

BENTHIC DIATOM AUTECOLOGY AND INFERENCE MODEL DEVELOPMENT FROM THE CANADIAN HIGH ARCTIC ARCHIPELAGO¹

Dermot Antoniades,² Marianne S. V. Douglas

Department of Geology, University of Toronto, 22 Russell St., Toronto, Ontario, M5S 3B1, Canada

and

John P. Smol

Paleoecological Environmental Assessment and Research Lab (PEARL), Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6, Canada

Diatom assemblages were analyzed from 64 lakes and ponds from Alert, Ellesmere Island and Mould Bay, Prince Patrick Island in the Canadian High Arctic Archipelago. Diverse water chemistry conditions and diatom communities were present in these sites. Small benthic taxa typically dominated diatom communities; however, assemblages were markedly different between Alert and Mould Bay sites in response to disparate water chemistry characteristics in the two regions. The most abundant taxa belonged to the genera *Navicula*, *Cymbella*, *Achnanthes*, *Nitzschia*, and *Pinnularia*. Canonical correspondence analysis indicated that pH, specific conductivity, dissolved organic carbon, and total phosphorus were the most important limnological variables in determining species composition. Diatom inference models were developed for pH, specific conductivity, and dissolved organic carbon using weighted averaging and weighted averaging partial least squares techniques; these had root mean square error of prediction/ r_{boot}^2 values of 0.40/0.77, 0.28/0.70, and 0.24/0.55, respectively. These models are applicable to sites with large ranges of taxonomic and limnological variation and will allow the reconstruction of past changes of climate-related limnological parameters from biostratigraphic records in future paleolimnological studies.

Key index words: autecology; benthic; diatoms; dissolved organic carbon; Ellesmere Island; High Arctic; inference models; pH; Prince Patrick Island; specific conductivity

Abbreviations: CCA, canonical correspondence analysis; DCA, detrended correspondence analysis; DCCA, detrended canonical correspondence analysis; DOC, dissolved organic carbon; MSC, Meteorological Service of Canada; RMSEP, root mean square error of prediction; TPU, total unfiltered phosphorus; WA, weighted averaging; WA_{CLA}, weighted averaging with classical deshrinking;

WA_{INV}, weighted averaging with inverse deshrinking; WA-PLS, weighted averaging partial least squares; WA(tol), weighted averaging models with tolerance down-weighting

The Canadian High Arctic represents one of the most extreme climatic regions on Earth. Biota there must survive its extremely cold and arid environment as well as alternating extremes of solar radiation. Polar regions are also especially susceptible to the effects of climate change because of positive feedback mechanisms such as decreasing surface albedo, cloud cover changes, and reductions in the extent of sea ice (Houghton et al. 2001). With recognition of the vulnerability of the High Arctic to changes in climate (Serreze et al. 2000, Houghton et al. 2001), more attention has been focused on the potential of limnological systems as sensitive biomonitors of environmental change (Rouse et al. 1997). Although arctic systems are subjected to the effects of long distance transport of some pollutants (Braune et al. 1999, Rose et al. 2004), most high arctic lakes and ponds are sufficiently remote to be largely isolated from anthropogenic effects such as acidification and eutrophication. As such, they allow assessment of climate change to be independent of many other complicating processes. However, no meteorological data are available from the Canadian High Arctic beyond about the last 50 years, which limits our ability to evaluate the inherent variability of these systems. Indirect proxy records developed using paleolimnological approaches can potentially address this shortcoming and allow us to better understand the significance of any recent climate change within the context of longer term climate dynamics (Smol and Cumming 2000).

Diatom communities have been shown to shift in response to changes in environmental conditions (Stoermer and Smol 1999). Because diatoms comprise an important component of most high arctic periphytic assemblages, they have been used increasingly in studies of environmental change in high arctic limnological systems (Douglas and Smol 1999). However, reliable inferences of past environmental conditions from

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²Author for correspondence: e-mail dermot.antoniades@utoronto.ca.

diatom sedimentary records first require the quantification of the autecological characteristics of diatom taxa in new geographical regions, which is typically done using surface sediment calibration sets or training sets (Smol 2002). Such investigations of diatom species–environment relationships in the Canadian High Arctic have been published from east-central Ellesmere Island (Douglas and Smol 1993, 1995), Bathurst Island (Lim et al. 2001a,b), northeastern Victoria Island (Michelutti et al. 2003b), and Isachsen, Ellef Ringnes Island (Antoniades et al. 2004). However, no research has yet been completed on modern diatom distributions in either the Alert (northeastern Ellesmere Island) or Mould Bay (southwestern Prince Patrick Island) regions (Fig. 1). Because Alert and particularly Mould Bay have been identified as two regions of distinctive water chemistry in the High Arctic (Antoniades et al. 2003a), knowledge of the associated diatom communities is important to our understanding of high arctic diatom autecology.

Diatoms have been used to infer past changes in environmental conditions in high arctic lake and pond sediment profiles using paleolimnological techniques. Qualitative interpretations of diatom sedimentary records include those from Ellesmere Island (Douglas et al. 1994, Doubleday et al. 1995, Wolfe 2000, Smith 2002), Devon Island (Gajewski et al. 1997, Wolfe and King 1999), Cornwallis Island (Michelutti et al. 2002, 2003a), and Svalbard (Jones and Birks 2004). However, whereas several publications have quantified environmental change in lower arctic regions (Andreev and Klimanov 2000, Sorvari et al. 2002, Rühland et al. 2003), similar studies from the High Arctic are still rare.

Because all our diatom and limnological surveys from the High Arctic used identical sampling techniques over the same short sampling window (July), we were able to use comparative approaches to explore several objectives. Our primary goal was to broaden the understanding of high arctic diatom distributions by establishing the taxonomic and autecological characteristics of taxa in two previously unstudied regions, thus expanding the geographical and environmental ranges of existing surveys. Second, we compared the composition of assemblages, both between regions and with those of previously completed high arctic diatom surveys, to assess the spatial variation of diatom assemblages and the influence of environmental characteristics. Finally, we developed rigorous inference models for the reconstruction of environmental change from sites with a wide range of environmental and taxonomic characteristics.

MATERIALS AND METHODS

Study areas. **Alert:** Alert (80° 30' N, 60° 20' W) is situated on the northern coast of Ellesmere Island in the Queen Elizabeth Islands of the Canadian Arctic Archipelago (Fig. 1). The infrastructure at Alert includes a Canadian military base and a weather station of the Meteorological Service of Canada (MSC). Alert has a cold dry climate, with a mean annual

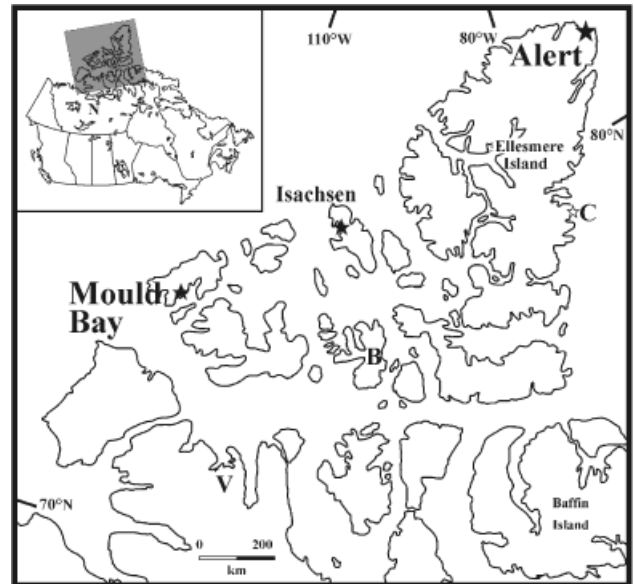


FIG. 1. Map of the Canadian High Arctic with locations of studies included in text. B, Bathurst Island; C, Cape Herschel, Ellesmere Island; N, mainland Northwest Territories; V, Victoria Island.

temperature of -18.0°C . February is the coldest month, with a mean temperature of -32.3°C ; July is the warmest month, with a mean temperature of 3.3°C (MSC 2002). Alert receives an average of 154 mm per year of precipitation, and the summer averages 28 degree days per year above 5°C (MSC 2002). As a result, very little vegetation grows in the Alert region, with primarily herbaceous shrubs and mosses present (Edlund and Alt 1989).

The bedrock of the Alert area is composed primarily of carbonates of Ordovician to Silurian age (Christie 1964) that are a dominant influence on the alkaline nature of local fresh waters (Antoniades et al. 2003a). Although tundra ponds are sparse in the Alert region relative to typical high arctic landscapes, several large (i.e. 1–3 km wide) lakes are present in the area. Further details concerning the limnology of the Alert region are summarized in Antoniades et al. (2003a).

Mould Bay: Mould Bay (76° 14' N, 119° 20' W) is situated on the south coast of Prince Patrick Island, along the western margin of the Queen Elizabeth Islands (Fig. 1). An MSC weather station at Mould Bay was inhabited from 1948 until 1995, after which it was closed and replaced with an automated station that continues to record meteorological data. Mould Bay's climate is similar to Alert's, with an annual daily mean temperature of -17.5°C , a February mean of -34.0°C , and a July mean temperature of 4.0°C . Mould Bay is among the driest areas of the High Arctic, with average annual precipitation of 111 mm per year, and a growing season of 27 degree days per year above 5°C (MSC2002).

Local bedrock is largely composed of Jurassic to Cretaceous sandstones and Devonian clastic sediments that are overlain by shallow, poorly drained, slightly acidic soils (Everett 1968). Although plant cover is extremely sparse in most high arctic landscapes, Mould Bay is lushly vegetated, with grasses and mosses blanketing the land surface. In many cases, lake and pond bottoms are also almost entirely covered with submerged mosses and emergent grasses. This dense vegetation influences the water chemistry of Mould Bay freshwater sites (Antoniades et al. 2003a), which were distinct from previously studied high arctic regions for their above average concentrations of dissolved organic carbon (DOC; mean, $6.7\text{ mg}\cdot\text{L}^{-1}$) and

nutrients (mean total phosphorus, $16.5 \mu\text{g} \cdot \text{L}^{-1}$; mean total nitrogen, $0.616 \text{mg} \cdot \text{L}^{-1}$). Further details of Mould Bay's water chemistry characteristics can be found in Antoniadou et al. (2003a).

Sampling and enumeration. Thirty-four sites in the Mould Bay region were sampled for water chemistry and diatom analysis between 12 and 21 July 1999, and 30 Alert sites were similarly sampled from 24 July to 7 August 2000. Sampling in both regions was conducted on foot or with all-terrain vehicles, and in each case the geographical extent of the study area was restricted to roughly a 25-km radius of our base camp. With the exception of several large Alert lakes, none of our sites was officially named. As such, each was simply given a name consisting of its location and an alphabetic designation (e.g. Alert, A-A to A-AE; Mould Bay, MB-A to MB-AH). For the latitudes and longitudes of each site as well as additional limnological data, please see Table 1 in Antoniadou et al. (2003a).

Most sites were considered to be ponds (i.e. <2 m depth, freezing completely in winter). Six Alert sites (i.e. Upper and Lower Dumbell lakes, Kirk Lake, Hilgard Lake, Moss Pond, and Self Pond) were considered to be lakes, whereas three Mould Bay sites (i.e. MB-K, MB-L, and MB-AD) were more than 2 m deep.

Where possible, surface sediment samples were collected using the same procedures as in previous high arctic surveys (Lim et al. 2001a). However, because of the high levels of vegetation, many pond bottoms in the Mould Bay region were completely covered with mosses, preventing the collection of sediment samples. In 16 sites where moss cover prevented sediment sampling (i.e. MB-C, MB-D, MB-F, MB-G, MB-I, MB-JE, MB-JW, MB-L, MB-N, MB-O, MB-P, MB-Q, MB-R, MB-W, MB-X, and MB-Y), a moss sample from the bottom of the pond was substituted for the diatom calibration. In these cases, samples were taken from a minimum of five different moss cushions and combined into the sample used for diatom

TABLE 1. Pearson correlation matrix for 90 Alert, Mould Bay, and Isachsen sites.

	Cl ⁻	SO ₄ ²⁻	SiO ₂	POC	PON	DOC	DIC	SRP	NH ₃	TKN	Al ³⁺	Zn ²⁺	Ba ²⁺	Cu ²⁺	Fe ²⁺	Li ⁺	Mn ²⁺	Sr ²⁺	
Cl ⁻	1.00																		
SO ₄ ²⁻	0.15	1.00																	
SiO ₂	-0.17	0.02	1.00																
POC	0.10	-0.01	0.16	1.00															
PON	0.10	-0.00	0.15	1.00	1.00														
DOC	-0.07	-0.12	-0.11	0.07	0.11	1.00													
DIC	0.12	0.09	0.03	-0.16	-0.15	0.05	1.00												
SRP	0.26	0.06	0.10	0.11	0.10	0.06	0.17	1.00											
NH ₃	-0.12	-0.14	-0.06	0.37	0.38	0.31	0.02	-0.02	1.00										
TKN	0.01	-0.21	-0.09	0.08	0.11	0.89	0.26	0.09	0.53	1.00									
Al ³⁺	0.31	-0.04	0.08	0.72	0.69	-0.27	-0.10	0.18	0.19	-0.18	1.00								
Zn ²⁺	0.04	0.10	0.37	0.54	0.53	-0.20	-0.25	-0.01	0.19	-0.18	0.67	1.00							
Ba ²⁺	0.43	0.29	-0.15	0.34	0.36	0.25	-0.25	0.17	0.13	0.13	0.22	0.21	1.00						
Cu ²⁺	0.05	-0.31	-0.19	0.03	0.04	0.22	0.32	0.01	0.04	0.26	0.10	-0.02	0.05	1.00					
Fe ²⁺	0.15	-0.07	0.17	0.89	0.89	0.11	-0.11	0.21	0.31	0.11	0.71	0.56	0.34	0.18	1.00				
Li ⁺	0.16	0.98	0.03	0.02	0.03	-0.10	0.07	0.08	-0.13	-0.20	-0.02	0.10	0.33	-0.30	-0.04	1.00			
Mn ²⁺	-0.01	0.32	0.20	0.02	0.03	-0.15	-0.16	-0.05	-0.07	-0.19	0.09	0.47	0.01	-0.17	-0.00	0.34	1.00		
Sr ²⁺	0.49	0.84	-0.01	-0.06	-0.06	-0.08	0.39	0.19	-0.12	-0.05	-0.00	0.04	0.38	-0.11	-0.07	0.80	0.14	1.00	
Ca ²⁺	0.15	0.87	0.13	-0.12	-0.11	-0.13	0.43	0.08	-0.14	-0.11	-0.10	0.09	0.14	-0.16	-0.15	0.80	0.24	0.89	
Mg ²⁺	0.29	0.96	-0.04	0.00	0.01	-0.09	0.24	0.13	-0.12	-0.14	-0.00	0.03	0.29	-0.22	-0.04	0.97	0.27	0.87	
Na ⁺	0.95	0.29	-0.15	0.08	0.07	-0.11	0.06	0.20	-0.15	-0.07	0.25	0.05	0.49	-0.05	0.10	0.29	0.08	0.54	
K ⁺	0.81	0.65	-0.14	0.12	0.12	-0.09	0.13	0.22	-0.14	-0.10	0.22	0.05	0.56	-0.16	0.12	0.66	0.07	0.80	
TPU	0.08	-0.02	0.12	0.92	0.91	-0.10	-0.18	0.07	0.29	-0.07	0.79	0.51	0.27	0.00	0.75	0.01	0.00	-0.08	
TPF	0.12	0.02	0.02	0.36	0.38	0.56	-0.16	0.49	0.11	<i>0.40</i>	0.07	0.02	0.37	0.02	0.37	0.05	-0.11	0.01	
TN	0.24	-0.17	-0.03	0.54	0.56	0.68	0.22	0.23	0.55	0.82	0.32	0.14	0.26	0.29	0.55	-0.16	-0.14	0.01	
Cond	0.75	0.70	-0.06	0.03	0.03	-0.13	0.36	0.25	-0.16	-0.08	0.19	0.07	0.34	-0.09	0.04	0.68	0.18	0.88	
pH	0.06	-0.25	-0.30	-0.19	-0.18	0.27	0.71	0.24	0.19	0.47	-0.21	0.54	-0.16	0.46	-0.13	-0.27	0.47	0.05	
Elev	-0.12	-0.00	0.22	-0.17	-0.15	-0.21	0.31	-0.04	0.04	-0.02	-0.02	-0.00	-0.30	0.07	-0.11	-0.04	0.03	0.04	
Diam	-0.08	-0.14	0.03	-0.01	-0.01	-0.26	0.16	-0.08	-0.08	-0.19	0.05	-0.05	0.23	0.13	0.02	0.13	0.07	0.11	
Dist	-0.03	0.12	0.14	0.04	0.03	-0.31	-0.25	0.01	-0.20	-0.33	0.07	0.07	-0.04	-0.35	-0.08	0.10	0.20	0.01	
	Ca ²⁺	Mg ²⁺	Na ⁺	K ⁺	TPU	TPF	TN	Cond	pH	Elev	Diam	Dist							
Ca ²⁺	1.00																		
Mg ²⁺	0.84	1.00																	
Na ⁺	0.25	0.39	1.00																
K ⁺	0.54	0.73	0.87	1.00															
TPU	-0.13	-0.01	0.07	0.09	1.00														
TPF	-0.11	0.04	0.10	0.14	0.27	1.00													
TN	-0.10	-0.07	0.14	0.11	0.38	0.47	1.00												
Cond	0.72	0.81	0.77	0.90	0.01	0.03	0.11	1.00											
pH	-0.00	-0.11	-0.03	-0.07	-0.21	-0.04	0.34	0.02	1.00										
Elev	0.18	-0.00	-0.12	-0.10	-0.13	-0.31	-0.06	0.01	0.20	1.00									
Diam	-0.05	-0.12	-0.11	-0.15	0.01	-0.27	-0.12	-0.10	0.17	0.16	1.00								
Dist	0.08	0.03	0.01	0.04	0.09	-0.11	-0.24	-0.01	-0.31	0.25	0.09	1.00							

Bold denotes $P < 0.01$, and italics denotes $P < 0.05$. Cond, specific conductivity; Diam, diameter; Dist, distance from ocean; DOC/DIC, dissolved organic/inorganic carbon; Elev, elevation; POC/N, particulate organic carbon/nitrogen; SRP, soluble reactive phosphorus; TKN, total Kjeldahl nitrogen; TN, total nitrogen; TPU, total unfiltered phosphorus; TPF, total dissolved phosphorus.

analysis. Similarly, the bottom of one pond (i.e. MB-E) was entirely covered by a thick cyanobacterial mat. Because this was the only substrate in the site, it was used for our calibration. In the Alert data set, one rock sample (i.e. A-H) and one cyanobacterial mat sample (i.e. A-X) were included from sites where no other substrates were present.

Diatom samples were processed according to standard techniques (Pienitz and Smol 1993), summarized briefly here. Carbonates were removed with 10% HCl, and organic material was digested with 1:1 H₂SO₄:HNO₃. The samples were heated in a 100° C hot water bath during each digestion step to accelerate the reaction and were subsequently rinsed with distilled water until they reached pH ≈ 7. An aliquot of the remaining slurries were dried onto coverslips and mounted on glass microscope slides in Naphrax[®] (refractive index, 1.74 Flemming 1954).

Diatom photomicroscopy, identification, and enumeration were carried out under oil immersion at 1000× magnification using a Leica DMRB microscope (Leica, Wetzlar, Germany) equipped with DIC optics (Nomarski). A minimum of 500 valves per sample was counted to the species or subspecies level. Taxonomy primarily followed Krammer and Lange-Bertalot (1986–1991), although several other references were important in making taxonomic determinations (Foged 1981, Germain 1981, Krammer 1992). Photographic images of all taxa from this study are available in Antoniadou (2004).

Samples for water chemistry analysis were collected and analyzed both in the field and subsequently at the National Laboratory for Environmental Testing of the National Water Research Institute in Burlington, Ontario following standard methodology (Environment Canada 1994). Details on methodology, results of the 38 water chemistry analyses, and discussion of the physical and chemical limnology of the sites can be found in Antoniadou et al. (2003a).

Statistical analyses. The species and water chemistry data sets were analyzed using several multivariate techniques. Before analysis, the data sets were transformed to reduce the effect of skewness in the environmental data set and to maximize the signal-to-noise ratio in the species data set (Walker et al. 1997). The water chemistry data sets were primarily log(x) transformed, whereas the species data set was square root transformed. Detrended correspondence analysis (DCA) was used to determine the gradient length and to explore trends in community structure within the species data set, whereas Hill's (1973) N₂, calculated as the reciprocal of Simpson's index, was used as a measure of diversity.

Canonical correspondence analysis (CCA) was subsequently used to investigate species–environment relationships in the data sets. To increase the applicability of our models, the 64 sites from this study were combined with the 26-site data set of a previous study from Isachsen, Ellef Ringnes Island (Antoniadou et al. 2004) before CCA and model construction. The addition of these sites increased the ranges of several key environmental variables, including pH, specific conductivity, and total unfiltered phosphorus (TPU). A Pearson correlation matrix (Table 1) was generated to identify correlated variables within this larger water chemistry data set. Environmental variables below detection limits at most sites in the data set were removed before running the CCA, and only environmental variables that contributed significantly to the analysis (as assessed using forward selection) were included in the final CCA. The effects of differing microhabitats on diatom assemblages were also assessed using variance partitioning in a partial CCA.

A series of detrended CCAs (DCCA) constrained to individual environmental variables was run to explore the explanatory power of each variable, and the resulting DCCA gradient length was used to indicate the suitability of linear or unimodal techniques in subsequent calibration steps (Birks 1995). The ratio of the eigenvalues of the constrained first axis to the second unconstrained axis was also examined, because this ratio is

typically indicative of the importance of a variable in controlling diatom distributions (ter Braak 1986). All DCA, CCA, and DCCA were carried out with the computer program CANOCO, version 4.0 (ter Braak 1998), and all axes were tested for significance using 999 unrestricted Monte Carlo permutations. Inference models were constructed for pH, specific conductivity, and DOC using weighted averaging (WA) and weighted averaging partial least squares (WA-PLS) approaches, and each model was cross-validated by bootstrapping. The strengths and weaknesses of each approach were then assessed to determine the best model, based on lowest root mean square error of prediction (RMSEP), lowest mean and maximum bias, and highest coefficient of determination (*r*²) (Birks 1998). All models were generated using the computer program C², version 1.3 (Juggins 2003).

RESULTS AND DISCUSSION

Water chemistry. The 64 sites in this study encompassed a diverse set of environmental conditions (Table 2), with sites ranging from ultraoligotrophic to hypereutrophic (i.e. total phosphorus = 3.4–77.9 μg · L⁻¹), from circumneutral to strongly alkaline (i.e. pH = 7.0–8.9), and from extremely dilute to relatively high conductivity waters (i.e. conductivity = 25–2000 μS · cm⁻¹).

Several regional water chemistry characteristics differentiated Alert sites from those at Mould Bay (Antoniadou et al. 2003a). Mould Bay sites were higher in nitrogen and DOC and particulate organic carbon concentrations than Alert sites, resulting from the much higher levels of vegetation at Mould Bay. High and low conductivity sites were present in both of our study areas; however, the factors influencing conductivity differed between regions. Carbonate bedrock and surficial materials predominantly influenced ionic chemistry in Alert sites, with high proportions of hydrogen carbonate and Ca²⁺. At Mould Bay, however, proximity to the ocean and the contribution of marine aerosols was the largest factor in determining the ionic composition of sites, and Na⁺ and Cl⁻ concentrations were of relatively greater importance. Although sites in both regions were alkaline, Alert sites generally had higher pH readings (8.1–8.9) than those at Mould Bay (7.0–8.6).

The Pearson correlation matrix (Table 1) identified several highly correlated groups of water chemistry variables. The largest group was composed of conductivity and related variables (i.e. Cl⁻, SO₄²⁻, Li⁺, Sr²⁺, Ca²⁺, Mg²⁺, Na⁺, K⁺). High concentrations of several variables (i.e. particulate organic carbon, particulate organic nitrogen, total nitrogen, TPU, Fe²⁺, Al³⁺) resulted from resuspended particulate matter (Antoniadou et al. 2003a,b). These variables were thus highly correlated, as were a group of dissolved nutrient related variables (i.e. total dissolved phosphorus, total Kjeldahl nitrogen, NH₃, DOC). A detailed analysis and discussion of water chemistry trends within the Alert and Mould Bay regions is available in Antoniadou et al. (2003a).

Description of diatom communities. A total of 265 diatom taxa from 26 genera was identified from our 64

TABLE 2. Summary of water chemistry variables from Alert ($n = 30$) and Mould Bay ($n = 34$) sites.

Variable	Alert			Mould Bay		
	Median	Range	SD	Median	Range	SD
Cl ⁻	7.5	0.6–703	155.6	9.3	3.2–212	47.8
SO ₄ ²⁻	3.2	0.2–111	26.9	4.0	0.6–38.4	9.6
SiO ₂	0.6	0.04–4.29	1.1	0.17	0.04–3.54	0.67
POC	0.328	0.108–3.090	0.6	0.552	0.375–7.090	1.44
PON	0.032	0.015–0.286	0.1	0.065	0.030–0.684	0.14
DOC	2.7	0.6–6.1	1.6	6.9	1.1–13.7	3.0
DIC	26.3	12.1–45.9	8.5	7.6	1.5–22.5	6.1
SRP (μg · L ⁻¹)	1.0	0.5–4.8	0.8	0.9	0.2–3.0	0.5
NO ₃ + NO ₂	0.061	0.016–0.888	0.204	<0.010	<0.010–0.146	0.090
NH ₃	0.022	0.006–0.229	0.054	0.028	<0.005–0.122	0.029
TKN	0.350	0.086–0.736	0.195	0.490	0.160–1.360	0.244
Al ³⁺	0.05	<0.01–2.15	0.45	0.03	<0.01–1.49	0.28
Fe ²⁺	0.107	0.008–3.700	0.768	0.267	0.083–7.200	1.392
Zn	0.003	<0.001–0.010	0.002	0.002	<0.001–0.015	0.003
Ca ²⁺	37.8	18.8–67.5	12.9	12.1	2.6–29.3	8.4
Mg ²⁺	9.3	1.4–56.5	11.4	3.3	0.8–22.8	4.8
Na ⁺	4.5	0.4–404.0	88.4	4.1	1.6–98.8	23.8
K ⁺	0.5	<0.2–18.4	4.0	1.0	<0.2–4.0	0.9
TPU (μg · L ⁻¹)	9.1	3.4–67.6	14.0	11.2	7.1–117.0	21.0
TPF (μg · L ⁻¹)	4.0	0.7–9.7	2.3	7.7	4.0–23.9	3.7
TN	0.465	0.107–1.631	0.296	0.591	0.206–1.430	0.288
Chl <i>a</i> (μg · L ⁻¹)	1.0	0.5–2.6	0.5	0.9	<0.1–6.9	1.6
Cond (μS · cm ⁻¹)	230	121–2000	408	75	25–530	119
Temperature (° C)	7.0	2–15	3.8	6.0	4–9.5	1.3
pH	8.4	8.1–8.9	0.2	7.8	7.0–8.6	0.4
Elev (m asl)	45	12–147	45.5	8	2–78	24
Diam (m)	55	7–1400	423	25	3–700	122
Dist (km)	1.08	0.10–4.75	0.87	1.33	0.20–2.45	0.72
Latitude	82° 26.180' – 82° 31.208' N			76° 12.912' – 76° 16.778' N		
Longitude	62° 01.618' – 63° 06.635' W			119° 16.884' – 119° 26.147' W		

All units are expressed in mg · L⁻¹ unless otherwise noted. Cond, specific conductivity; Diam, diameter; Dist, distance from ocean; DOC/DIC, dissolved organic/inorganic carbon; Elev, elevation; POC/N, particulate organic carbon/nitrogen; SRP, soluble reactive phosphorus; SD, standard deviation; TKN, total Kjeldahl nitrogen; TN, total nitrogen; TPU, total unfiltered phosphorus; TPF, total dissolved phosphorus.

sites (Table 3). Of these, 106 taxa were common to both regions, an additional 70 taxa were present only in Alert sites, and a further 89 taxa were identified only from Mould Bay samples (Table 3). Most taxa were from the genera *Navicula* (30% of taxa), *Cymbella* (16%), *Achnanthes* (10%), *Nitzschia* (9%), and *Pinnularia* (7%). Because of the shallow nature of most high arctic water bodies, sites were overwhelmingly dominated by benthic diatoms, and, with few exceptions, no planktonic species were recorded. Diatom assemblages at individual sites ranged from a minimum of 12 to a maximum of 58 identified taxa, and Hill's N2 site values varied from 2.8 to 22.9.

Although there were broad similarities in the species composition of diatom assemblages between both Alert and Mould Bay sites, certain components of the diatom communities in each region were distinct both from each other and from those reported in previous high arctic diatom surveys. Most sites were dominated by taxa from the genera *Navicula sensu lato* (*s.l.*), *Nitzschia*, *Achnanthes*, and *Cymbella s.l.* However, there were large regional differences in the diversity and relative importance of these genera (Table 4). Significant differences between mean DCA axis 1 from Alert and Mould Bay reflected these differences in taxonomic composi-

tion (Alert mean, 0.46 [range, 0–1.49]; Mould Bay mean, 1.90 [range, 0.71–2.43]; $P < 0.0001$).

The most common and abundant species in Alert sites included *Nitzschia perminuta* (Grunow) Peragallo, *Navicula soehrensensis* Krasske, *N. cryptocephala* Kützing, *N. chiarae* Lange-Bertalot and Genkal, *N. bryophila* (Peterson) Lange-Bertalot, *N. cincta* (Ehrensberg) Ralfs, and *Diploneis oculata* (Brébisson) Cleve. With the exception of *N. chiarae*, these taxa have been reported as common components of high arctic diatom assemblages (Douglas and Smol 1995, Joynt and Wolfe 2001, Lim et al. 2001a,b, Michelutti et al. 2003b, Antoniaades et al. 2004). The absence of *N. chiarae* from these other studies may simply result from differences in taxonomic determinations, because *N. chiarae* is a newly defined species (Lange-Bertalot and Genkal 1999) that is easily confused with smaller forms of *N. cryptocephala* (Lange-Bertalot 2001).

Two sites (i.e. A-A, A-B) had diatom assemblages that were distinct from all others in the Alert data set, likely in response to their greatly elevated specific conductivities (i.e. 2000 μS · cm⁻¹ and 1650 μS · cm⁻¹, respectively; median, 230 μS · cm⁻¹). Distinct components of these diatom assemblages included *Amphipleura rutilans* (Trentepohl) Cleve, *Amphora spitzbergensis*

TABLE 3. Diatom taxa and authorities for the 108 diatom taxa with N2 > 5.

Taxon no.	Taxon name	Regions	N	Hill's N2	pH WA Opt.	Conductivity WA Opt. ($\mu\text{s} \cdot \text{cm}^{-1}$)	DOC WA Opt. ($\text{mg} \cdot \text{L}^{-1}$)
1	<i>Achnanthes bioretii</i> Germain	A MB	11	6.1	8.1	109	1.80
2	<i>A. broenlundensis</i> Foged	A MB	I 14	6.0	8.0	122	5.09
3	<i>A. chlidanos</i> Hohn & Hellerman	A MB	I 25	16.2	8.0	117	2.35
6	<i>A. flexella</i> Kützing	A MB	I 22	13.1	8.0	128	3.16
7	<i>A. helvetica</i> Hustedt	A MB	I 32	11.5	7.7	96	1.95
10	<i>A. kryophila</i> Petersen	A MB	I 41	19.7	8.0	148	2.40
12	<i>A. laevis</i> Østrup	A MB	I 47	22.5	8.2	162	2.83
13	<i>A. marginulata</i> Grunow in Cleve & Grunow	A MB	I 43	10.6	7.5	102	2.30
14	<i>A. minutissima</i> Kützing	A MB	I 66	26.2	8.1	132	4.50
18	<i>A. petersenii</i> Hustedt	A MB	I 69	23.3	7.9	109	4.01
20	<i>A. rossii</i> Hustedt	A MB	I 7	5.3	8.0	117	1.35
24	<i>A. ventralis</i> Krasske	A MB	I 18	11.6	7.7	82	2.10
32	<i>Amphora inariensis</i> Krammer	A MB	I 33	14.1	8.3	192	2.20
33	<i>A. libyca</i> Ehrenberg	A MB	30	14.7	8.2	142	3.79
34	<i>A. pediculus</i> (Kützing) Grunow ex Schmidt	MB	I 8	5.4	7.8	102	4.58
35	<i>Amphora spitzbergenensis</i> VanLandingham	A MB	I 22	12.1	7.6	309	2.42
38	<i>Aulacoseira</i> sp. I1		I 13	10.8	7.0	246	2.10
40	<i>Caloneis aerophila</i> Bock	A	I 23	5.0	6.7	95	1.55
45	<i>C. hendeyi</i> Lange-Bertalot	A MB	22	6.6	8.2	155	2.60
46	<i>C. silicula</i> (Ehrenberg) Cleve	A MB	I 48	21.3	8.1	171	2.79
49	<i>Caloneis</i> sp. I2		I 15	5.0	7.1	337	2.63
50	<i>C. subclevei</i> Krammer		I 9	7.2	6.5	88	1.55
52	<i>Cyclotella antiqua</i> W. Smith	A MB	11	8.9	8.0	86	6.03
57	<i>Cymbella amphicephala</i> Naegeli	A MB	17	11.8	8.3	176	4.01
58	<i>C. angustata</i> (W. Smith) Cleve	A MB	I 41	24.9	8.0	105	4.45
59	<i>C. arctica</i> (Lagerstedt) Schmidt	A MB	I 40	23.4	8.0	114	4.79
62	<i>C. botellus</i> (Lagerstedt) A. Schmidt	A MB	16	7.4	8.3	132	4.67
63	<i>C. cesatii</i> (Rabenhorst) Grunow ex Schmidt	A MB	13	5.4	8.1	110	5.87
64	<i>C. cistula</i> (Ehrenberg) Kirchner	MB	11	6.7	7.8	82	7.31
65	<i>C. cuspidata</i> Kützing	MB	I 17	10.1	7.8	66	4.95
66	<i>C. descripta</i> (Hustedt) Krammer & Lange-Bertalot	A MB	I 16	10.1	8.0	121	3.07
67	<i>C. designata</i> Krammer	A MB	21	10.0	8.3	154	3.49
68	<i>Encyonema elginense</i> (Krammer) Mann	A MB	11	8.5	7.9	85	4.52
70	<i>E. fogedii</i> Krammer	A MB	49	24.9	8.0	108	4.95
71	<i>E. gauemannii</i> (Meister) Krammer	A MB	16	12.0	8.4	208	2.19
72	<i>C. incerta</i> (Grunow) Cleve	A MB	17	11.2	8.3	185	3.58
73	<i>Encyonema lange-bertalotii</i> Krammer	A MB	28	20.2	7.9	87	6.13
74	<i>Cymbella lapponica</i> Grunow	A MB	I 23	10.7	7.9	109	2.26
75	<i>C. latens</i> Krasske	A MB	I 17	7.6	7.6	108	1.92
77	<i>C. microcephala</i> Grunow in Van Heurck	A MB	I 41	13.8	8.1	114	4.87
78	<i>Encyonema minutum</i> (Hilse) Mann	A MB	I 31	14.3	7.8	78	4.32
79	<i>C. obscura</i> Krasske	A MB	I 21	12.6	7.9	91	3.38
82	<i>C. silesiaca</i> Bleisch in Rabenhorst	A MB	I 51	31.2	8.0	120	3.29
83	<i>C. stauroneiformis</i> Lagerstedt	A MB	15	7.7	8.0	107	6.26
90	<i>Encyonema ventricosum</i> (Agardh) Grunow	A MB	9	6.5	8.4	310	2.96
100	<i>Denticula kuetzingii</i> Grunow	A MB	I 27	11.6	8.2	138	4.73
102	<i>Diademsis contenta</i> (Grunow) Mann	A MB	I 20	7.1	7.8	80	4.58
104	<i>D. paracontenta</i> Lange-Bertalot & Werum	A MB	I 26	7.3	7.0	159	2.26
107	<i>Diatoma moniliformis</i> Kützing	A MB	13	7.3	8.0	166	5.34
108	<i>D. tenuis</i> Agardh	A MB	I 32	16.7	7.8	220	4.52
112	<i>Diploneis oculata</i> (Brébisson) Cleve	A MB	35	13.1	8.3	205	2.38
113	<i>D. parma</i> Cleve	A MB	13	9.1	8.1	135	4.04
120	<i>Eunotia praerupta</i> Ehrenberg	A MB	I 30	13.8	7.7	62	4.43
124	<i>Fragilaria capucina</i> Desmazières	A MB	I 39	14.1	7.8	79	4.61
125	<i>F. capucina</i> var. <i>gracilis</i> (Østrup) Hustedt	MB	25	12.4	8.0	81	7.31
129	<i>F. vaucheriae</i> (Kützing) Petersen	A MB	I 21	9.0	7.4	48	2.57
133	<i>Gomphonema angustatum</i> Agardh	MB	I 19	12.0	7.9	82	6.26
144	<i>Gyrosigma obtusatum</i> (Sullivan & Wormley) Boyer	A	8	5.4	8.5	193	2.49
145	<i>Hammaea arcus</i> (Ehrenberg) Patrick	A	I 7	5.4	7.5	103	1.31
149	<i>Navicula bacillum</i> Ehrenberg	A MB	I 16	9.8	7.9	105	5.13
151	<i>N. bryophila</i> (Petersen) Lange-Bertalot	A MB	I 28	14.1	8.4	209	2.53
155	<i>N. chiarae</i> Lange-Bertalot & Genkal	A MB	56	33.0	8.2	143	3.74
156	<i>N. cincta</i> (Ehrenberg) Ralfs	A MB	I 35	18.8	7.9	340	1.92
157	<i>N. clementis</i> Grunow	MB	7	5.7	8.0	181	6.54
158	<i>N. cocconeiformis</i> Gregory ex Greville	A MB	I 8	5.3	7.1	66	1.67
159	<i>N. cryptocephala</i> Kützing	A MB	I 48	22.3	8.1	133	2.23
160	<i>Navicula</i> sp. aff. <i>cryptocephala</i> Kützing	A MB	19	5.6	8.0	111	2.55

TABLE 3. (Contd.)

Taxon no.	Taxon name	Regions	N	Hill's N2	pH WA Opt.	Conductivity WA Opt. ($\mu\text{s} \cdot \text{cm}^{-1}$)	DOC WA Opt. ($\text{mg} \cdot \text{L}^{-1}$)
165	<i>Navicula</i> sp. aff. <i>phyllepta</i> Kützing	A	12	7.4	8.3	212	1.24
166	<i>N. gandrufii</i> Krasske	A MB	I 38	12.5	7.2	247	2.03
168	<i>N. gerloffii</i> Schimanski	A MB	I 26	15.8	7.8	120	2.00
170	<i>N. globulifera</i> Hustedt	A MB	I 10	6.0	7.4	544	3.19
173	<i>N. halophiloides</i> Hustedt	A MB	I 19	12.1	7.8	97	1.76
175	<i>N. insociabilis</i> Krasske	A	I 16	6.6	8.3	197	1.53
179	<i>N. krasskei</i> Hustedt	A MB	I 18	14.5	8.0	148	2.25
180	<i>Navicula</i> sp. 1 aff. <i>krasskei</i> Hustedt	A	I 21	10.9	7.6	158	2.16
184	<i>N. lenzii</i> Hustedt in Schmidt	A MB	I 7	5.4	8.1	145	3.03
188	<i>N. mutica</i> Kützing	A	I 17	9.4	6.9	282	1.79
192	<i>N. phyllepta</i> Kützing	A MB	I 22	7.8	7.7	455	3.57
195	<i>N. pseudotenelloides</i> Krasske	A MB	I 20	9.6	7.9	248	1.52
196	<i>N. pupula</i> var. <i>mutata</i> (Krasske) Hustedt	MB	I 13	8.7	7.8	64	5.11
206	<i>N. soehrensensis</i> Krasske	A	25	16.9	8.4	236	2.46
208	<i>N. egregia</i> Hustedt	A	15	9.9	8.4	245	2.30
216	<i>N. vulpina</i> Kützing	A MB	I 27	6.8	8.0	98	6.38
219	<i>Navicula</i> sp. A2	A	13	7.8	8.3	195	1.48
227	<i>Navicula</i> sp. MB1	A MB	I 13	7.7	8.2	126	3.59
237	<i>Navicula</i> sp. I1		I 10	5.8	7.2	327	1.97
252	<i>Neidium ampliatum</i> (Ehrenberg) Krammer	A MB	I 16	12.7	7.2	72	2.68
253	<i>N. bergii</i> (Cleve) Krammer	A MB	I 25	13.0	8.0	130	2.00
266	<i>Nitzschia amphibia</i> Grunow	A MB	I 13	7.2	8.3	183	2.27
268	<i>N. clausii</i> Hantzsch	A MB	I 22	5.7	7.5	469	2.12
269	<i>N. commutata</i> Grunow	A MB	I 17	5.5	7.6	272	2.36
271	<i>N. debilis</i> Arnott	A	I 15	9.0	7.4	272	2.45
272	<i>N. dissipata</i> var. <i>media</i> (Hantzsch) Grunow in Van Heurck	A MB	I 29	12.8	7.9	215	1.93
276	<i>N. inconspicua</i> Grunow		MB I 35	14.1	7.8	86	4.71
281	<i>N. palea</i> (Kützing) W. Smith	A MB	I 66	25.0	7.8	132	2.92
282	<i>N. paleacea</i> Grunow	A MB	I 18	9.2	7.9	140	5.09
283	<i>N. palustris</i> Hustedt		I 14	10.6	7.0	146	1.94
284	<i>N. perminuta</i> (Grunow) Peragallo	A MB	I 89	54.3	7.8	135	3.19
285	<i>N. pura</i> Hustedt	A MB	I 23	12.2	8.0	86	3.42
286	<i>N. pusilla</i> Grunow	A	I 25	9.4	7.6	338	1.39
295	<i>Pinnularia borealis</i> Ehrenberg		MB I 19	9.5	6.7	235	1.80
298	<i>P. divergens</i> W. Smith	A	I 10	7.2	7.1	96	1.58
304	<i>P. intermedia</i> (Lagerstedt) Cleve	A	I 24	8.4	6.7	177	1.57
305	<i>P. interrupta</i> W. Smith	A MB	I 10	8.7	7.7	85	3.19
307	<i>P. obscura</i> Krasske	A MB	I 23	7.9	7.0	98	2.06
312	<i>P. subrostrata</i> (A. Cleve) Cleve-Euler	A MB	I 25	15.0	7.4	98	3.20
324	<i>Stauroneis anceps</i> Ehrenberg	A MB	I 42	9.2	7.3	80	2.31
325	<i>S. phoenicenteron</i> (Nitzsch) Ehrenberg	MB	I 15	12.1	7.6	100	4.21

A/MB/I denotes presence/absence in each region. WA Opt., species optima as calculated by weighted averaging.

VanLandingham, *Denticula subtilis* Grunow, *Diatoma tenuis* Agardh, *Navicula gregaria* Donkin, *N. phyllepta* Kützing, *N. salinarum* Grunow, *Nitzschia clausii* Hantzsch, and *N. commutata* Grunow, each of which were absent or found in trace amounts at all other Alert sites. Excluding *D. tenuis*, these taxa have been infrequently recorded as components of electrolyte-rich high arctic diatom communities (Douglas and Smol 1993, Lim et al. 2001b, Antoniaades et al. 2004) and are considered to be brackish or high conductivity indicators (Lowe 1974, Foged 1981, Krammer and Lange-Bertalot 1986–1991, Lange-Bertalot 2001, Antoniaades et al. 2004). *Diatoma tenuis* has been commonly reported around the Canadian High Arctic and is present in sites of variable conductivity (Douglas and Smol 1995, Lim et al. 2001a, Michelutti et al. 2003a, Antoniaades et al. 2004). Further, the most common diatom in the Alert data set, *Nitzschia perminuta*, was present only in trace abundances (i.e. <1%) in site A-A. Although it is perhaps the most

common and abundant taxon in the Canadian High Arctic, *N. perminuta* was also observed to be intolerant of high conductivity waters on Ellef Ringnes Island (Antoniaades et al. 2004).

In contrast to most other regions, diatom diversity did not differ markedly between lakes and ponds in the Alert region. Diatom samples from the lakes were collected from near-shore shallow habitats to make them more directly comparable with the pond samples that form the majority of any high arctic calibration set. As a result, these samples may exclude any planktonic component of their diatom communities. Despite similar diversity values, however, there were differences in the species composition of shallow ponds and larger deeper lakes. Lakes typically had higher relative abundances of *Navicula* spp. than ponds (i.e. 41% vs. 29%) and lower relative frequencies of *Cymbella* spp. (6% vs. 11%) and *Nitzschia* spp. (14% vs. 20%). However, the difference in mean lake and pond DCA

TABLE 4. Relative abundances by genus.

	Alert		Mould Bay	
	Mean	Max	Mean	Max
<i>Achnanthes</i>	18.9	65.4	25.9	59.5
<i>Amphora</i>	4.9	19.4	1.7	9.6
<i>Caloneis</i>	3.4	17.7	1.7	13.6
<i>Cymbella s.l.</i>	9.6	42.6	16.3	32.8
<i>Denticula</i>	1.3	15.0	0.6	6.3
<i>Diadesmis</i>	0.1	0.8	1.1	15.0
<i>Diatoma</i>	0.3	3.5	1.9	11.1
<i>Diploneis</i>	6.4	37.6	0.6	7.1
<i>Eunotia</i>	0.3	7.1	1.4	8.1
<i>Fragilaria</i>	1.0	6.6	5.2	19.7
<i>Gomphonema</i>	0.1	3.4	1.0	6.6
<i>Navicula</i>	31.9	58.6	12.4	67.5
<i>Neidium</i>	1.1	7.0	0.4	3.9
<i>Nitzschia</i>	18.6	43.2	23.0	60.8
<i>Pinnularia</i>	0.4	2.0	4.1	59.4

Genera with mean abundance > 1% in one site are included. *Cymbella s.l.* includes *Encyonema* spp.

axis 1 scores was not significant (lake mean, 0.27; pond mean, 0.51; $P = 0.16$), partially due to the small sample size for lakes ($n = 6$).

Divergent diatom assemblages, with several different dominant taxa, characterized the Mould Bay sites. The most common diatom taxa in the Mould Bay data set included, in descending order of abundance, *Nitzschia perminuta*, *Achnanthes minutissima* Kützing, *A. petersenii* Hustedt, *Encyonema fogedii* Krammer, *E. lange-bertalotii* Krammer, and *Nitzschia inconspicua* Grunow. The growth of *A. minutissima* has been shown to be particularly sensitive to increases in UV radiation (Vinebrooke and Leavitt 1996). As such, the relatively higher DOC concentrations of Mould Bay sites may allow this taxon to reach higher abundances than in more transparent sites elsewhere in the High Arctic. *Encyonema fogedii* and *E. lange-bertalotii* (Krammer 1997) have not been reported in previous high arctic diatom surveys but likely occur as the commonly recorded *Cymbella silesiaca* Bleisch and *C. minuta* Hilse in these other regions (Douglas and Smol 1995, Lim et al. 2001b, Michelutti et al. 2003b).

Two sites, MB-O and MB-AH, had diatom assemblages that were distinct from all others in the Mould Bay data set. Taxa from the genus *Pinnularia* represented 48% and 59%, respectively, of diatoms at these sites but reached a maximum of only 7% elsewhere in Mould Bay sites. MB-O is a small pond that was a water chemistry outlier, resulting from greatly elevated total phosphorus ($77.9 \mu\text{g} \cdot \text{L}^{-1}$) and Fe^{2+} ($7.2 \text{mg} \cdot \text{L}^{-1}$), above average total nitrogen ($1.394 \text{mg} \cdot \text{L}^{-1}$), and the lowest pH in the Mould Bay data set (7.0) (Antoniades et al. 2003a). Four taxa comprised over 68% of the enumerated diatoms at MB-O: *Pinnularia* cf. *humilis* Krammer and Lange-Bertalot (30.9%), *Nitzschia perminuta* (18.8%), *Pinnularia angustiborealis* Krammer and Lange-Bertalot (13.9%), and *Achnanthes petersenii* (4.7%). No other taxon exceeded 2.5% relative abundance in MB-O. The ecological implications of the

presence of these taxa are unclear, because *N. perminuta* and *A. petersenii* were the only two taxa recorded in all 35 Mould Bay sites, whereas *P. angustiborealis* was present only in MB-O, has only been identified elsewhere from two sites, and has poorly defined ecological preferences (Krammer 2000).

The second outlier, site MB-AH, was situated immediately adjacent to the Arctic Ocean, which not surprisingly resulted in unusual water chemistry (Antoniades et al. 2003a). MB-AH had the highest specific conductivity and the highest concentrations of conductivity-related variables. In response to this disparate water chemistry, *Pinnularia balfouriana* Grunow and *Diatoma moniliformis* Kützing dominated the diatom assemblage, representing 59.0% and 8.2%, respectively, of diatoms enumerated. All other taxa were present below 4% relative abundance at MB-AH. *Pinnularia balfouriana* occurs commonly throughout shallow arctic sites (Douglas and Smol 1995, Krammer 2000, Lim et al. 2001b, Michelutti et al. 2003b). It was present in several other Mould Bay sites at lower relative abundances (i.e. $\leq 5\%$). *Diatoma moniliformis* is a species commonly found in coastal high electrolyte to brackish waters in northern Europe (Krammer and Lange-Bertalot 1986–1991). It was present in 10 other Mould Bay sites, all of which were in close proximity to the ocean and/or at the high end of the conductivity spectrum.

Of the 176 taxa identified in the Alert region, 75% have previously been reported in at least one diatom survey from the Canadian Arctic Archipelago (Table 3) (Douglas and Smol 1995, Joynt and Wolfe 2001, Lim et al. 2001a,b, Michelutti et al. 2003b, Antoniades et al. 2004), and an additional 9% have been identified from mainland arctic North America (Foged 1981, Fallu et al. 2000, Rühland and Smol 2002). Similarly, 74% of Mould Bay's 195 identified diatom taxa were previously recorded elsewhere in the Canadian High Arctic (Table 3) (Douglas and Smol 1995, Joynt and Wolfe 2001, Lim et al. 2001b, Michelutti et al. 2003b, Antoniades et al. 2004) and a further 9% from arctic North America (Foged 1981, Fallu et al. 2000, Rühland and Smol 2002).

It has been hypothesized that the duration of the growing season controls diatom diversity in high arctic sites (Smol 1988, Douglas and Smol 1999), and previous high arctic surveys suggested that diatom diversity decreases at more extreme latitudes in response to changes in climate and solar radiation (Michelutti et al. 2003b). Hill's N2 values were examined from seven arctic regions (Table 5), and one-way analysis of variance testing indicated that the differences in assemblage N2 between these regions were significant ($F = 10.1$, $P < 0.001$, $df = 6$; Table 5a). However, the highest mean diversity in our study was found in the most northerly location, Alert, where mean N2 was significantly higher ($P = 0.01$) than all regions except the central Northwest Territories (Table 5b). In fact, the mean Hill's N2 values from each of our regions exceed those of all previous high arctic diatom surveys,

TABLE 5. (a) Mean N2 values for Canadian Arctic diatom surveys.

Location	Mean N2	SD
Alert	13.09	5.22
Isachsen	9.16	5.06
Cape Herschel	6.72 ^a	3.40
Mould Bay	10.08	5.30
Bathurst Island	8.32 ^a	4.35
Victoria Island	7.81 ^a	4.35
Central Northwest Territories	13.88 ^a	5.22

Regions are arranged according to decreasing latitude.

^aFrom Michelutti et al. (2003b).

(b) Matrix of pair-wise least squares mean differences, with Bonferroni adjusted significances.

	Alert	Isachsen	Cape Herschel	Mould Bay	Bathurst Island	Victoria Island	Central Northwest Territories
Alert	0.00						
Isachsen	4.78	0.00					
Cape Herschel	6.13	1.36	0.00				
Mould Bay	-2.78	2.00	3.36	0.00			
Bathurst Island	- 4.53	0.24	1.60	-1.76	0.00		
Victoria Island	- 5.04	-0.27	1.09	-2.27	-0.51	0.00	
Central Northwest Territories	1.03	5.80	7.16	3.80	5.56	6.07	0.00

Bold denotes $P < 0.01$, and italics denotes $P < 0.05$.

and no correlation between latitude and diversity was apparent (Table 5, a and b). The average growing seasons of Alert and Mould Bay are of similar duration (i.e. 28 vs. 27 days; MSC 2002), whereas the closest weather station to the Bathurst and Victoria island study areas, Resolute, Cornwallis Island (74° 43' N, 94° 58' W), records an equally short growing season (32 days; MSC 2002). In addition, most sites in these studies are located within relatively short distances of the Arctic Ocean and thus are affected by similar microclimatic processes. Therefore, differences in growing season length may not be pronounced enough to account for the diversity differences between these high arctic regions. As such, these differences in mean diversity may be caused by other factors, such as regional water chemistry characteristics and microhabitat availability.

Although its overall taxonomic composition was similar to those of other high arctic studies, differing relative abundances and diversity within individual genera distinguished Mould Bay's diatom assemblages from those of other regions. Epiphytic taxa were more diverse in the Mould Bay region, as illustrated by the increased diversity of *Cymbella*, *Eunotia*, and *Gomphonema* species. *Achnanthes* spp. were also more abundant in Mould Bay sites than in other high arctic regions (Douglas 1989, Lim 1999, Michelutti 2003). These taxonomic differences appear to result from the high DOC concentrations and higher levels of submerged vegetation present at Mould Bay.

Multivariate analyses. Major diatom taxa (those present in at least 12 sites) from our 64 lakes and ponds are shown in Figure 2 according to increasing DCA site and species scores. The first DCA axis had a gradient length of 3.6 SDs, and the analysis showed a clear segregation of Alert and Mould Bay sites. The

Navicula-dominated Alert sites are situated along the top of the y -axis, separated from the *Achnanthes* and *Cymbella s.l.* dominated Mould Bay sites. Generalist taxa common to many sites in both study regions (e.g. *Navicula chiorae*, *Nitzschia perminuta*) are located in the middle of Figure 2, whereas taxa increase in their specificity to either the Alert (e.g. *Navicula soehrensensis*) or Mould Bay regions (e.g. *Fragilaria capucina* var. *gracilis* (Østrup) Hustedt) toward the left and right, respectively.

Moss samples within the Mould Bay data set tended to have the highest DCA site scores, potentially suggesting distinct diatom communities that resulted from microhabitat differences (i.e. moss vs. sediment). However, variance partitioning by partial CCA indicated that water chemistry was the primary determinant of diatom assemblages in these sites. Of the 54.9% of species variance explained in the analysis, water chemistry accounted for 46.2%, whereas microhabitat explained only 3.8% of the variance, and 4.8% was explained by a combination of both water chemistry and substrate. Because the grouping of diatom communities from these moss-covered sites was explained primarily by the environmental data, this may suggest a relationship between water chemistry and substrate availability (i.e. degree of moss cover). Water chemistry characteristics may determine the extent of moss growth within these ponds, or alternately, moss cover may be exerting influence on the water chemistry of these sites.

The first axis length of the species DCA (3.6 SDs) indicated that unimodal methods (i.e. CCA) were appropriate for further data exploration. Forward selection indicated that 13 environmental variables explained significant ($P \leq 0.05$) portions of the variance (i.e. pH, Mg^{2+} , DOC, SiO_2 , TPU, Cu^{2+} , Ba^{2+} , conductivity,

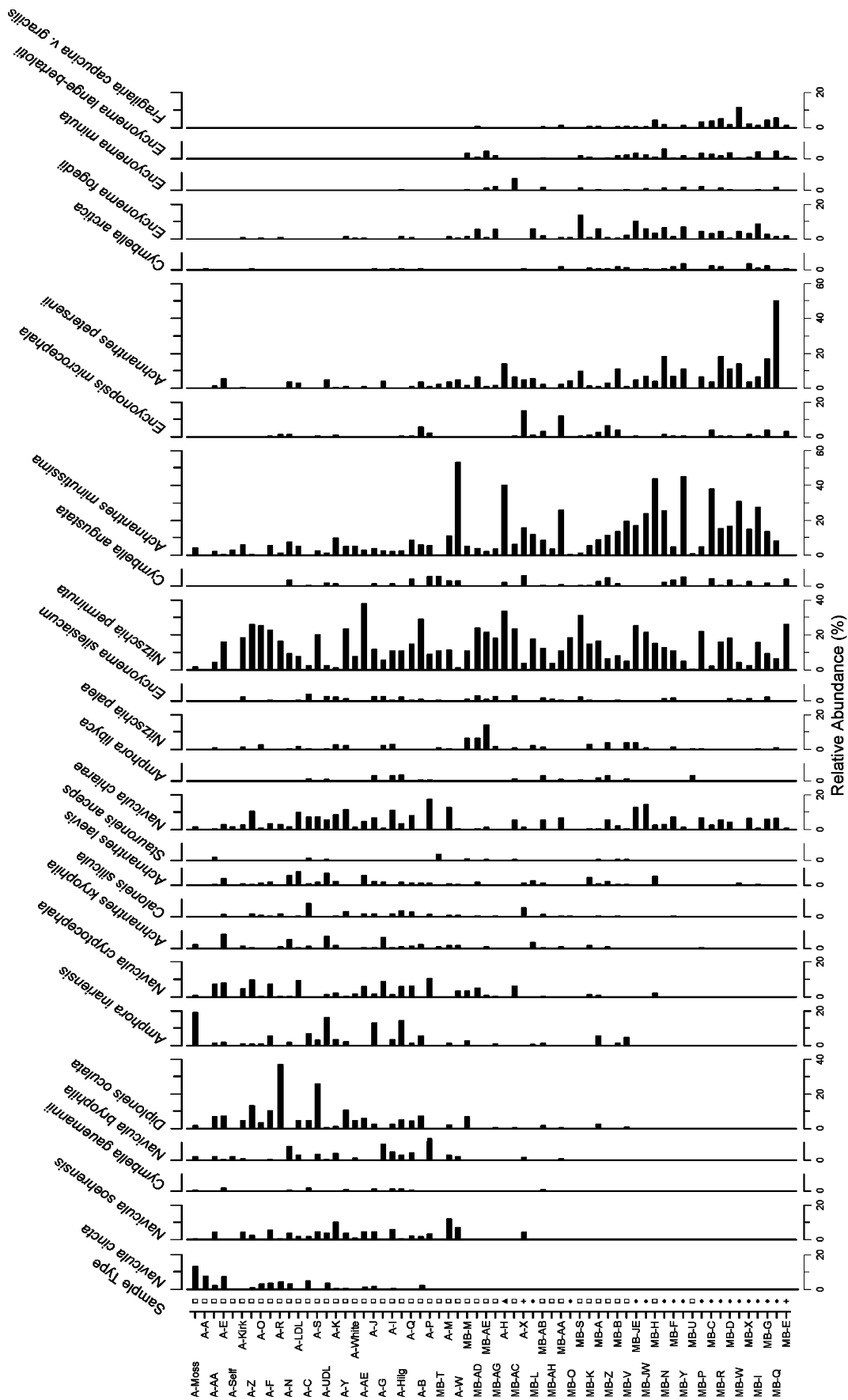


FIG. 2. Major diatom taxa in the Alert and Mould Bay regions, arranged according to increasing DCA axis 1 site/species scores. Open squares denote surface sediment samples, cross signs indicate microbial mat samples, filled circles represent moss samples, and filled triangles indicate rock samples.

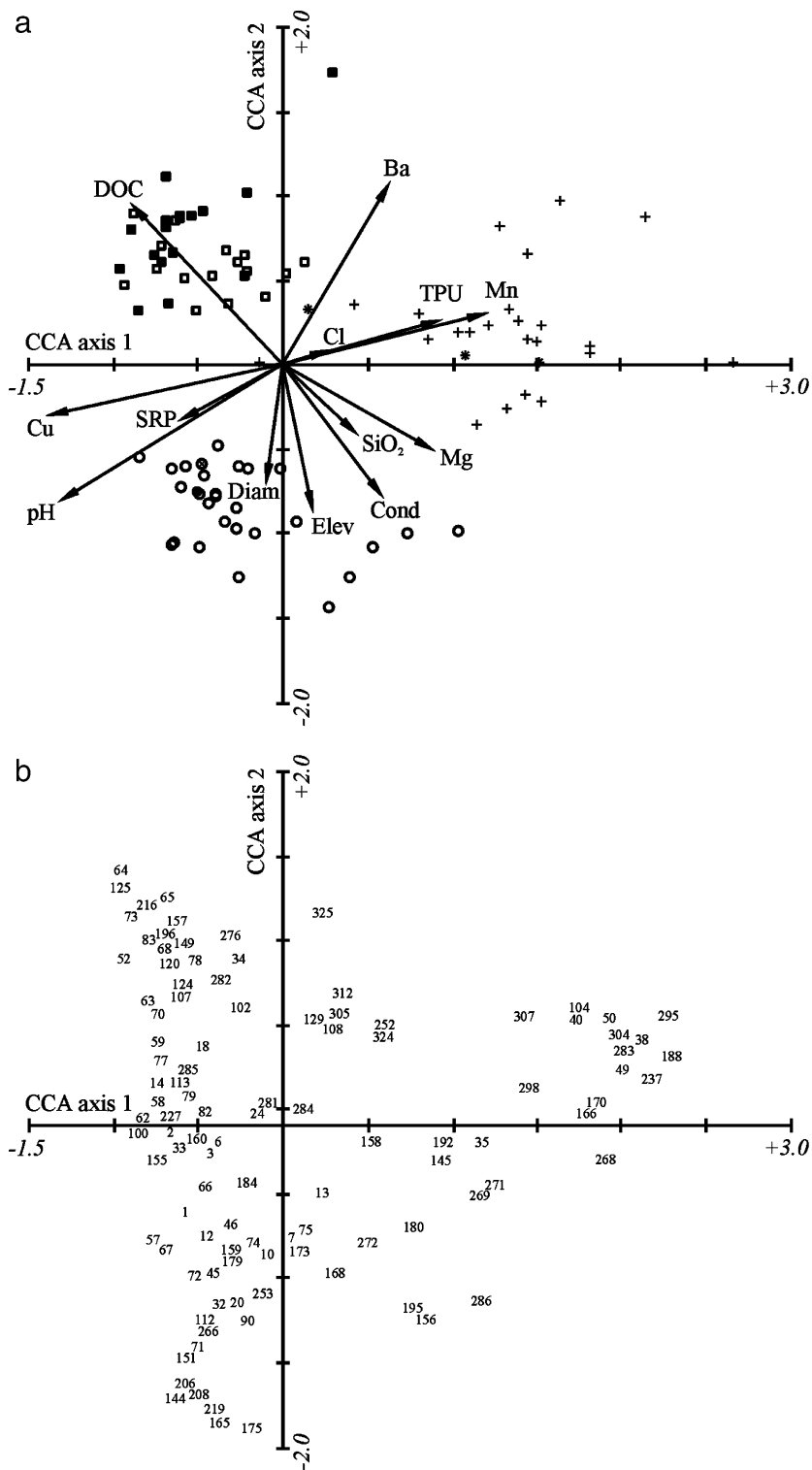


Fig. 3. CCA biplots of sites (a) and species (b). Squares represent Mould Bay samples, circles represent Alert samples, and crosses represent Isachsen samples. Open/filled shapes denote sediment/moss and microbial mat samples, whereas hatched symbols denote rock samples. Species codes for (b) can be found in Table 3.

soluble reactive phosphorus, elevation, Cl^{2+} , Mn^{2+} , and diameter). The first two axes of a CCA including these 13 variables explained 18.2% of the variance and 51.1% of the species–environment relationship (Fig. 3).

On the CCA biplot shown in Figure 3, the lengths of the arrows indicate the relative importance of variables in explaining the species data set, whereas their angles relative to the axes and to each other indicate the

strength of their correlation. Acute angles indicate high correlations, and right angles indicate no relationship between variables (Jongman et al. 1995). The positions of sites on the biplot are determined by the relationships between their diatom assemblages and the environmental variables. Given the disparate species compositions and water chemistry of the respective regions, it is not surprising that Alert, Mould Bay, and Isachsen sites are largely segregated on the CCA biplot (Fig. 3a).

Interset correlations indicated that pH had strong negative correlations with axes 1 and 2. The diatom communities of the more alkaline sites typical of the Alert region are thus found in the bottom left of Figure 3a. Common taxa most strongly associated with this quadrant included *Diploneis oculata*, *Amphora inariensis* Krammer, *Navicula bryophila*, *N. soehrensii*, and *N. egregia* Hustedt, which had pH optima between 8.3 and 8.5 (Table 3). With the exception of *N. egregia*, which has not previously been identified from the Canadian Arctic, these species are cosmopolitan high arctic forms, commonly found on Ellesmere, Bathurst, and Victoria islands (Douglas and Smol 1995, Lim et al. 2001b, Michelutti et al. 2003b).

Dissolved organic carbon was also negatively correlated with axis 1 but positively correlated with axis 2. Mould Bay sites, with their relatively higher DOC and lower pH values, were clustered in the upper left quadrant in close association with the DOC arrow, reflecting the influence of the dense local vegetation on diatom assemblages in the region. Taxa most strongly associated with these high DOC sites included several *Cymbella s.l.* taxa (i.e. *Encyonema fogedii*, *E. lange-bertalotii*, *E. minutum* (Hilse) Mann) as well as *Fragilaria capucina* Desmazières, *Eunotia praeurupta* Ehrenberg, and *Navicula vulpina* Kützing. Accordingly, these taxa had DOC optima ranging from 4.3 to 7.3 mg · L⁻¹ and pH optima from 7.7 to 8.0. *Fragilaria capucina* and *N. vulpina* were common in low abundances elsewhere in the High Arctic, whereas *E. praeurupta* was reported commonly from Victoria Island, rarely from Ellesmere Island, and was not present in

Bathurst Island sites (Douglas and Smol 1995, Lim et al. 2001b, Michelutti et al. 2003b). As discussed above, these *Encyonema* spp. may have been recorded in these other regions as *Cymbella silesiaca* and *C. minuta*.

Sites with relatively low pH dominate the positive side of CCA axis 1, with a secondary gradient from low conductivity in the upper portion to higher conductivity sites in the bottom right quadrant. As such, most of these sites are the weakly acidic to circumneutral ponds of the Isachsen region. However, alkaline sites with elevated solute concentrations from Alert are also present in the lower right quadrant, in close association with the conductivity arrow, and driven by the presence of taxa such as *Navicula cincta*, *N. pseudotenelloides* Krasske, *Nitzschia dissipata* var. *media* (Hantzsch) Grunow, and *N. pusilla* Grunow. These taxa are typically found in high conductivity to brackish waters (Lowe 1974, Lange-Bertalot 2001) and in our study had relatively high conductivity optima of 344, 248, 215, and 338 $\mu\text{S} \cdot \text{cm}^{-1}$, respectively. High relative abundances in these sites also implied alkaliphilic preferences, and, not surprisingly, the pH optima of these taxa ranged from 7.6 to 7.9. Among this group of taxa, only *N. dissipata* was previously reported from the Canadian High Arctic, and then only as a rare low abundance component of ultraoligotrophic Victoria Island diatom assemblages (Michelutti et al. 2003b).

Conversely, the diatom assemblages from sites of lower pH and low conductivity are situated in the upper left of the biplot of Figure 3. Acidophilic taxa from the genus *Pinnularia* were present in greater relative abundances at these sites. The most common species included *P. borealis* Ehrenberg, *P. intermedia* (Lagerstedt) Cleve, and *P. obscura* Krasske as well as *Diademesmis paracontenta* Lange-Bertalot and Werum, *Navicula mutica* Kützing, *Nitzschia palustris* Hustedt, and *Aulacoseira* sp. II, with pH optima ranging from 6.6 to 7.0. These taxa reached their highest abundances in the low conductivity weakly acidic sites present on gabbro substrates in the Isachsen region (Antoniades et al. 2004).

TABLE 6. Comparison of WA and WA-PLS inference models.

	WA _{INV}	WA _{CLA}	WA(tol) _{INV}	WA(tol) _{CLA}	WA-PLS(1)	WA-PLS(2)	WA-PLS(3)
RMSEP	0.419	0.416	0.448	0.446	0.428	0.400	0.411
r_{boot}^2	0.716	0.720	0.738	0.740	0.709	0.765	0.756
Max. Bias _{boot}	1.210	0.933	1.490	1.308	1.361	1.373	1.400
Mean Bias _{boot}	-0.025	-0.031	-0.089	-0.102	-0.028	-0.040	-0.042
			<i>pH</i>				
RMSEP	0.308	0.308	0.361	0.370	0.310	0.282	0.275
r_{boot}^2	0.617	0.620	0.563	0.567	0.614	0.703	0.725
Max. Bias _{boot}	0.615	0.504	0.682	0.599	0.622	0.440	0.404
Mean Bias _{boot}	0.004	0.005	0.002	0.002	0.006	0.009	0.005
			<i>Conductivity</i>				
RMSEP	0.240	0.254	0.270	0.287	0.241	0.234	0.233
r_{boot}^2	0.548	0.553	0.494	0.498	0.543	0.590	0.611
Max. Bias _{boot}	0.481	0.427	0.552	0.530	0.475	0.407	0.419
Mean Bias _{boot}	0.001	-0.001	-0.019	-0.026	0.006	-0.005	-0.005
			<i>DOC</i>				

WA, weighted averaging; WA_{CLA}, WA with classical deshrinking; WA_{INV}, WA with inverse deshrinking; WA-PLS, weighted averaging partial least squares; WA(tol), weighted averaging with tolerance down-weighting.

Generalist taxa clustered around the origin of the CCA biplot, including *Nitzschia perminuta*, *N. palea* (Kützing) Smith, *Diatoma tenuis*, *Achnanthes flexella* Kützing, and *A. ventralis* Krasske, had Hill's N2 values of 54, 25, 17, 13, and 12, respectively. Their pH optima were within the narrow range of 7.7 to 7.9, whereas conductivity optima ranged from 82 to 220 $\mu\text{S}\cdot\text{cm}^{-1}$. These optima were centered on the median values of 7.8 and 162 $\mu\text{S}\cdot\text{cm}^{-1}$, confirming the lack of strong environmental preferences of these taxa.

Model construction. CCAs constrained to individual environmental variables indicated that the four variables selected from the original CCA each accounted for a significant portion of the variance in the species data set ($P \leq 0.01$). Analyses constrained to pH ($\lambda_1/\lambda_2 = 0.76$), DOC ($\lambda_1/\lambda_2 = 0.53$), and conductivity ($\lambda_1/\lambda_2 = 0.44$) yielded ratios that suggested the potential for further investigation of inference model development. The TPU first axis eigenvalue and λ_1/λ_2 ratio (0.37) were low; thus, TPU inference models were not generated.

A single variable DCCA indicated that pH alone explained 7.9% of the species variance, with a gradient length (G.L.) of 3.41 SDs ($P = 0.005$). Dissolved organic carbon alone explained 5.9% of the variance (G.L. = 2.116, $P = 0.005$), whereas conductivity alone explained 5.2% (G.L. = 2.466, $P = 0.005$). As such, unimodal methods were deemed appropriate for subsequent model generation. Diatom inference models were constructed for each of these three variables using WA methods, and models both with (WA(tol)) and without (WA) tolerance down-weighting were considered (Table 6).

Initially, pH, conductivity, and DOC models were developed with the Alert ($n = 30$), Mould Bay ($n = 34$), and Isachsen ($n = 26$; Antoniaades et al. 2004) data sets separately as well as with a larger, combined, regional, 90-site model representing all three regions. Species optima and tolerances from the three smaller models were then compared with those from the 90-site model using *t*-tests. Only the conductivity optima from the Isachsen model ($r^2 = 0.58$) were significantly correlated ($P = 0.05$) with values generated by the larger model, and there were no significant correlations between tolerances calculated by the individual and regional models. This suggests that the individual data sets were either too small or did not encompass sufficiently large environmental gradients to accurately predict these variables (Wilson et al. 1994). As such, all species optima and tolerances reported here were generated on the basis of the combined 90-site data set.

Simple WA produced pH models that were slightly better than those generated with tolerance down-weighting (WA(tol)), based on RMSEP and bootstrapped mean bias, although the coefficient of determination (r^2) of the WA(tol) models was slightly higher (Table 6). WA with classical (WA_{CLA}) and inverse (WA_{INV}) deshrinking produced similar RMSEP, bootstrapped mean bias, and r^2 values; however, WA_{CLA} had a 23% lower maximum bias and was thus the best

WA model. Typically, a higher component WA-PLS model is selected only if it improves RMSEP by at least 5% over a simpler one-component model (Birks 1998). The second WA-PLS pH component (WA-PLS(2)) improved RMSEP by 6.5% over WA-PLS(1) and by 4% over WA_{CLA}, with little difference in mean bias between models. Because no model clearly outperformed all others, 10 intervals along the pH gradient were examined to determine whether model performance was related to pH level (Birks 1998). All models were prone to underestimation at high pH and overestimation at the low end of the gradient. However, WA_{CLA} had lower mean and maximum bias at the ends of the pH gradient (i.e. ≥ 8.3 and ≤ 7.0), whereas WA-PLS(2) improved bias relative to simpler models in moderate pH sites (i.e. 7.1–8.2). Because 48 of our sites fall in the former category and 42 in the latter, selection of the appropriate paleolimnological model may be made based on the modern pH of the site chosen for reconstruction.

Simple WA models clearly outperformed WA(tol) in the construction of conductivity models according to RMSEP and r^2 (Table 6). WA_{INV} and WA_{CLA} produced models with almost identical RMSEP, mean bias, and r^2 values, with lower maximum bias in the WA_{CLA} model. The second WA-PLS component clearly improved over simple WA models, with an 8% reduction in RMSEP, a 13% decrease in maximum bias, and a 13% increase in r^2 relative to the best one-component model, although WA-PLS(2) mean bias was slightly higher than in other models. Although WA-PLS(3) represented a further improvement over the second component, the decrease in RMSEP (2.5%) was not sufficient to warrant its selection over the simpler model. As such, the best conductivity model for paleolimnological reconstruction is the two-component WA-PLS model.

In the construction of DOC models, simple WA again clearly outperformed WA(tol), with lower RMSEP, lower mean and maximum bias, and higher bootstrapped r^2 (Table 6). WA_{INV} RMSEP was 5.5% lower than that of the WA_{CLA} model, whereas WA_{CLA} improved maximum bias by 11%. Bootstrapped r^2 and mean bias were roughly equal between the two models (Table 6). The second WA-PLS component improved RMSEP by 3% over WA-PLS(1) and WA_{CLA} and was thus rejected in favor of the "minimal adequate" WA models (Birks 1998).

Because of the similarity of the performance measures of WA_{INV} and WA_{CLA}, model estimates along the DOC gradient were examined in greater detail to determine whether model performance was related to DOC concentration. Again, both WA models tended to underestimate DOC at high concentrations while overestimating it at the low end of the DOC gradient. Mean bias was lower for WA_{INV} than WA_{CLA} at moderate DOC values (i.e. $\log_{10}\text{DOC} \geq 0.21$ and ≤ 0.62), whereas WA_{CLA} improved mean bias at higher and lower DOC concentrations. Maximum bias values followed similar trends, although WA_{INV} maximum bias was greater only

at more extreme concentrations (i.e. $\log_{10}\text{DOC} \leq 0.08$ and ≥ 0.91). As such, WA_{INV} represents the superior model and, except perhaps in cases of extremely high or low DOC sites, is the model appropriate for use in reconstructions.

Inferences generated by each of these three models may provide important insights into the environmental history of lakes and ponds in the Canadian High Arctic. The three environmental variables in question are directly or indirectly related to climate processes and may be dramatically affected by any change in climate regime in the region. For example, alpine lakes appear to sensitively record changes in seasonal ice cover: pH reconstructions in acidic alpine lakes have revealed trends that closely mirror changes in annual air temperature (Sommaruga-Wögrath et al. 1997), which the authors attribute to the effects of ice cover duration on site chemistry. These temperature-dependent variations in pH may result from the effect of ice cover on CO_2 exchange with the atmosphere, rates of primary productivity and decomposition, and changes in the input of cations from the catchment (Koinig et al. 1998). Ratios of periphytic to planktonic diatoms have also been shown to record ice cover changes in an alkaline alpine lake (Lotter and Bigler 2000).

The prolonged ice cover, sparsely vegetated catchments, and lack of direct human impacts that characterize high alpine lakes are also common to high arctic lakes and ponds. High arctic sites also appear to be similarly sensitive to changes in pH, as pH increases due to productivity have been observed during the short arctic summer in shallow tundra ponds (Douglas and Smol 1999). Changes of approximately 0.8 pH units over the last approximately 5500 years have been inferred from diatom biostratigraphic records from Baffin Island to represent neoglacial cooling (Wolfe 2002). However, no studies yet exist that reconstruct pH in the Canadian High Arctic or from shallow arctic ponds.

Similar to trends in pH, specific conductivity increases after early summer runoff throughout the arctic summer due to the evaporative concentration of solutes (Douglas and Smol 1999). These changes in conductivity may affect diatom communities directly or through indirect effects on pH in these largely carbonate dominated sites. Proxy records of pH and conductivity could therefore potentially provide information about past climates in the High Arctic.

Typical arctic fresh waters are also extremely vulnerable to the effects of harmful UV radiation as a result of their low DOC concentrations (Vincent and Pienitz 1996), although DOC can be dramatically higher in regions of atypically high vegetative growth such as Mould Bay (Antoniades et al. 2003a). The UV attenuation depth of lakes below $2 \text{ mg} \cdot \text{L}^{-1}$ DOC is highly sensitive to changes in DOC concentrations (Williamson et al. 1996), and UV radiation has been shown to suppress periphytic diatom productivity in alpine lakes with similarly low DOC (Vinebrooke and Leavitt 1996). Because of their typically shallow nature

and low DOC concentrations, it is plausible to suggest that diatom growth in most Alert and Isachsen sites could be inhibited by high UV levels and thus indirectly controlled by DOC. Changes in DOC inputs from vegetation can be two orders of magnitude more important than ozone depletion in determining UV penetration and the inhibition of algal photosynthesis (Pienitz and Vincent 2000). Although reconstruction of past DOC levels should provide insights into long-term vegetational change in our sites, it may also give an indication of the degree to which productivity may historically have been affected by changing levels of UV attenuation.

The effects that changes in DOC concentrations may have on diatom communities is well illustrated by the taxonomic differences between Mould Bay and other high arctic regions. High DOC levels, mediated by increased levels of vegetation, exert strong influences on the diatom communities of Mould Bay. As such, increases in DOC concentrations may not only protect organisms from the harmful effects of UV radiation, but may affect diatom species compositions as well. High modern DOC concentrations at Mould Bay may provide important insights into future conditions at other less vegetated high arctic sites under climate amelioration scenarios. In addition, paleolimnological records from the Mould Bay region may provide insights into the influence of long-term vegetational change on diatom communities.

Conclusions. The sampling sites included in this study encompass broad spatial and limnological gradients. Because of this diversity, our inference models may allow for the accurate reconstruction of climate-related trends in pH, conductivity, and DOC from sites of diverse geographical, limnological, and biological characteristics. Although it is recognized that recent climate warming has been amplified in the circumpolar Arctic (Overpeck et al. 1997), the spatial variability of this warming across the Canadian Arctic Archipelago is not yet clearly documented. Because of the relationships between climate and pH, conductivity, and DOC, quantitative paleolimnological reconstructions of these variables in the Canadian High Arctic may allow us to more completely understand the climatic and environmental history of the region.

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