.17	2.3	709	7.3	NR
171	*N. gregaria* Donkin	2	1.96	9.4	1100	7.8	
173	*N. halophilioides* Hustedt	5	4.16	2.7	31	7.0	NR

Table 2. (Continued)

Taxon #	Taxon Name	# Occur.	Hill's N2	Max. abun. (%)	Cond WA opt. (μS/cm)	pH WA opt.	pH resp. model
175	*N. insociabilis* Krasske	1	1.00	0.4	66	6.8	
179	*N. krasskei* Hustedt	3	2.93	0.6	98	7.0	NR
180	*N.* sp. 1 aff. *krasskei* Hustedt	9	7.18	7.1	79	6.8	NR
181	*N.* sp. 2 aff. *krasskei* Hustedt	11	8.43	4.2	86	6.9	NR
182	*N. lapidosa* Krasske	1	1.00	0.4	295	6.7	
184	*N. lenzii* Hustedt in Schmidt	1	1.00	0.3	49	7.1	
188	*N. mutica* Kützing	17	14.15	4.8	281	6.9	NR
190	*N. nivaloides* Bock	1	1.00	1.1	17	6.9	
191	*N. perminuta* Grunow in Van Heurck	1	1.00	2.6	89	7.8	
192	*N. phyllepta* Kützing	7	5.21	15.9	854	7.4	SI
193	*N. porifera* Hustedt	2	2.00	0.4	13	6.8	
194	*N. pseudoscutiformis* Hustedt	6	3.92	19.9	24	6.6	NR
195	*N. pseudotenelloides* Krasske	8	5.83	10.6	269	7.2	SU
196	*N. pupula* var. *mutata* (Krasske) Hustedt	2	1.79	2.2	14	6.6	
209	*N. tripunctata* (Muller) Bory	1	1.00	1.0	2138	7.9	
216	*N. vulpina* Kützing	1	1.00	0.3	89	7.8	
217	*N. wulffii* Petersen	3	2.62	1.3	33	6.9	UM
237	*Navicula* sp. I1	10	7.94	8.8	332	7.2	SU
238	*Navicula* g.v. sp. 1	1	1.00	17.7	1380	7.5	
239	*Navicula* sp. I10	1	1.00	0.3	19	6.5	
240	*Navicula* sp. I11	1	1.00	0.5	19	6.5	
241	*Navicula* sp. I12	1	1.00	1.6	19	6.5	
242	*Navicula* sp. I1B	4	3.79	1.0	167	6.8	NR
243	*Navicula* sp. I2	3	2.97	1.3	355	6.4	NR
244	*Navicula* sp. I3	1	1.00	1.4	275	5.1	
245	*Navicula* sp. I4	1	1.00	1.9	741	5.6	
246	*Navicula* sp. I5	1	1.00	1.9	457	7.7	
247	*Navicula* sp. I6	1	1.00	0.6	49	7.1	
248	*Navicula* sp. I7	1	1.00	0.4	17	6.9	
249	*Navicula* sp. I8	1	1.00	0.7	12	6.7	
250	*Navicula* sp. I9	1	1.00	0.2	513	6.7	
251	*Neidium affine* (Ehrenberg) Pfitzer	5	4.30	2.5	18	6.7	UM
252	*N. ampliatum* (Ehrenberg) Krammer	8	7.61	0.9	54	6.6	NR
253	*N. bergii* (Cleve) Krammer	7	6.35	1.9	54	6.9	NR
254	*N. bisulcatum* (Lagerstedt) Cleve	1	1.00	0.8	158	5.9	
255	*N. decoratum* Brun	1	1.00	2.6	49	7.1	
259	*N. iridis* (Ehrenberg) Cleve	1	1.00	0.9	355	7.7	
262	*Neidium* sp. I1	1	1.00	0.4	275	5.1	
264	*Nitzschia acicularis* (Kützing) W. Smith	1	1.00	0.8	891	7.0	
266	*N. amphibia* Grunow	1	1.00	0.7	10	6.7	
268	*N. clausii* Hantzsch	14	8.63	47.5	491	7.3	UM
269	*N. commutata* Grunow	7	5.70	5.2	172	7.0	UM
270	*N. commutatoides* Lange-Bertalot	5	4.06	5.2	374	6.9	NR
271	*N. debilis* Arnott	8	6.82	3.6	192	6.8	NR
272	*N. dissipata* var. *media* (Hantzsch) Grunow in Van Heurck	9	6.66	9.0	455	7.2	UM

Table 2. (Continued)

Taxon #	Taxon Name	# Occur.	Hill's N2	Max. abun. (%)	Cond WA opt. (μS/cm)	pH WA opt.	pH resp. model
273	*N. dubia* W. Smith	5	4.28	3.0	138	7.4	UM
274	*N. fonticola* Grunow in Van Heurck	1	1.00	0.4	32	6.8	
275	*N. homburgiensis* Lange-Bertalot	15	9.45	32.3	186	6.9	UM
276	*N. inconspicua* Grunow	6	4.34	23.2	84	7.4	SU
277	*N. lacuna* Patrick and Freese	5	4.68	3.2	103	7.4	UM
279	*N. normannii* Grunow in Van Heurck	8	4.94	15.3	335	6.1	SD
281	*N. palea* (Kützing) W. Smith	17	15.13	3.2	209	7.0	NR
282	*N. paleacea* Grunow	3	2.64	2.8	580	7.1	NR
283	*N. palustris* Hustedt	14	12.89	2.6	137	7.0	NR
284	*N. perminuta* (Grunow) Peragallo	23	18.01	67.9	136	6.9	NR
285	*N. pura* Hustedt	2	1.83	0.7	12	6.8	
286	*N. pusilla* Grunow	9	6.58	13.7	453	6.7	NR
289	*N. tubicola* Grunow	1	1.00	0.6	49	7.1	
290	*N. vitrea* Norman	1	1.00	4.2	457	7.7	
294	*Pinnularia balfouriana* Grunow ex Cleve	4	1.84	22.2	221	6.0	UM
295	*P. borealis* Ehrenberg	18	14.69	4.4	240	6.6	SD
298	*P. divergens* W. Smith	9	8.24	1.2	87	7.0	NR
301	*P. divergentissima* (Grunow) Cleve	3	2.32	4.6	73	6.2	UM
302	*P. gebhardii* (Krasske) Hustedt	1	1.00	0.4	295	6.7	
303	*P. humilis* Krammer and Lange-Bertalot	1	1.00	0.4	513	6.7	
304	*P. intermedia* (Lagerstedt) Cleve	22	16.55	12.0	179	6.6	SD
305	*P. interrupta* W. Smith	3	2.94	0.8	51	7.2	NR
307	*P. obscura* Krasske	18	13.02	9.4	95	6.8	NR
309	*P. microstauron* (Ehrenberg) Cleve	5	4.91	0.7	30	6.8	UM
311	*P. subinterrupta* Krammer and Schroeter	5	4.68	1.9	25	6.8	UM
312	*P. subrostrata* (A. Cleve) Cleve and Euler	7	6.04	3.4	168	6.3	UM
313	*P. suchlandtii* Hustedt in Schmidt	4	3.35	2.9	26	7.0	NR
317	*Pinnularia* sp. I1	1	1.00	0.6	36	7.5	
318	*Pinnularia* sp. I2	2	2.00	0.6	67	7.3	
319	*Pinnularia* sp. I3	1	1.00	1.8	123	7.1	
320	*Pinnularia* sp. I4	1	1.00	0.4	66	6.8	
321	*Pinnularia* sp. I5	1	1.00	1.2	275	5.1	
322	*Pinnularia* sp. I6	1	1.00	0.6	741	5.6	
323	*Pinnularia* sp. I7	1	1.00	0.7	32	6.8	
324	*Stauroneis anceps* Ehrenberg	14	9.88	17.9	76	6.4	SD
325	*S. phoenicenteron* (Nitzsch) Ehrenberg	4	3.96	1.0	92	6.9	NR
326	*S. prominula* (Grunow) Hustedt	9	5.61	17.6	351	7.0	NR
327	*S. pseudosubobtusoides* Germain	1	1.00	2.1	355	7.7	
329	*S. thermicola* (Petersen) Lund	1	1.00	3.5	19	6.5	
330	*Surirella angusta* Kützing	2	1.94	0.7	20	6.8	
331	*S. brebissonii* Krammer and Lange-Bertalot	1	1.00	0.3	89	7.8	
332	*S. minuta* Brebisson	5	4.09	5.4	48	7.2	UM

pH response models as determined by HOF are included for all taxa present in three or more sites. UM = unimodal, SD = sigmoidal decreasing, SI = sigmoidal increasing, NR = no significant relationship. Taxon numbers listed are those used in Figure 2.
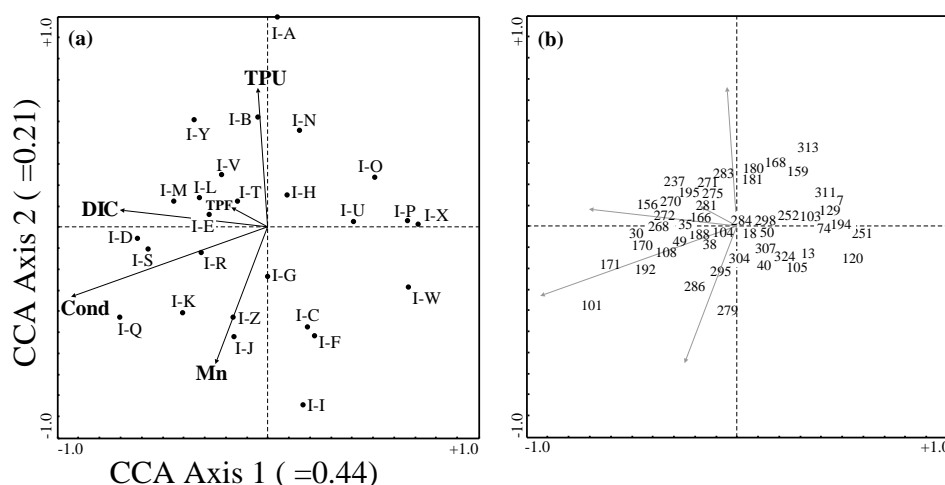
Figure 3. CCA biplot of analysis with five forward selected environmental variables. (a) Environmental variables vs. sites. (b) Environmental variables vs. species. See Table 2 for index of taxon numbers.

relative to the axes and to other variables indicate the strength of their correlations. Acute angles indicate highly correlated variables, while right angles indicate that no relationship exists between variables (Jongman et al., 1995). The first CCA axis ($\lambda = 0.44$) was most closely associated with conductivity and DIC, while axis 2 ($\lambda = 0.21$) was controlled primarily by TPU and Mn concentrations. TPU was highly correlated with POC, PON, and Fe, but uncorrelated with dissolved nutrient variables (i.e., TPF, TKN). As such, axis 2 most likely represents a gradient of particulate concentrations rather than nutrients, as evidenced by the wide angle between TPU and TPF in the biplot.

Major diatom taxa (i.e., present in at least 10 sites) are plotted in Figure 4. Although sites and taxa in Figure 4 were ordered according to increasing DCA axis 1 scores, this arrangement also produced a species gradient of descending COND optima (see Table 2). Therefore, while DCA is an analysis of community composition independent of environmental data, Figure 4 suggested a close relationship between changes in conductivity and diatom assemblages.

The diatom communities from the highest conductivity sites clustered at the negative end of DCA axis 1, and thus at the top of Figure 4. Hill's N2 values for these sites were low, reflecting the exclusion of many taxa in these high conductivity conditions. In addition to the taxa shown in Figure 4, *Denticula subtilis, Amphipleura rutilans,*

Amphora spitzbergensis, and *Navicula phyllepta* were abundant in high conductivity sites. These species were largely restricted to sites at the extreme of the conductivity gradient and had the lowest DCA species scores.

The CCA biplot confirmed the relationship between diatom assemblages and changes in conductivity, with high and low conductivity sites located at the extremes of the first CCA axis. Diatom communities from the highest conductivity sites were clustered at the negative end of axis 1. Taxa common in these assemblages were typically those associated with high electrolyte and brackish waters (e.g., Patrick & Reimer, 1966; Lowe, 1974; Lange-Bertalot, 2001), including *Amphipleura rutilans, Denticula subtilis, Diatoma tenuis, Navicula cincta, Navicula globulifera, Navicula gregaria, Navicula phyllepta, Nitzschia clausii, Nitzschia commutatoides,* and *Nitzschia dissipata* var. *media.* As expected, these taxa had COND optima ranging from 374 to 1886 μS/cm (Table 2). Of these taxa, only *D. tenuis, N. cincta, N. phyllepta,* and *N. dissipata* var. *media* have been previously reported in the Canadian High Arctic.

By contrast, diatom taxa with broad environmental ranges characterized moderate conductivity sites (i.e., 100–400 μS/cm), where they typically reached their maximum relative abundances. These generalist species, including *Navicula gandrupii, Diadesmis paracontenta, Pinnularia intermedia,* and *Nitzschia perminuta,* were identified in at least 20 of
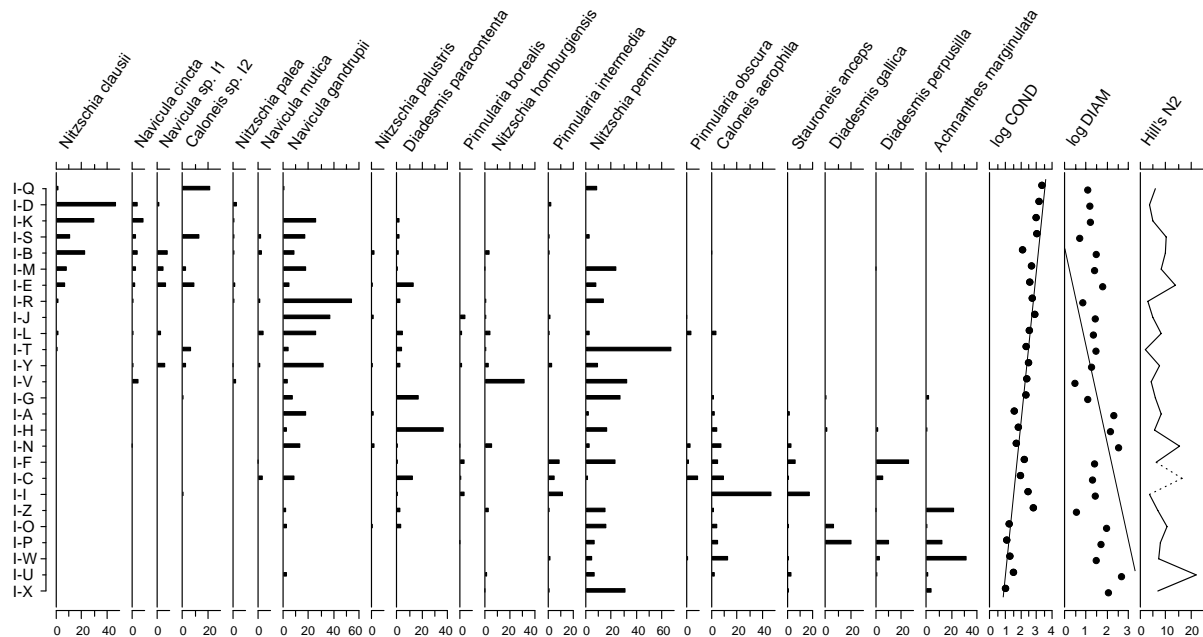
Figure 4. Relative abundances of major diatom taxa (i.e., $n > 10$) in Isachsen sites.

our 26 sites (Fig. 4), had moderate COND optima (i.e., 136–249 μS/cm; Table 2), and were located at or near the center of the CCA biplot (Fig. 3), indicating that they had no strong affinity towards any of the environmental variables in the CCA.

Nitzschia perminuta is a common and abundant component of high arctic diatom assemblages, and has been identified from Bathurst, northern Ellesmere, Victoria, and Prince Patrick islands (Lim et al., 2001a, c; Michelutti et al., 2003a, unpublished data). Despite wide distributions and ecological tolerances in this study, however, *N. gandrupii* was not common on northern Ellesmere and Prince Patrick Islands (unpublished data), and not recorded in previous high arctic studies (Douglas & Smol, 1993; Lim et al., 2001a; Michelutti et al., 2003a). *D. paracontenta* was a rare component of Ellesmere and Prince Patrick Island diatom assemblages (Douglas & Smol, 1995, unpublished data), whereas *P. intermedia* occurred rarely in sites on Victoria and northern Ellesmere islands (Michelutti et al., 2003a, unpublished data).

Taxa with high DCA axis 1 species scores included *Achnanthes marginulata*, *A. petersenii*, *A. helvetica*, *Diadesmis gallica*, *D. perpusilla*, *Fragilaria vaucheriae*, and *Eunotia praerupta*. These taxa, found to be moss epiphytes characteristic of

low alkalinity assemblages elsewhere in the Canadian High Arctic (Douglas & Smol, 1995; Lim et al., 2001c; Michelutti et al., 2003a), were primarily restricted to the low conductivity sites found near the bottom of Figure 4.

Low conductivity diatom assemblages at Isachsen differed from those in other high arctic surveys, driven by several key taxa. *Caloneis aerophila* was present in 19 Isachsen sites at the low end of the conductivity spectrum, but was not previously recorded in high arctic diatom surveys (Douglas & Smol, 1995; Lim et al., 2001a, c; Michelutti et al., 2003a). Similarly, *Navicula pseudoscutiformis* and *Stauroneis anceps* were present in low conductivity Isachsen sites, but were reported only from Bathurst Island as a rare component of diatom assemblages (Lim et al., 2001a, c).

Low conductivity sites (i.e., <100 μS) underlain by gabbro (Antoniades et al., 2003a) dominated the positive end of the first CCA axis, indicating a common diatom response to limnological conditions resulting from this chemically resistant substrate. In addition to the taxa above, these sites were further characterized by increased relative abundances of other oligohalobous diatoms, including *Cymbella lapponica*, *Navicula pseudoscutiformis*, *Neidium affine*, *Pinnularia mi-*

crostauron, *P. subinterrupta*, and *P. suchlandtii* (Patrick & Reimer, 1966; Lowe, 1974; Krammer, 2000). Not surprisingly, these taxa all had COND optima below 40 μS/cm (Table 2). Several of these taxa with pH optima below 7.0 also distinguished Isachsen from other high arctic sites (i.e., *Achnanthes helvetica*, *Cymbella lapponica*, *Diadesmis gallica*, *Pinnularia subinterrupta*). Their absence from other high arctic surveys is likely due to the paucity of non-alkaline sites in these other regions.

Previous high arctic studies have suggested higher diversity diatom communities in ponds vs. lakes (see Douglas & Smol, 1999). However, in our sites, more diverse assemblages were associated with increases in diameter. In addition to many taxa present in small sites, other small, benthic taxa from the genera *Achnanthes*, *Diadesmis*, and *Navicula* appeared or increased in abundance as site diameter increased. In our dataset, the lone lake (I-U) had the highest Hill's N2 value, and *t*-tests indicated that diameter and N2 were positively correlated ($r = 0.77$). These diversity increases do not appear to be an artefact of the weaker negative correlation between diameter and conductivity ($r = 0.68$), as conductivity and N2 were uncorrelated ($r = 0.37$).

The higher diversity of I-U may reflect increasing community structure due to the more heterogeneous microhabitats present in this lake relative to the smaller, shallower ponds. Eight diatom taxa (i.e., *Achnanthes rossii*, *Amphora pediculus*, *Cyclotella pseudostelligera*, *Cymbella cuspidata*, *Cymbella obscura*, *Gomphonema parvulum*, *Nitzschia fonticola*, and *Pinnularia* sp. I7) were present in our one lake (I-U) that did not occur in any of the ponds. I-U was, however, located amongst ponds of similar chemistry on the CCA biplot (Fig. 3), suggesting that water chemistry is more influential than morphometric characteristics in determining overall community composition.

Three epilithic samples were examined from sites where no sediments were present (i.e., I-C, I-W, I-Z). However, these epilithic samples in the dataset were not distinguished from sediment samples in either the DCA or CCA results (Figs. 3 and 4), indicating that water chemistry was more important than substrate in determining diatom species composition. Nonetheless, there were certain taxa that were distinct to each of these three samples. Only one species was unique to I-Z (i.e., *Achnanthes rupestris*), however, it represented 24.4% of the diatoms counted from that site. It has not been recorded in previous high arctic surveys, and is a rare nordic-alpine taxon with poorly defined autecological characteristics (Krammer & Lange-Bertalot, 1986–1991).

Site I-W was located near other, similarly low conductivity sites on the CCA biplot (Fig. 3), although seven taxa were found only in this pond (i.e., *Achnanthes broenlundensis*, *A. subatomoides*, *Frustulia rhomboides*, *Navicula* sp. I10, I11, and I12, and *Stauroneis thermicola*). *S. thermicola* was the most abundant of these diatoms (3.6% relative abundance), as the other taxa each represented less than 1% of the total diatom sum. *A. subatomoides* was recorded in epilithic and epiphytic microhabitats on Bathurst Island, but not from sediment samples (Lim et al., 2001a, c), and was absent in other high arctic studies. None of these other taxa have previously been identified in the Canadian High Arctic.

In addition to being an epilithic sample, sample I-C was taken from a stream environment. Despite these differences in habitat, I-C had site scores that placed it amidst the shallow ponds on the CCA biplot. Despite this, eight taxa were unique to I-C (i.e., *Achnanthes chlidanos*, *Amphora inariensis*, *Navicula atomus* var. *permitis*, *N. elginensis*, *N. perminuta*, *N. vulpina*, and *Surirella brebissonii*). *A. chlidanos*, *N. atomus*, and *S. brebissonii* have previously been identified from arctic streams (Moore, 1974; Potapova, 1996; Antoniades & Douglas, 2002), and thus may have rheophilic habitat preferences. *Hannaea arcus* and *Meridion circulare*, two taxa characteristic of high arctic streams (Antoniades & Douglas, 2002), were also present in I-C.

Notwithstanding the relative geographic isolation of Ellef Ringnes Island, only 38% of diatom taxa from Isachsen were previously identified from high arctic surface sediment collections (Douglas & Smol, 1993; Lim et al., 2001a; Michelutti et al., 2003a). Even after excluding rare taxa (i.e., present in <3 sites), 53% of Isachsen's diatom taxa have yet to be reported from the Canadian High Arctic. The distinct nature of the diatom communities of the Isachsen region may result from several factors, acting alone or in concert. The unique chemistry of Isachsen's freshwaters (Antoniades

et al., 2003a), in particular their weak acidity, and the extreme climate of the Isachsen region each account for some of the floral differences between Isachsen and other high arctic regions. While pH appears to play a secondary role (after conductivity) in determining diatom community change within the Isachsen dataset, it may still be a factor in determining floristic differences between Isachsen and other more alkaline regions of the Canadian High Arctic.

Model development

A series of single variable DCCA analyses were run to determine the influence of each water chemistry variable on diatom assemblages. Conductivity alone explained 13.1% of the variance in the diatom dataset, with a gradient length (GL) of 2.94 standard deviations ($p \leq 0.001$). After conductivity-related variables, DIC explained the greatest proportion of the variance (i.e., 9.3%, GL = 2.55, $p = 0.001$), followed by diameter (7.6%, 1.76, 0.005), Al (6.8%, 2.18, 0.01), pH (6.7%, 2.10, 0.01), and DOC (6.7%, 1.95, 0.02).

Diatom inference models were constructed for conductivity and pH. pH has been shown to be dependent on temperature and ice cover in sensitive alpine lakes (Koinig et al., 1998). As such, pH inferences from sediment cores could provide valuable insights into past climate-related changes in ice-dominated arctic sites. Conductivity in high arctic lakes and ponds increases through the summer, as evaporation increases solute concentrations (Douglas & Smol 1999). Similarly, during warmer years, increased evaporation should result in higher conductivity. As diatom communities respond to these changes in pH and conductivity,

sediment cores from these sites may thus record important information about high arctic climate change.

The conductivity gradient length (2.94 SD) indicated that unimodal calibration techniques were most appropriate (Birks, 1995). To compare the strengths and weaknesses of several approaches, inference models were developed using weighted-averaging, both with and without tolerance downweighting (WA, WA_{tol}), with inverse (WA_{inv}) and classical (WA_{cla}) deshrinking, and (WA-PLS). All inference models were evaluated with jackknifing. The length of the pH gradient (2.13 SD) was intermediate between values that clearly suggest linear or unimodal calibration methods (Birks, 1995); therefore, in addition to the aforementioned unimodal methods, pH models were constructed based on partial least squares regression. WA_{tol} inference models developed for both variables performed poorly relative to WA-PLS and simple WA, based on RMSEP and r^2 values. As such, while their results are presented for comparison purposes in Tables 3 and 4, they are not discussed further.

WA and WA-PLS produced similar conductivity models based on jackknifed RMSEP, r^2 and maximum bias (Table 3, Fig. 5). While the second WA-PLS component improved $RMSEP_{jack}$ and r^2_{jack} relative to the best one-component model, the improvement was not sufficient to warrant its selection over simpler models (Birks, 1998). WA_{cla} therefore represented the superior conductivity model (Table 3).

WA-PLS outperformed simple WA and PLS in reconstructing pH (Table 4, Fig. 6a). The second WA-PLS component improved RMSEP by a minimum of 6.6% compared with WA, and improved r^2 by at least 28%. However, all pH models

Table 3. Summary of results of conductivity models

Model	Apparent RMSE	r^2	Jackknifed RMSEP	r^2	Avg bias	Max bias
WA(inv)	0.1974	0.9066	0.3283	0.7486	0.0303	0.4107
WA(cla)	0.2074	0.9066	0.3196	0.7582	0.0327	0.3929
WA_{tol}(inv)	0.1672	0.9330	0.3904	0.6392	−0.0083	0.9146
WA_{tol}(cla)	0.1731	0.9330	0.3844	0.6465	−0.0082	0.9509
WAPLS(1)	0.1975	0.9066	0.3323	0.7521	0.0303	0.4148
WAPLS(2)	0.0763	0.9861	0.3067	0.8000	0.0379	0.4100
WAPLS(3)	0.0386	0.9965	0.3084	0.7900	0.0360	0.4186

Table 4. Summary of results of pH models

	Apparent RMSE	r^2	Jackknifed RMSEP	r^2	Avg bias	Max bias
All species ($n = 169$)						
WA(inv)	0.2990	0.8039	0.5549	0.3294	−0.0164	1.3938
WA(cla)	0.3334	0.8039	0.5626	0.3488	−0.0175	1.2435
WA$_{tol}$(inv)	0.3122	0.7861	0.6029	0.2174	0.0429	1.4360
WA$_{tol}$(cla)	0.3521	0.7861	0.6125	0.2378	0.0581	1.2869
WA-PLS(1)	0.3012	0.8039	0.5536	0.3343	−0.0533	1.4574
WA-PLS(2)	0.1339	0.9608	0.5183	0.4216	−0.0372	1.3220
WA-PLS(3)	0.0780	0.9869	0.5354	0.3804	−0.0631	1.3195
PLS(1)	0.4620	0.5315	0.6502	0.1258	−0.0093	1.5571
Species with significant unimodal relationships only ($n = 25$)						
WA(inv)	0.3129	0.7852	0.3833	0.6781	−0.0129	0.8253
WA(cla)	0.3531	0.7852	0.3991	0.6948	−0.0138	0.6309
WA$_{tol}$(inv)	0.3132	0.7848	0.4223	0.6111	−0.0121	0.8294
WA$_{tol}$(cla)	0.3535	0.7848	0.4217	0.6359	−0.0096	0.6944
WA-PLS(1)	0.3322	0.7852	0.3918	0.6938	−0.0336	0.9440
WA-PLS(2)	0.2909	0.8300	0.3947	0.6618	0.0110	0.7831
WA-PLS(3)	0.2847	0.8371	0.4588	0.5490	0.0307	1.0320
PLS(1)	0.5631	0.3040	0.6275	0.1576	−0.0178	1.7239

performed poorly when jackknifed, as there were large differences between the apparent and jackknifed predictive abilities of all pH models (e.g., WA-PLS(2): $r^2 = 0.96$, $r^2_{jack} = 0.42$). This implied that these models, as constructed, were not statistically rigorous.

In an attempt to strengthen the pH models by increasing the 'signal to noise' ratio in the dataset, species that had no significant response to pH were

Figure 5. Observed vs. WA(cla)$_{jack}$ inferred log Conductivity.

removed. Modeling of species-environment relationships using HOF (Oksanen, 1998) indicated that, of the 81 species present in at least three sites, 47% had significant responses to pH, and 31% had significant unimodal responses. Two additional pH models were examined including: (a) only those species whose distributions had significant relationships to pH ($n = 38$), and (b) only those species with significant unimodal relationships to pH ($n = 25$) (Table 2).

While pH models constructed using species with significant pH responses did not greatly improve over the original species dataset, the model based on unimodal species only greatly improved RMSEP$_{jack}$ and r^2_{jack} over our other pH models (Table 4, Fig. 6b). Simple WA was again superior, as additional WA-PLS components did not improve RMSEP or r^2, and only marginally improved mean bias. WA$_{cla}$ and WA$_{inv}$ produced similar jackknifed RMSEP and r^2, however WA$_{cla}$ was chosen as the best model based on lower maximum bias.

The unimodal WA$_{cla}$ improved RMSEP$_{jack}$ by 23%, and r^2_{jack} by 65% over the original pH model. This model was also more rigorous, as indicated

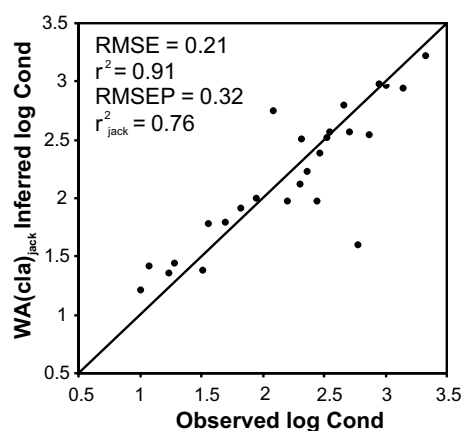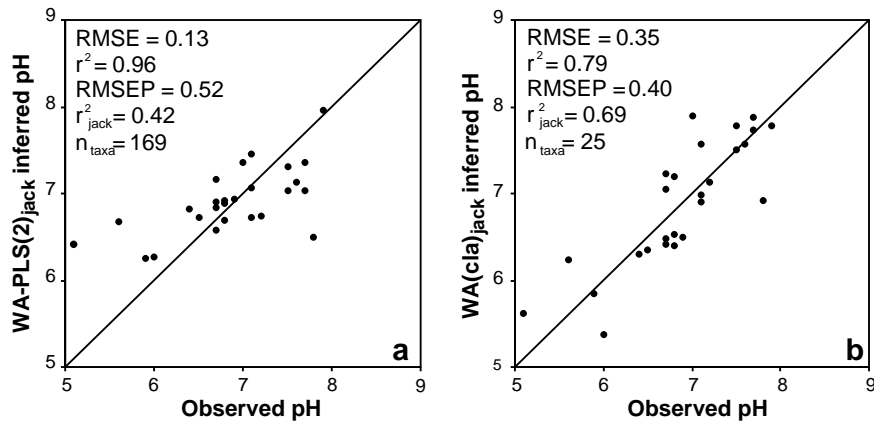*Figure 6.* (a) Observed vs. WA-PLS(2)$_{jack}$ inferred pH with 168 taxon model. (b) Observed vs. WA(cla)$_{jack}$ inferred pH with unimodal taxon ($n = 25$) model.

by the better performance during jackknifing (Table 4). However, it should be noted that, because of the lower number of taxa included, reliable inferences based on this model may be limited to those sites in which these 25 species comprise a large proportion of the diatom assemblage.

Conclusions

This study is the first examination of diatom distribution and ecology from Ellef Ringnes Island, one of the most climatically extreme sites in the northern hemisphere. The diatom flora of the Isachsen region proved to be as distinct as its limnology from other high arctic regions. Conductivity was the most important influence on diatom community change between sites, although several other limnological variables were also significantly related to diatom distributions (e.g., K, pH). pH also appeared to play an important role in determining the differences in diatom communities between Isachsen and other regions of the Canadian High Arctic. Future research in other acidic sites in the High Arctic may clarify the importance of pH on floral differences. The predictive abilities of the inference models constructed for conductivity and pH values suggest that they may form the basis for reliable environmental reconstructions in this region of the Canadian High Arctic using paleolimnological techniques.

References

Andreev, A. A. & V. A. Klimanov, 2000. Quantitative Holocene climate reconstruction from Arctic Russia. Journal of Paleolimnology 24: 81–91.

Antoniades, D. & M. S. V. Douglas, 2002. Characterization of high arctic stream diatom assemblages from Cornwallis Island, Nunavut, Canada. Canadian Journal of Botany 80: 50–58.

Antoniades, D., M. S. V. Douglas & J. P. Smol, 2003a. The physical and chemical limnology of 24 ponds and one lake from Isachsen, Ellef Ringnes Island, Canadian High Arctic. International Review of Hydrobiology 88: 519–538.

Antoniades, D., M. S. V. Douglas & J. P. Smol, 2003b. Comparative physical and chemical limnology of two Canadian High Arctic regions: Alert (Ellesmere Island, NU) and Mould Bay (Prince Patrick Island, NWT). Archiv für Hydrobiologie 158: 485–516.

Birks, H. J. B., 1995. Quantitative palaeoenvironmental reconstructions. In Maddy, D. & J. S. Brew (eds), Statistical

Modelling of Quaternary Science Data – Technical Guide 5. Quaternary Research Association, Cambridge: 161–254.

Birks, H. J. B., 1998. D.G. Frey & E.S. Deevey review 1: numerical tools in palaeolimnology – progress, potentialities, and problems. Journal of Paleolimnology 20: 307–332.

Birks, H. J. B., J. M. Line, S. Juggins, A. C. Stevenson & C. J. F. ter Braak, 1990. Diatoms and pH reconstruction. Philosophical Transactions of the Royal Society of London B 327: 263–278.

Doubleday, N. C., M. S. V. Douglas & J. P. Smol, 1995. Paleoenvironmental studies of black carbon deposition in the High Arctic: a case study from Northern Ellesmere Island. The Science of the Total Environment 160/161: 661–668.

Douglas, M. S. V. & J. P. Smol, 1993. Freshwater diatoms from high arctic ponds (Cape Herschel, Ellesmere Island, N.W.T.) Nova Hedwigia 54: 511–552.

Douglas, M. S. V. & J. P. Smol, 1995. Periphytic diatom assemblages from high arctic ponds. Journal of Phycology 31: 60–69.

Douglas, M. S. V. & J. P. Smol, 1999. Freshwater diatoms as indicators of environmental change in the High Arctic. In Stoermer, E. F. & J. P. Smol, (eds), The Diatoms: Applications for the Environmental and Earth Sciences. Cambridge University Press, Cambridge: 227–244.

Douglas, M. S. V., J. P. Smol & W. Blake Jr., 1994. Marked post-18th century environmental change in High-Arctic ecosystems. Science 266: 416–419.

Edlund, S. A. & B. T. Alt, 1989. Regional congruence of vegetation and summer climate patterns in the Queen Elizabeth Islands, Northwest Territories, Canada. Arctic 42: 3–23.

Environment Canada, 1994. Manual of Analytical Methods – National Laboratory for Environmental Testing, Canadian Centre for Inland Waters, Burlington, Ontario, 2 volumes, 1097 pp.

Finney, B. P., I. Gregory-Eaves, M. S. V. Douglas & J. P. Smol, 2002. Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. Nature 416: 729–732.

Foged, N., 1981. Diatoms in Alaska. Bibliotheca Phycologica, Vol. 53. J. Cramer, Vaduz, 317 pp.

Foscolos, A. E. & H. Kodama, 1981. Mineralogy and chemistry of Arctic desert soils on Ellef Ringnes Island, Arctic Canada. Soil Science Society of America Journal 45: 978–993.

Germain, H., 1981. Flore des Diatomées – eaux douces et saumâtres. Société Nouvelle des Éditions Boubée, Paris, 444 pp.

Hamilton, P. B., K. Gajewski, D. E. Atkinson & D. R. S. Lean, 2001. Physical and chemical limnology of 204 lakes from the Canadian Arctic Archipelago. Hydrobiologia 457: 133–148.

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

Jones, V. J & H. J. B. Birks, 2004. Lake-sediment records of recent environmental change on Svalbard: results of diatom analysis. Journal of Paleolimnology 31: 445–466.

Jongman, R. H. G., C. J. F. ter Braak & O. F. R. van Tongeren (eds), 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press, New York, 299 pp.

Juggins, S., 2003. C^2: software for ecological and palaeoecological data analysis and visualisation, version 1.3. Department of Geography, University of Newcastle.

Juggins, S. & C. J. F. ter Braak, 2000. WAPLS, version 1.2. Unpublished computer program.

Koinig, K. A., R. Schmidt, S. Sommaruga-Wögrath, R. Tessadri & R. Psenner, 1998. Climate change as the primary cause for pH shifts in a high alpine lake. Water, Air, and Soil Pollution 104: 167–180.

Krammer, K., 1992. Pinnularia: eine monographie der europäischen taxa. Bibliotheca Diatomologica, 26. J. Cramer, Berlin, 353 pp.

Krammer, K., 2000. Diatoms of Europe. The Genus Pinnularia, Vol. 1. A. R. G. Ganter Verlag, Ruggell, 703 pp.

Krammer, K. & H. Lange-Bertalot, 1986–1991. Bacillariophyceae. In Ettl, H., J. Gerloff, H. Heynig & D. Mollenhauer (eds), Süßwasserflora von Mitteleuropa, Band 2(1–4). Gustav Fischer Verlag, Stuttgart, 2485 pp.

Lange-Bertalot, H., 2001. Diatoms of Europe. Navicula sensu stricto, 10 genera separated from Navicula sensu lato, Frustulia, Vol. 2. A. R. G. Ganter Verlag, Ruggell, 526 pp.

Lim, D. S. S., M. S. V. Douglas & J. P. Smol, 2001a. Diatoms and their relationship to environmental variables from lakes and ponds on Bathurst Island, Nunavut, Canadian High Arctic. Hydrobiologia 450: 215–230.

Lim, D. S. S., M. S. V. Douglas, J. P Smol & D. R. S. Lean, 2001b. Physical and chemical limnological characteristics of 38 lakes and ponds on Bathurst Island, Nunavut, Canadian High Arctic. International Review of Hydrobiology 86: 1–22.

Lim, D. S. S., C. Kwan & M. S. V. Douglas, 2001c. Periphytic diatom assemblages from Bathurst Island, Nunavut, Canadian High Arctic: an examination of community relationships and habitat preferences. Journal of Phycology 37: 379–392.

Line, J. M., C. J. F. ter Braak & H. J. B. Birks, 1994. WACALIB version 3.3 – a computer program to reconstruct environmental variables from fossil assemblages by weighted-averaging and to derive sample specific errors of prediction. Journal of Paleolimnology 10: 147–152.

Lowe, R. L., 1974. Environmental requirements and pollution tolerance of freshwater diatoms. US Environmental Protection Agency, Cincinnati, 334 pp.

MacDonald, G. M., B. Felzer, B. P. Finney & S. L. Forman, 2000. Holocene lake sediment records of Arctic hydrology. Journal of Paleolimnology 24: 1–13.

Maxwell, J. B., 1981. Climatic regions of the Canadian High Arctic Islands. Arctic 34: 224–240.

Maxwell, J. B., 1982. The Climate of the Canadian Arctic Islands and Adjacent Waters, 2 volumes, Vol. 2. Canadian Government Publishing Centre, Ottawa, 589 pp.

Michelutti, N., M. S. V. Douglas, D. R. S. Lean & J. P. Smol, 2002a. Physical and chemical limnology of 34 ultra-oligotrophic lakes and ponds near Wynniatt Bay, Victoria Island, Arctic Canada. Hydrobiologia 482: 1–13.

Michelutti, N., M. S. V. Douglas, D. C. G. Muir & J. P. Smol, 2002b. Limnological characteristics of 38 lakes and ponds on

Axel Heiberg Island, High Arctic Canada. International Review of Hydrobiology 87: 385–399.

Michelutti, N., A. J. Holtham, M. S. V. Douglas & J. P. Smol, 2003a. Periphytic diatom assemblages from ultra-oligotrophic and UV transparent lakes and ponds on Victoria Island and comparisons with other diatom surveys in the Canadian Arctic. Journal of Phycology 39: 465–480.

Michelutti, N., M. S. V. Douglas & J. P. Smol, 2003b. Diatom response to recent climatic change in a high arctic lake (Char Lake, Cornwallis Island, Nunavut). Global and Planetary Change 38: 257–271.

Moore, J. W., 1974. The benthic algae of southern Baffin Island. I. Epipelic communities in rivers. Journal of Phycology 10: 50–57.

Nahir, M., 1996. Isachsen high arctic weather station decommissioning and cleanup: environmental screening report. Edmonton, Public Works and Government Services Canada.

Oksanen, J., 1998. HOF: ecological gradient analysis using Huisman–Olff–Fresco models, version 2.3. Unpublished computer program, University of Oulu, Finland.

Overpeck, J., K. Hughen, D. Hardy, R. Bradley, R. Case, M. Douglas, B. Finney, K. Gajewski, G. Jacoby, A. Jennings, S. Lamoureux, A. Lasca, G. MacDonald, J. Moore, M. Retelle, S. Smith, A. Wolfe & G. Zielinski, 1997. Arctic environmental change of the last four centuries. Science 278: 1251–1256.

Patrick, R. & C. W. Reimer, 1966. The Diatoms of the United States Exclusive of Alaska and Hawaii. Academy of Natural Sciences, Philadelphia, 2 volumes, Vol. 1, 688 pp.

Pienitz, R. & J. P. Smol, 1993. Diatom assemblages and their relationship to environmental variables in lakes from the boreal forest-tundra ecotone near Yellowknife, Northwest Territories, Canada. Hydrobiologia 269/270: 391–404.

Potapova, M., 1996. Epilithic algal communities in rivers of the Kolyma Mountains, NE Siberia, Russia. Nova Hedwigia 63: 309–334.

Rouse, W. R., M. S. V. Douglas, R. E. Hecky, A. E. Hershey, G. W. Kling, L. Lesack, P. Marsh, M. McDonald, B. J. Nicholson, N. T. Roulet & J. P. Smol, 1997. Effects of climate change on the waters of Arctic and Subarctic North America. Hydrological Processes, 11: 973–902.

Rühland, K., A. Priesnitz & J. P. Smol, 2003. Paleolimnological evidence from diatoms for recent environmental changes in 50 lakes across Canadian Arctic treeline. Arctic, Antarctic and Alpine Research 35: 110–123.

Smith, I. R., 2002. Diatom-based Holocene paleoenvironmental records from continental sites on northeastern Ellesmere Island, high Arctic, Canada. Journal of Paleolimnology 27: 9–28.

Smol, J. P., 2002. Pollution of Lakes and Rivers: A Paleoenvironmental Perspective. Arnold Publishers, London, 280 pp.

Smol, J. P. & Cumming, B. F. 2000. Tracking long-term changes in climate using algal indicators in lake sediments. Journal of Phycology 36: 986–1011.

Sorvari, S., A. Korhola & R. Thompson, 2002. Lake diatom response to recent Arctic warming in Finnish Lapland. Global Change Biology 8: 153–163.

ter Braak, C. J. F., 1998. CANOCO and CANOPost, Version 4 for Windows. Microcomputer Power, Ithaca, NY, USA.

Wolfe, A. P., 2000. A 6500-year diatom record from southwestern Fosheim Peninsula, Ellesmere Island, Canadian High Arctic. In Garneau, M. & B. T. Alt (eds), Environmental Response to Climate Change in the High Arctic. Geological Survey of Canada Bulletin 529: 249–256.

Wolfe, A. P. & R. H. King, 1999. A paleolimnological constraint to the extent of the last glaciation on Northern Devon Island, Canadian High Arctic. Quaternary Science Reviews 18: 1563–1568.