

Distribution of freshwater diatoms in 64 Labrador (Canada) lakes: species–environment relationships along latitudinal gradients and reconstruction models for water colour and alkalinity

Marie-Andrée Fallu, Nancie Allaire, and Reinhard Pienitz

Abstract: The distribution of modern diatom assemblages in surficial sediments of 64 Labrador (Canada) lakes across broad vegetational biomes was studied in order to explore species–environment relationships and to develop transfer functions for paleoenvironmental reconstruction. The study sites were situated along a latitudinal gradient (51°27' to 57°37'N) and classified according to six catchment vegetation types: wetland (peatland) forest, spruce/fir forest, lichen woodland, forest–tundra, coastal tundra, and tundra. Canonical correspondence analysis revealed that among 28 environmental variables determined for each site, water colour and alkalinity accounted for most of the variance in the diatom data. Using weighted-averaging partial least squares techniques, we developed transfer functions for inference of water colour (CLR) ($r^2_{\text{jack}} = 0.85$, root mean square error of prediction (RMSEP) = $0.18\log(\text{CLR} + 1)$ or 1.51 Pt units) and alkalinity (ALK) ($r^2_{\text{jack}} = 0.63$, RMSEP = $0.25\log(\text{ALK} + 1)$ or $1.78 \mu\text{eq}\cdot\text{L}^{-1}$) from the percent abundance of the 132 most abundant diatom taxa. By determining diatom distribution in relation to more detailed vegetation types within the boreal forest zone (wetland forest, spruce/fir forest, and lichen woodland), this calibration data set demonstrated the potential of these assemblages for revealing more subtle changes in lake catchment vegetation over time.

Résumé : La répartition des assemblages fossiles de diatomées dans les sédiments de surface de 64 lacs du Labrador (Canada) situés dans différentes régions géographiques a été étudié afin de déterminer les relations existantes entre les espèces et leur environnement et de développer des fonctions de transfert pour effectuer des reconstitutions environnementales. Les lacs sont situés le long d'un transect latitudinal (51°27' à 57°37'N) et se classent selon six zones de végétation; forêt des milieux humides (tourbières), pessière/sapinière, pessière à lichen, toundra forestière, toundra côtière et toundra. Des analyses canoniques de correspondances ont été utilisées pour les 28 variables environnementales et ont révélé que la couleur de l'eau et l'alcalinité expliquaient le mieux la répartition des espèces de diatomées. En utilisant l'analyse des moyennes pondérées des moindres carrés partiels, des fonctions de transfert ont été développées pour inférer la couleur de l'eau (CLR) ($r^2_{\text{jack}} = 0.85$, erreur des moindres carrés partiel de prédiction (RMSEP) = $0.18\log(\text{CLR} + 1)$ ou 1.51 unités Pt) et l'alcalinité (ALK) ($r^2_{\text{jack}} = 0.63$, RMSEP = $0.25\log(\text{ALK} + 1)$ ou $1.78 \mu\text{eq}\cdot\text{L}^{-1}$) à partir des 132 taxa de diatomées les plus abondants. En déterminant la répartition des diatomées selon des zones de végétation plus détaillées à l'intérieur de la forêt boréale (forêt des milieux humides (tourbières), pessière/sapinière, pessière à lichen), ces données permettent aussi de démontrer le potentiel des assemblages de diatomées pour déceler des changements plus subtiles du couvert végétal du bassin versant des lacs.

Introduction

Global warming scenarios predict that the greatest changes in climate will occur within the boreal and north polar regions (e.g., Kattenberg et al. 1996). The consequences of such climatic changes could translate into major shifts in vegetation in these high latitude areas, which in turn could further modify climate via albedo and other feedback mechanisms (Bonan et al. 1995). In northern and alpine regions, a close relationship between climate and vegetation has been

observed (Payette et al. 1989; Pielke and Vidale 1995). This interdependence is also reflected in the limnological conditions of northern and high altitude lakes, which change abruptly across vegetational boundaries within the tree-line ecotone (e.g., Duff et al. 1999). Paleolimnological studies within this ecotone and in recently deglaciated landscapes have similarly revealed that there have been large-scale modifications of the aquatic environment in response to past catchment vegetation changes brought about by climate-related shifts in tree line (e.g., Pienitz et al. 1999; Pienitz

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and Vincent 2000) and by successional changes following deglaciation (Engstrom et al. 2000).

The striking physical and chemical changes in lakes across arctic and alpine tree lines are also reflected in the zonal distributional patterns of freshwater diatoms (class Bacillariophyceae). Studies of modern diatom assemblages in high latitude and high altitude regions have contributed to a better understanding of diatom species–environment relationships and the development of transfer functions to predict past environmental changes (reviewed in Lotter et al. 1999). In the circumpolar region of the northern hemisphere, inference models have been developed for the reconstruction of dissolved organic carbon (DOC), which is derived from terrestrial vegetation and soils (e.g., Pienitz and Smol 1993; Fallu and Pienitz 1999). Other diatom-based inference models have been developed for the reconstruction of water colour (e.g., Korsman and Birks 1996; Seppä and Weckström 1999), alkalinity (e.g., Korsman and Birks 1996; Rühland 1996), dissolved inorganic carbon (DIC) (Pienitz and Smol 1993), total organic carbon (TOC) (e.g., Seppä and Weckström 1999; Rosén et al. 2000), pH (e.g., Rosén et al. 2000; Bigler and Hall 2002), water depth, lake surface water temperature (e.g., Pienitz et al. 1995; Weckström et al. 1997), and air temperature (e.g., Rosén et al. 2000; Bigler and Hall 2002). These models provide the starting point for more detailed, quantitative paleolimnological reconstructions in high latitude regions and, in the case of the DOC/TOC and water colour models, a means for the study of the links between terrestrial (vegetation) and aquatic environments. However, studies of relationships between diatoms and catchment vegetation to date have focused only on distinguishing coarse lake catchment vegetation zones (i.e., boreal forest, forest–tundra, or tundra lakes). The present study encompasses six different catchment vegetation types (wetland forest, spruce/fir forest, lichen woodland, forest–tundra, coastal tundra, tundra) and therefore provides an opportunity to evaluate how vegetation within the boreal forest and the degree of paludification affect diatom community structure.

Only a few studies focusing on the postglacial stratigraphies of diatom assemblages have been completed to date in northeastern Québec – Labrador (e.g., Clark et al. 1989; Allaire 1997), and no extensive studies examining diatom distributions have yet been carried out in this vast territory. The present paper aims to provide the first detailed inventory of these important bioindicators through a survey of diatom distributions in the surface sediments of 64 lakes located across steep ecoclimatic gradients and ecotonal boundaries. We used a multivariate statistical approach to determine which environmental variables best explained the observed distributional patterns. The variation in diatom assemblages across the latitudinal gradient from boreal forest to arctic tundra conditions in Labrador were analyzed, and the autecological preferences of the identified diatom taxa were determined. The second part of the paper assesses the applicability and predictive ability of two weighted-averaging partial least squares (WA-PLS) inference models for alkalinity and water colour developed using the diatom and environmental data for future use with diatom-based paleolimnological studies in Labrador. Finally, we evaluated the usefulness of diatoms as proxies of catchment vegetation changes in the northern region.

Materials and methods

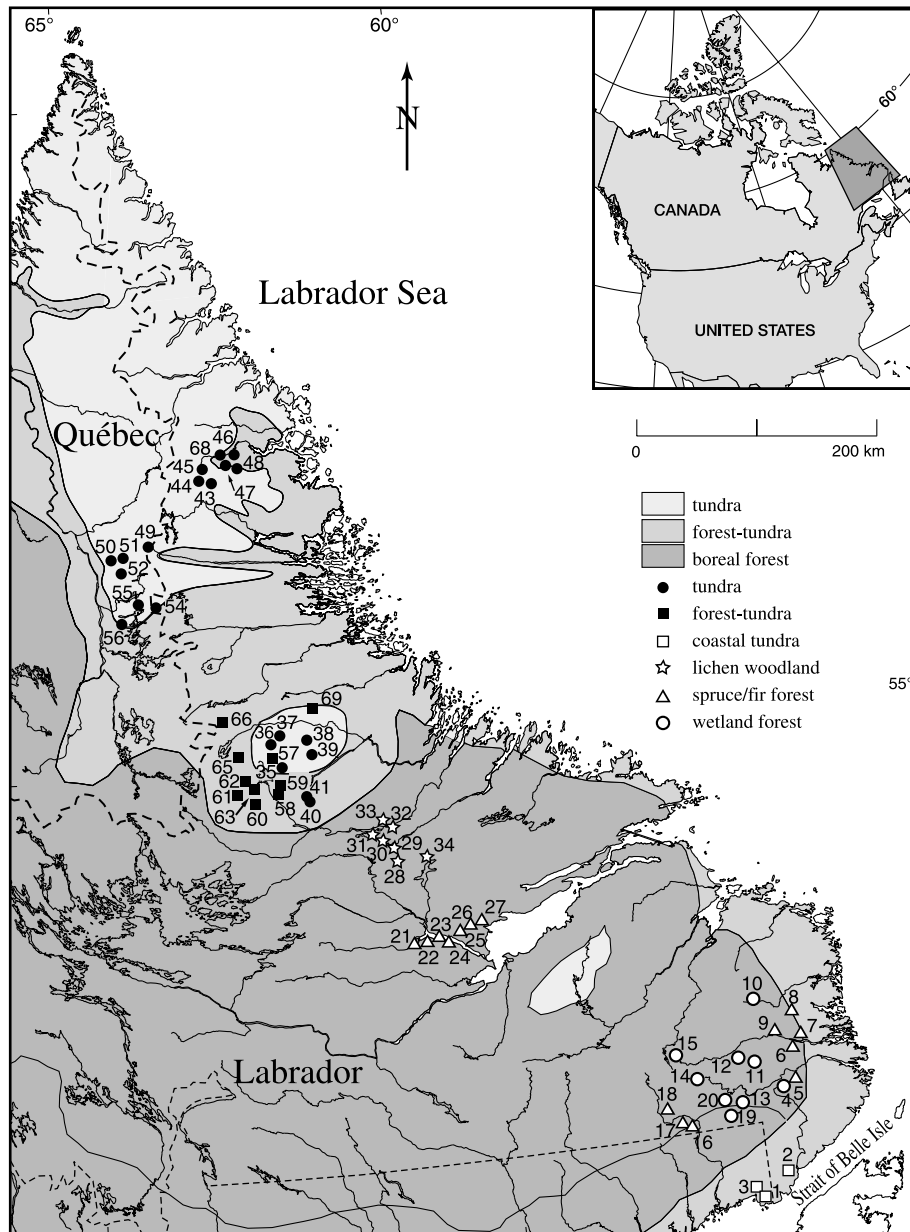
Description of study region and sites

The 64 lake sites in Labrador and adjacent Québec are situated between 51°27' to 57°37'N and 56°11' to 64°32'W (Fig. 1). The lakes were specifically chosen to span a broad climatic gradient so that the study area included different ecoclimatic zones. Most of the lakes were unnamed and therefore were given sampling numbers. Of the 64 lakes studied, sites 4, 10–15, 19, and 20 are situated within catchments dominated by wetland (peatland) forests; sites 5–9, 16–18, and 21–27 are within spruce/fir forests; sites 28–34 are within lichen woodland; sites 57–63, 65, 66, and 69 are within forest–tundra; sites 1–3 are within coastal tundra; and sites 35–41, 43–52, and 54–56 are within tundra catchments.

The study region has been described in detail in earlier studies on the Holocene history of vegetation and soils in Labrador (Lamb 1980; Engstrom and Hansen 1985) and the present-day influence of vegetation and hydrology on the humus budgets of lakes (Engstrom 1987), as well as within the context of modern training sets for pollen (Lamb 1984) and chironomids (Walker et al. 1991). These studies also review the geology, deglaciation history, climatology, and limnology of the area.

In summary, the bedrock geology is dominated by granites and granodiorites of Precambrian age that belong to the Canadian Shield. The sites are located on bedrock belonging to three different geological provinces (Grenville, Churchill, and Nain). Till of differing thickness sporadically occurs throughout the area. Sites 30–33 are located on postglacial marine sediments deposited during high sea level stands and are composed of gravel, sand, silt, and clay (Water Resources Division 1992). The climate of Labrador comprises three major ecoclimatic regions (Oceanic High Boreal through the Low Arctic) (Ecoregions Working Group 1989). From south to north, annual precipitation ranges from 900 to 750 mm, and annual temperature ranges from 1.5 to –2°C (Water Resources Division 1992).

Three major physiognomic zones can be distinguished along a latitudinal gradient in Labrador (Hare 1959): boreal forest, forest–tundra, and tundra (Fig. 1). Within the boreal forest zone, three different vegetation types can be found in the catchments of lakes: wetland forest, spruce/fir forest, and lichen woodland (Hare 1959). In maritime southeastern Labrador, the denser spruce/fir forests are restricted to sheltered areas in river valleys (*Abies balsamea*, *Picea mariana*, and *P. glauca*), whereas the open wetland forests are characterized by sparsely forested (*Picea mariana*) mires and muskegs (Lamb 1984). The lichen woodland zone is characterized by an open forest of *Picea mariana* with a lichen-dominated ground flora, a vegetation type that can also be found in the forest–tundra zone and on xeric sites in the closed forest region (Lamb 1984). The lichen woodland zone with its open *Picea mariana* forests and extensive lichen ground cover represents the transition towards the forest–tundra zone (Lamb 1984). The latter consists of patches of open *Picea* and *Larix* woodlands in lowlands and tundra-covered uplands. The vegetation of the tundra zone is composed of small dwarf shrubs (*Betula glandulosa*, *Alnus crispa*, and a few species of *Salix*), graminoids, herbs, mosses, and lichens (Lamb 1984).

Fig. 1. Map illustrating the location of the 64 Labrador lakes, Eastern Canada.

Sampling and measurement procedures

The surficial sediments of the 64 study sites were sampled by the Limnological Research Centre (LRC) of the University of Minnesota during July–August of 1979. The top 3 cm of sediments was collected at the deepest point of each lake basin (Lamb 1984), none of which was connected to upstream lakes or fed by large affluents (Engstrom 1987). Sediments were collected with a free-fall modified Hongve sampler (Wright 1990). Field sampling techniques (sediment and water samples) and laboratory analysis (water chemistry) procedures have been described in detail by Lamb (1984), Engstrom and Hansen (1985), and Engstrom (1987). Specific conductance, pH, apparent water colour (measured by a comparator method with calibrated platinum–cobalt (Pt–Co) standards), water transparency (Secchi depth), and alkalinity were measured in the field, whereas all other water chemistry analyses were performed in the laboratory.

Topographic maps (1 : 50 000) and aerial photographs (1 : 17 000) were used to determine catchment and lake area as well as to determine predominant vegetation, along with field observations (Engstrom 1987). The physical and chemical characteristics for the 64 lakes where diatoms were studied are summarized in Table 1.

The preparation and analysis of diatom samples followed standard techniques. Diatoms were extracted from sediments using acid digestion techniques (HNO_3 and H_2SO_4 , 50:50) before being mounted on microscope slides using Naphrax[®]. Some of the surficial sediments were previously counted by Keith Camburn (4435 Huntington Drive, Gastonia, NC 28056, U.S.A.). The taxonomy was standardized by recounting several levels and assuring similar results. For each sample, approximately 500 diatom valves were counted. Identifications were made to the lowest taxonomic level possible (e.g., variety) at 1000 \times magnification. Diatom taxon-

Table 1. Summary of selected limnological data for the 64 study lakes in Labrador, arranged according to catchment vegetation type.

Variable	Coastal tundra (3 lakes)			Spruce/fir forest (15 lakes)			Wetland forest (9 lakes)			Lichen woodland (7 lakes)			Forest-tundra (10 lakes)			Tundra (20 lakes)			Total (all 64 lakes)		
	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
ALK ($\mu\text{eq}\cdot\text{L}^{-1}$)	66	2154	763	7	106	35	3	68	33	28	463	217	34	138	84	10	94	36	3	2154	97
CLR (Pt units)	5	40	18	10	70	50	50	130	89	5	10	8	5	20	14	5	20	6	5	130	30
Depth (m)	5	23	14	3	50	14	1	2	2	3	29	19	3	15	8	3	50	15	1	50	12
ORG (g)	12	20	16	20	44	33	3	33	20	10	44	22	17	42	29	2	36	18	2	44	24
pH	5.9	7.9	6.8	5.2	6.7	5.7	5.0	6.4	6.0	6.4	7.6	7.0	5.9	7.0	6.5	6.0	7.1	6.5	5.0	7.9	6.3
Specific cond. ($\mu\text{S}\cdot\text{cm}^{-1}$)	2.5	203	85	8	74	19	5	16	11	6	50	28	5	17	10	1	11	4	1	203	16
Trans. (m)	4	105	56	40	135	78	38	235	128	62	195	119	73	105	86	27	173	83	4	235	91
AREA (ha)	43	195	94	57	385	203	221	406	340	126	306	267	352	589	507	260	623	513	43	623	369
Catch. (ha)	61	341	204	84	2086	627	200	1570	744	168	635	410	421	3944	1125	159	3829	991	61	3944	791
Temp. ($^{\circ}\text{C}$)	12.4	14.0	13.5	11.5	16.0	14.0	13.8	18.0	16.7	12.8	15.2	13.5	10.9	12.0	11.5	7.6	12.0	10.4	7.6	18.0	12.8
Ca ($\text{mg}\cdot\text{L}^{-1}$)	1.5	36.7	13.3	0.7	2.2	1.2	0.9	2.1	1.2	0.8	8.0	4.2	0.6	2.1	1.4	0.4	2.0	0.9	0.4	36.7	2.0
Mg ($\text{mg}\cdot\text{L}^{-1}$)	0.6	7.4	2.9	0.2	0.4	0.3	0.2	0.5	0.3	0.1	0.8	0.5	0.2	0.4	0.3	0.1	0.4	0.2	0.1	7.4	0.4
Na ($\text{mg}\cdot\text{L}^{-1}$)	2.0	3.7	2.6	0.6	1.7	1.0	0.6	1.2	0.8	0.3	1.3	0.7	0.4	1.1	0.6	0.2	0.6	0.4	0.2	3.7	0.8
K ($\text{mg}\cdot\text{L}^{-1}$)	0.3	0.6	0.5	0.1	1.7	1.7	0.2	4.5	0.7	0.1	0.3	0.2	0.1	0.2	0.1	0.0	0.3	0.1	0.0	1.7	0.6
Cl ($\text{mg}\cdot\text{L}^{-1}$)	3.3	4.9	3.9	0.3	18.4	2.3	0.5	4.5	1.1	0.3	0.5	0.4	0.1	0.4	0.2	0.0	0.5	0.2	0.0	18.4	1.0
SO ₄ ($\text{mg}\cdot\text{L}^{-1}$)	1.8	2.8	2.3	1.0	5.6	1.6	0.6	1.7	0.9	0.7	4.1	1.7	0.6	1.0	0.8	0.4	1.0	0.7	0.4	5.6	1.1
Fe ($\text{mg}\cdot\text{L}^{-1}$)	0.1	0.1	0.1	0.1	0.4	0.2	0.3	3.0	1.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	3.0	0.3
PO ₄ ($\mu\text{g}\cdot\text{L}^{-1}$)	6	14	11	6	28	14	10	74	38	1	7	5	4	13	7	2	65	8	1	74	13
Si ($\text{mg}\cdot\text{L}^{-1}$)	0.1	0.7	0.4	0.3	2.7	1.2	0.4	2.9	0.9	0.1	1.6	1.0	0.6	2.8	1.3	0.1	2.4	0.8	0.1	2.9	1.0

Note: Min., minimum; Max., maximum; ALK, alkalinity; CLR, colour; Depth, maximum depth; ORG, organic content (LOD); Specific cond., specific conductivity; Trans., Secchi disk transparency; AREA, lake area; Alt., lake elevation; Catch., catchment area; Temp., surface water temperature.

omy followed that outlined and illustrated in Fallu et al. (2000).

Numerical analysis

The diatoms preserved in the surface lake sediments and the measured physical, chemical, and biological data were used to develop a calibration set to estimate the environmental optima and tolerances of the diatom taxa. The diatom species data are based on the relative abundance (percent of total diatoms) of taxa identified in surficial sediment samples. The available environmental data consist of 28 physical (9), chemical (13), and biological (6) variables measured for each lake including six vegetation zones (Table 1). The six main vegetation zones (wetland forest, spruce/fir forest, lichen woodland, coastal tundra, forest-tundra, and tundra) included in the calibration set of lakes were entered as binary codes (value 0 or 1). All variables and their abbreviations are presented in Table 1 except longitude (long.) and latitude (lat.). The distribution of the environmental data was verified using the computer program CALIBRATE version 0.3 (Juggins and ter Braak 1992). The positively skewed nature of most of the environmental variables was eliminated by a $\log(x)$, $\log(x + 1)$, or square root transformation, whereas normally distributed environmental variables were not transformed.

The data screening process followed Fallu and Pienitz (1999). Diatom taxa attaining a relative abundance of $\geq 1\%$ in at least one of the 64 lakes were included in the numerical analyses and in the development of the inference models. Samples were deleted if they had environmental variables with extreme ($>10\times$) influence, as detected by leverage diagnostics in a preliminary canonical correspondence analysis (CCA) (Birks et al. 1990a). Species and sample ordinations were performed using the computer program CANOCO for Windows, version 4.0 (ter Braak and Šmilauer 1998).

A principal components analysis (PCA) was performed to summarize the major patterns of variation within the environmental data and to examine relationships among environmental variables and sampling sites. Environmental variables were centered and standardized to allow them to be directly comparable. Detrended correspondence analysis (DCA; Hill and Gauch 1980), with detrending by linear segments and nonlinear rescaling of axes, was used to explore the principal patterns of floristic variation within the set of sampling sites. DCA also determined the compositional gradient lengths along DCA axes 1 (3.84 standard deviation (SD) units) and 2 (2.87 SD units), which justified the subsequent use of unimodal ordination methods (ter Braak and Prentice 1988). The results of DCA analyses are presented in Allaire (1997). A canonical variate analysis (CVA) was used to determine which environmental variables accounted for significant variance between the groups. The latter (site clusters) are based on catchment vegetation type. In the CVA, site clusters are used as binary variables instead of species data. Sites with extreme environmental values ($>20\times$) were removed, as detected by the leverage diagnostic. Because the number of vegetation zones used in the CVA is far fewer than the number of species used in the CCA, a different cut-off criterion for leverage diagnostic was applied. CCA was also used to identify which environmental variables were the

most important in explaining diatom assemblage distributions.

To remove the effects of collinearity (= amount of redundancy within the environmental information) in the CVA and CCA, only those variables were selected that explained a significantly additional proportion of the variance independent of the other variable. In the CVA and CCA, environmental variables with a variance inflation factor (VIF) exceeding 15 were eliminated (ter Braak 1988). Next, a series of CVAs and CCAs constrained to one variable were run to test the significance of each environmental variable on the first axis using Monte Carlo permutation tests with 199 unrestricted permutations ($P \leq 0.05$). The variables that did not have a significant influence on the data distribution were excluded from further analysis. Finally, in the CCA, the remaining variables were used to find pairs of highly correlated ($r > 0.6$) environmental variables identified from a Pearson correlation matrix. For each pair, partial CCAs were performed with one variable as the sole variable and the other as a covariable. The variable was then tested for its significance on the first canonical axis (Monte Carlo permutation test with 999 unrestricted permutations, $P \leq 0.05$). When the test was not significant (variables explaining the same part of the variance), the variable explaining the highest amount of variance in the diatom distributions was kept from the pair. This data screening process resulted in a group of variables with statistically independent and significant correlations with distributions of diatom assemblages.

The forward selection option of the CVA and CCA was then used to identify the smallest subset of variables explaining the most variation in the diatom data. Each variable was tested through Monte Carlo permutation tests (with 999 unrestricted permutations), with variables added to the model until the significant level of $P \leq 0.05$ was exceeded. Rare species were downweighted in the CCA ordinations. The selected variables in the CCA are those that can be used to develop environmental reconstruction models.

The quantitative transfer functions were developed using the computer program CALIBRATE, version 0.3 (Juggins and ter Braak 1992). Both linear-based partial least squares regression and calibration (PLS) and unimodal weighted-averaging (WA) regression and calibration models were tested and their predictive capacities were compared (Table 2). A $WA_{(tol)}$ option (with tolerance downweighting) was also used (with both inverse and classical deshrinking) in order to downweight the taxa with high tolerances (Birks et al. 1990b). The recently developed WA-PLS, which uses the weighted residual correlations in the species data to improve estimates of taxon optima in the final WA predictor (ter Braak and Juggins 1993), was also applied. The program CALIBRATE enabled the creation of Gaussian logit regression graphs for all of the species. These graphs show the distribution (unimodal vs. linear vs. sigmoidal) of the species in the data set. Only the data for the potential indicator taxa are presented in Appendix A.

All models were tested twice, once with the original relative abundance (%) values and a second time following square root transformation of the percentage species data. The r^2 , root mean square error of prediction (RMSEP), and maximum bias of the models were calculated by "leave-one-out" (or jackknifing) cross-validation procedures (e.g., ter

Table 2. Performance statistics for different water colour (log(CLR + 1)) and alkalinity (log(ALK + 1)) inference models.

Models		Untransformed species data		Square root transformed species data	
		Classical	Inverse	Classical	Inverse
Water colour					
WA	r^2	0.74	0.73	0.71	0.71
	RMSEP	0.24	0.24	0.26	0.25
WA _(tot)	r^2	0.60	0.60	0.45	0.44
	RMSEP	0.33	0.30	0.40	0.35
PLS 3 components	r^2		0.72		
	RMSEP		0.26		
PLS 4 components	r^2				0.83
	RMSEP				0.19
WA-PLS 2 components	r^2		0.77		
	RMSEP		0.22		
WA-PLS 4 components	r^2				0.85
	RMSEP				0.18
Alkalinity					
WA	r^2	0.61	0.60	0.62	0.61
	RMSEP	0.28	0.26	0.28	0.25
WA _(tot)	r^2	0.60	0.59	0.57	0.57
	RMSEP	0.28	0.26	0.31	0.27
PLS 1 component	r^2		0.30		
	RMSEP		0.53		
PLS 2 components	r^2				0.60
	RMSEP				0.26
WA-PLS 1 component	r^2		0.60		
	RMSEP		0.26		
WA-PLS 2 components	r^2				0.63
	RMSEP				0.25

Note: RMSEP, root mean square error of prediction; WA, weighted-averaging; PLS, partial least squares.

Braak and Juggins 1993). The transfer functions considered to be the best ("minimum adequate model", sensu Crawley 1993 in Birks 1998) were those with the highest coefficient of determination (r^2_{jack}), lowest RMSEP, and low mean and maximum bias.

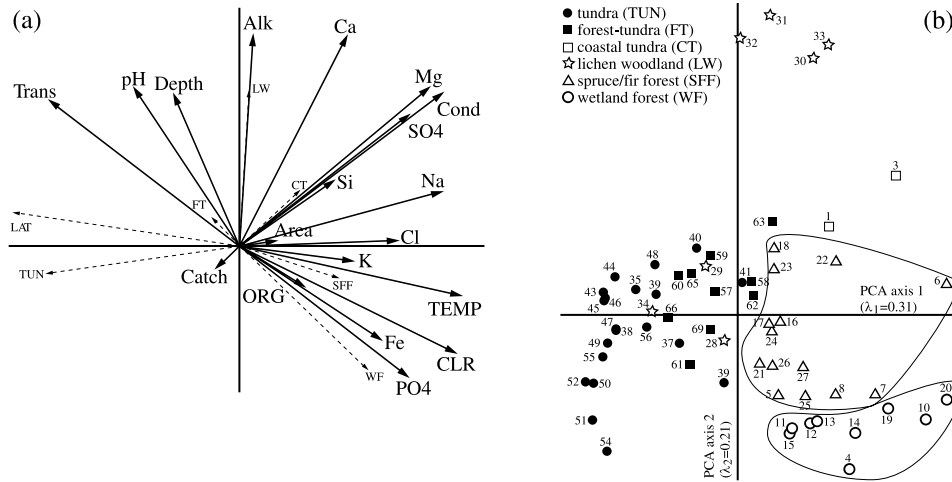
Results

Principal components analysis

The PCA indicates good separation of calibration lakes along major environmental and vegetational gradients (Fig. 2). Two sites had to be removed from the data set as they showed extreme values for some of the environmental variables as detected by the leverage diagnostics in a preliminary CCA. Site 2 had extreme values for magnesium ($7.4 \text{ mg}\cdot\text{L}^{-1}$), calcium ($36.7 \text{ mg}\cdot\text{L}^{-1}$), conductivity ($203 \text{ }\mu\text{S}\cdot\text{cm}^{-1}$), and alkalinity ($2154 \text{ }\mu\text{eq}\cdot\text{L}^{-1}$), whereas site 9 had high values of potassium ($17.7 \text{ mg}\cdot\text{L}^{-1}$), chloride ($18.4 \text{ mg}\cdot\text{L}^{-1}$), and sulphate ($5.6 \text{ mg}\cdot\text{L}^{-1}$). The variables longitude and altitude were eliminated; however, latitude and the vegetation zones were retained as passive variables (e.g., with no direct influence on the ordination axes) in order to gain a better understanding of how the limnological variables are distributed geographically in the data set.

The PCA was performed on a data set of 62 lakes and 19 environmental variables (plus 7 passive variables). The cumulative percentage of variance within the environmental data explained by the first two PCA axes is 51.4%, with eigenvalues of $\lambda_1 = 0.31$ and $\lambda_2 = 0.21$, respectively. The lakes located in the wetland forest form a distinct group in the lower right quadrant, reflecting dark water colour (CLR) associated with high water temperature, high PO_4 concentrations, high iron (Fe) concentration, high organic matter content (ORG) of the sediments, and low pH and water depth. The spruce/fir forest lakes are grouped in the right half of the ordination, well separated from wetland forest sites. Tundra sites are mostly positioned on the left. They are characterized by high water transparency (Trans.) and low summer water temperature (Temp.), also by low conductivity and ion concentrations. The lakes situated in the coastal tundra are characterized by high conductivity and ion concentration. The forest-tundra and some of the lichen woodland lakes occupy a median position in the ordination, indicating similar chemical and limnological conditions among sites. Four lichen woodland sites are positioned separately in the top right quadrant, reflecting marked differences in water chemistry related to high alkalinity values as a result of marine deposit in the area. Overall, the relative positioning of the sample sites reflects environmental and limnological gradi-

Fig. 2. Principal components analysis (PCA) ordination of 19 environmental variables (a) in the 62 lake data set (b). Dashed arrows in (a) indicate passive environmental variables.



ents that are closely associated with changing vegetation zones along the latitudinal transect from tundra conditions in the north to spruce/fir and wetland-dominated forests in the south.

Canonical variates analysis

The original data set was composed of 64 lakes and 28 environmental variables including six vegetation zones. Because there were only three sites in the coastal tundra zone and one of them (site 2) had variables of extreme influence (see above), the latter vegetation zone was removed. Sites 6, 9, 10, 19, and 20 had to be removed because of environmental variables with extreme influence. Longitude, latitude, and altitude were removed for reasons mentioned above. The conductivity variable was deleted because of a high VIF. In a series of CVAs, Catch., Area, K, and Si were removed because they did not explain a significant amount of the variance in the vegetation types.

The CVA analysis included 56 lakes, 14 environmental variables, and five groups representing vegetation zones. After forward selections, only five environmental variables remained: water colour, calcium, iron, alkalinity, and water temperature (Fig. 3). The cumulative percentage variance of cluster grouping–environment relationship explained by axes 1 and 2 is 65.9%. Axis 1 clearly separates the vegetation zones along a colour gradient that is closely related to changes in temperature and iron. The wetland forest sites are concentrated in the lower right quadrant, representing high colour and iron content. Along the same axis, they are followed by spruce/fir forest sites, also influenced by water colour but to a lesser degree. The three other lake types are characterized by low water colour. Division between forest–tundra and tundra sites is less striking than between wetland forest and spruce/fir forest, but it is still perceptible. It also appears that the tundra sites are characterized by low water temperature. Lichen woodland sites are split into two groups, as seen in the PCA (Fig. 2). The first group occupies the central part of the ordination, between the forest–tundra and the spruce/fir forest sites, and represents the transition between these two catchment types. The other group is positioned in the upper part of the ordination, well separated from all other sites. These four sites are influenced by high

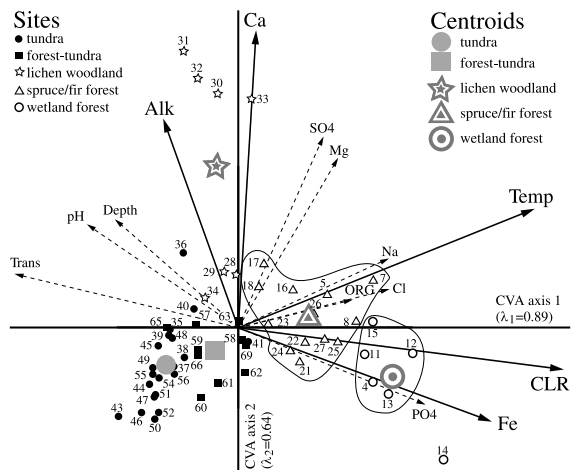
water alkalinity resulting from local marine sediment, which is represented by axis 2. The CVA ordination confirms the environmental similarities of sites within vegetation zones and the limnological differences among sites from different vegetation zones.

Canonical correspondence analysis

After the data screening, several species, sites, and environmental variables were removed from the original data set of 303 diatoms, 64 lakes, and 28 environmental variables. Of the 303 diatom taxa (in 21 genera) identified in the surface sediment samples of the study lakes, a total of 132 taxa met the selection criteria ($\geq 1\%$ in at least one lake). Most of these were periphytic species belonging to the genera *Achnanthes*, *Cymbella*, *Eunotia*, *Fragilaria*, and *Navicula*. Lakes 2, 3, 9, and 20 were deleted as they had environmental data having an extreme influence, as assessed by the leverage diagnostics. Vegetation zones and latitude were run as passive variables, whereas longitude was removed. The variables of conductivity and chloride (Cl) were deleted for their high VIF values. In the CCAs constrained to one variable, catchment (Catch.) and potassium (K) did not have a significant influence on diatom distributions and therefore were excluded from further analysis. From all pairs tested for their correlations, only temperature and phosphate (PO_4) did not show independent influences on diatom distributions. Temperature was retained, representing an association with the eliminated variable of PO_4 .

A CCA analysis was performed with 60 lakes, 15 environmental variables, and 132 species. Axes 1 and 2 of the final CCA, with eigenvalues of $\lambda_1 = 0.40$ and $\lambda_2 = 0.32$, accounted for 18.6% of the cumulative variance of the diatom data. CCA axes 1 and 2 explained a large proportion of the variance in the diatom–environment relationship (42.7%). The diatom–environment correlations for axes 1 and 2 were also high, with values of 0.91 and 0.95, respectively, indicating a strong relationship between the diatom species and the 15 environmental variables. Forward selection and unrestricted Monte Carlo permutation tests showed that eight environmental variables explained a significant proportion ($P \leq 0.05$) of the variance in the species data. In decreasing order of importance, these are water colour, alkalinity, lake

Fig. 3. Canonical variate analysis (CVA) ordination of five vegetation groups (one centroid representing each group) and 14 environmental variables for the 56 lake data set. Dashed arrows indicate passive environmental variables.



depth (Depth), iron, water transparency, sediment organic content, calcium (Ca), and summer surface-water temperature. These eight forward-selected variables accounted for 76.7% of the variance explained by the initial 15 variables. A final CCA performed with these eight variables yielded eigenvalues of $\lambda_1 = 0.38$ and $\lambda_2 = 0.31$, and together they capture 17.8% of the variance in the diatom data. The diatom–environment correlations for CCA axes 1 (0.89) and 2 (0.94) were high, and the cumulative variance proportion explained in the diatom–environment relationship was 53.8%.

The results of this CCA are illustrated by a simultaneous ordination representing the taxa and the samples, which are directly related to the environmental variables (Fig. 4). The CCA biplot of the environmental-site scores (Figs. 4a, 4b) shows a clear separation between the lakes belonging to different catchment vegetation zones based on the underlying patterns in diatom assemblage composition. In particular, the strongly coloured, iron-rich, warmer wetland forest (peatland) lakes occupy distinct positions in the lower right quadrant, reflecting dystrophic conditions that seem to favour a distinct subset of diatoms (Fig. 4c; see Appendix B for complete names). Diatom assemblages from the spruce/fir forest zone are quite different from those in tundra lakes, although some overlap is present, presumably because the zonal boundaries are not as sharp as with the wetland forest zone. The distinction between the diatom assemblages found in the tundra zones and in the lichen woodland zone was less evident from the CCA (Figs. 4a, 4c). This can be explained by the greater limnological and floristic similarity between these lake types and their catchments. However, among this group, some lichen woodland lakes (30–33) showed the strongest affinity with high water alkalinity values, likely resulting from the influence of carbonate-rich deposits of post-glacial marine origin.

Overall, water colour and alkalinity were the two most important variables determining diatom community structure. The floristic composition of the tundra lakes was characterized by the dominance of small species typical of dilute oligotrophic lakes, such as *Achnanthes marginulata* (14), *Navicula* sp. [cf. *begerii*] (95), *N. digitulus* (106), *N. krasskei* (103), *N. para-*

subtilissima (116), *Aulacoseira distans* var. *nivalis* (27), and *A. distans* var. *nivaloides* (28). These taxa occur in the left quadrants of the biplot corresponding to most of the tundra lakes (Fig. 4c). In the upper right quadrant, lichen woodland lakes are dominated by alkaliphilous species, such as *Cocconeis neothumensis* (38), *Cymbella descripta* (41), *Cyclotella kuetszingiana* (51), *C. michiganiana* (52), *Fragilaria construens* (74), *F. lapponica* (77), *F. pseudoconstruens* (84), *Navicula absoluta* (92), and *N. sp.* [cf. *submuralis*] (115). Other alkaliphilous species can also be found in that quadrant, but they could also be related to forest tundra lakes. These taxa include *Achnanthes laterostrata* (11), *A. pusilla* (16), *Fragilaria capucina* (69), *Navicula pseudoscutiformis* (108), and *N. seminuloides* (112). The floristic composition of diatom communities in the spruce/fir forest lakes showed higher species richness, the most common taxa being *Achnanthes subatomoides* (5), *Aulacoseira ambigua* (25), *Cymbella* sp. [cf. *schubartii*] (48), *Eunotia paludosa* var. *trinacria* (68), *Fragilaria lata* (78), *Navicula cocconeiformis* (98), *N. disjuncta* (99), *N. soehrensensis* var. *hassiacca* (114), and *N. ventralis* (118). These taxa are located in the two lower quadrants of the biplot. The diatom taxa typically found in wetland forest lakes (lower right quadrant, Figs. 4b, 4c) include *Fragilaria construens* var. *binodis* (72), *F. construens* sp. [cf. var. *pumila*] (73), *F. construens* var. *venter* (75), *F. pinnata* var. *acuminata* (80), *F. pinnata* var. *lancettula* (81), and *Navicula* spp. (e.g., *N. arvensis* (94)), which seem to be associated with strongly coloured warm lakes with high Fe concentration and low alkalinity conditions (Figs. 4b, 4c).

Weighted-averaging models

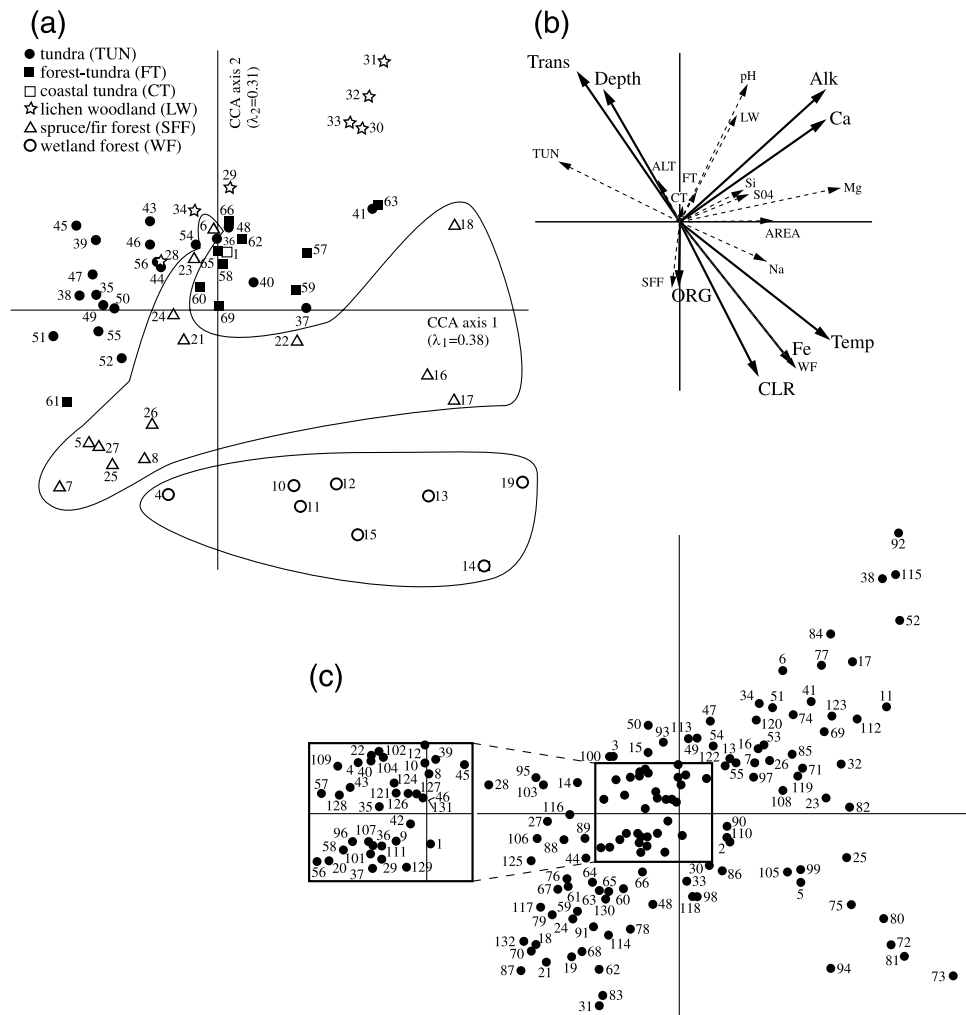
CCA showed that water colour and alkalinity are the two environmental variables with the statistically greatest significance ($P \leq 0.05$) influencing diatom distribution in the Labrador data set. In constrained CCAs with water colour and alkalinity as the only variables, the eigenvalues for the first and the second axes produced ratios of 0.58 and 0.61, respectively. Thus, water colour and alkalinity promised to be appropriate variables for the development of reliable inference models.

Among all models tested, the four-component WA-PLS model with square root transformation of percent species data best represented the diatom – water colour relationship (Table 2). The model predicts water colour values that are closely related to the actual observed values (Fig. 5), with a jackknifed r^2_{jack} of 0.85 between observed and predicted colour values, a RMSEP of $0.18 \log(\text{CLR} + 1)$ (backtransformed value = 1.51 Pt units), and a maximum bias of 0.12. A two-component WA-PLS provided the best model for alkalinity, with a slightly lower r^2_{jack} (0.63), a RMSEP of $0.25 \log(\text{ALK} + 1)$ (backtransformed value = 1.78 $\mu\text{eq}\cdot\text{L}^{-1}$), and a maximum bias of 0.26 (Table 2, Fig. 5).

Optima and tolerances of diatom taxa

The WA model allowed the calculation of alkalinity and water colour optima and tolerances for the 132 diatom species, as well as their effective number of occurrences (Appendix B). The WA optima for water colour range from 5 Pt units (*Cocconeis neothumensis*, *Navicula absoluta*, *N. agrestis*, *N. submolesta*, and *Nitzschia hantzschiana*) to 83 Pt units (*Fragilaria polygonata*). Alkalinity optima range

Fig. 4. Biplot of 60 sites (a), eight environmental variables (b), and 132 species (c) scores in the final canonical correspondence analysis (CCA) of the lake data set. Taxon names are presented in Appendix B. Dashed arrows in (b) indicate passive environmental



from $8 \mu\text{eq}\cdot\text{L}^{-1}$ (*Eunotia paludosa* var. *trinacria*) to $467 \mu\text{eq}\cdot\text{L}^{-1}$ (*Navicula absoluta*). The optima calculated here are in close agreement with those reported from northern Sweden for alkalinity and water colour (Korsman and Birks 1996; see Table 3) and from Canada's Northwest Territories for alkalinity (Rühland 1996; see Table 3).

Potential indicator taxa

For the selection of potential indicator taxa, the criteria outlined in Stevenson et al. (1991), Pienitz et al. (1995), and Fallu and Pienitz (1999) were followed: (i) more than 10% of the variance of a particular species had to be explained by the variable of interest in the constrained CCA; (ii) the tolerance of the species had to be less than the mean tolerance for all the taxa; and (iii) the species had to be present in 10 or more of the study lakes. Nine taxa fulfilled these criteria for water colour and 19 for alkalinity (Table 4), and their distribution is shown in Appendix A. These taxa give only a first approximation of lake water colour and alkalinity and should be used only for preliminary interpretations. For example, *Cyclotella michiganiana*, which has a very high WA alkalinity optimum of $306.5 \mu\text{eq}\cdot\text{L}^{-1}$, was not accepted as a potential indicator taxon because its WA tolerance is broader than the mean tolerance of all taxa and because it occurred

in only five lakes. However, this species was found only in high alkalinity lakes. Further research should aim at expanding the calibration set to increase the overall gradient length of alkalinity.

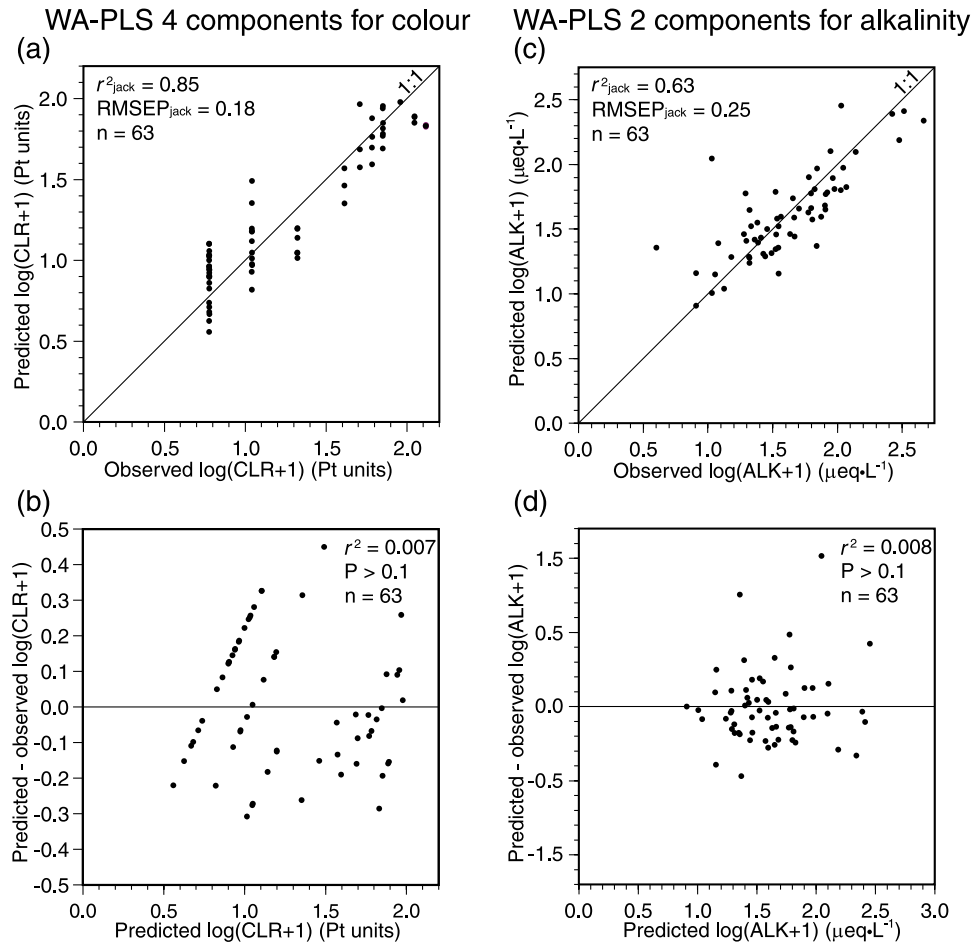
Gaussian logit regressions

With respect to alkalinity, many taxa (80) follow a Gaussian unimodal response model, whereas several (36) follow a linear-logit (sigmoidal) model, increasing (20 taxa) or decreasing with alkalinity (16). Some taxa (16) show no relation with alkalinity. As for colour, 78 taxa follow a Gaussian unimodal response model, whereas 20 taxa follow an increasing sigmoidal model and 18 taxa follow a decreasing one. Only 16 taxa show no relationship with colour. The Gaussian logit regression curves are presented for the potential indicator taxa in Appendix A. All potential alkalinity indicator taxa follow a unimodal response, whereas six out of nine taxa show this response among the potential colour indicator taxa.

Discussion

The ordination analyses of the Labrador data set showed a clear separation between lakes from forested and unforested

Fig. 5. (a) Plot of observed versus diatom-predicted colour and (b) observed versus residual values, based on WA-PLS with four components. (c) Plot of observed versus diatom-predicted alkalinity and (d) observed versus residual values, based on WA-PLS with two components.



regions. The PCA enabled the differentiation of sites by their chemical and physical characteristics, whereas the CVA showed distinct divisions between groups of sites classified by vegetation zones. The CCA indicated that a relatively large proportion of the variance in the diatom data was accounted for by the environmental variables included in the calibration set. Most striking are the well-defined differences between the wetland forest and the spruce/fir forest lakes when comparing the results of PCA, CVA, and CCA. Wetland forest sites are characterized by darkest water colour, highest iron concentrations, and highest temperature (correlated with high PO_4 values). These two vegetation types have been grouped under the term boreal forest in many previous studies (e.g., Rühland 1996; Fallu and Pienitz 1999; Laing and Smol 2000). Our study shows that by distinguishing these two types, a finer understanding of diatom distribution in these lakes will allow more detailed reconstructions of lake catchment environments. This kind of information will be beneficial to paleohydrological and paleoclimatological studies.

The floristic composition of the diatom assemblages in the surface sediment samples showed several distinct changes along the sampling transect. The most apparent trend observed is a shift from communities dominated by centric taxa considered to be benthic-tychoplanktonics (e.g., *Aula-*

coseira spp.) in the more acidic and coloured wetland lakes to those dominated by small periphytic pennate taxa (e.g., *Achnanthes* spp.) in the transparent and cold arctic tundra lakes. The overall declining relative abundance of large-celled centric and pennate diatoms with increasing latitude has previously been observed in lakes distributed along latitudinal transects crossing the tree line in North America (Pienitz et al. 1995; Fallu and Pienitz 1999; Lotter et al. 1999). Fallu and Pienitz (1999) and Laing et al. (1999) compared the floristic patterns between their study sites and those reported from other circumpolar regions and found strong floristic similarities. Despite the geographic distance and differences in the degree of anthropogenic disturbances, these species seem to have similar environmental preferences.

The strong alkalinity signal found in the Labrador data set confirms numerous previous regional studies that found this variable and its related factors to be influential in explaining diatom distributions. Alkalinity-related variables (e.g., DIC, pH) are often found to be the most important variables influencing the distribution and the abundance of diatom taxa (e.g., Dixit et al. 1993; Lotter et al. 1997; Weckström et al. 1997), including the assemblages from subarctic and arctic regions (Pienitz and Smol 1993; Pienitz et al. 1995). In Labrador, higher alkalinity values were observed in the lichen woodland region because of local bedrock dominated by a

Table 3. Comparison of diatom alkalinity optima inferred from calibration data sets in Québec–Labrador (present study), northern Sweden (Korsman and Birks 1996), and Canada’s Northwest Territories (Rühland 1996) and comparison of water colour optima inferred from Québec–Labrador (present study) and northern Sweden (Korsman and Birks 1996).

Taxa	ALK optimum ($\mu\text{eq}\cdot\text{L}^{-1}$)*			CLR optimum (Pt units)	
	Korsman and Birks	This study	Rühland	Korsman and Birks	This study
<i>Achnanthes altaica</i>		37	~48		
<i>A. didyma</i>	85	71	~70		
<i>A. kuelbsii</i>	42	42			
<i>A. laterostrata</i>				20	17
<i>A. levanderi</i>		54	~62		
<i>A. marginulata</i>		34	~36		
<i>Asterionella ralfsii</i> var. <i>americana</i>	16	17			
<i>Aulacoseira distans</i> var. <i>humilis</i>				17	14
<i>A. distans</i> var. <i>nivalis</i>	33	24	~18		
<i>A. lirata</i>	40	30	~24		
<i>A. perglabra</i>	36	30	~30		
<i>A. perglabra</i> var. <i>floriniae</i>	35	28			
<i>Cymbella gaeumannii</i>		35	~36		
<i>C. gracilis</i>		35	~40		
<i>C. hebridica</i>		25	~34		
<i>C. microcephala</i>				20	10
<i>C. silesiaca</i>		41	~40		
<i>Eunotia exigua</i>	22	29			
<i>E. faba</i>		24	~28		
<i>E. incisa</i>				54	53
<i>Fragilaria brevistriata</i>				22	15
<i>F. construens</i> var. <i>venter</i>				31	30
<i>F. lapponica</i>				13	8
<i>F. lata</i>	28	18			
<i>F. pseudoconstruens</i>				13	8
<i>F. virescens</i> var. <i>exigua</i>		34	~34		
<i>Frustulia rhomboides</i>		22	~26		
<i>F. rhomboides</i> var. <i>saxonica</i>		27	~22		
<i>Gomphonema parvulum</i>		48	~48		
<i>Navicula digitulus</i>				16	19
<i>N. laevissima</i>				25	26
<i>N. leptostriata</i>	30	34			
<i>N. pseudoscutiformis</i>		61	~74		
<i>N. vitiosa</i>				25	18
<i>Nitzschia perminuta</i>		37	~44	21	14
<i>Pinnularia microstauron</i>		39	~40		
<i>Stauroneis anceps</i>		33	~34	26	19

Note: ALK, alkalinity; CLR, water colour.

*Because Rühland (1996) reported alkalinity values measured in $\text{mg CaCO}_3\cdot\text{L}^{-1}$, her data were transformed into $\mu\text{eq}\cdot\text{L}^{-1}$, see Wetzel and Likens (2000) for formula used in transformations ($20 \times \text{mg CaCO}_3\cdot\text{L}^{-1} = 1 \mu\text{eq}\cdot\text{L}^{-1}$).

drift-covered belt composed of carbonate-rich sedimentary rocks (Colman-Sadd and Scott 1994). Most of the alkaliphilous diatoms were found in this region, indicating that the particular geological substrate in this part of the study region may strongly influence the lake water chemistry and the composition of diatom communities. For example, Laing and Smol (2000) demonstrated the importance of geological conditions in northern Russia where substrate-related changes in water chemistry overrode climatic gradients in explaining diatom distributions among different regions.

Water colour is the other environmental variable that appears to explain much of the variability in the distribution of diatoms in Labrador. Water colour was measured in the field to avoid error resulting from humus losses during lengthy

field storage of samples (Engstrom 1987). It provides a measure of humic content, or a degree of lake dystrophy, and represents a proxy for DOC. The strong colour signal in this data set was not surprising, as changes in lake water DOC and related processes (e.g., changes in water colour, transparency, and spectral composition of transmitted light; chemical interactions affecting the bioavailability of nutrients and trace metals) are known to strongly influence diatom distributions (e.g., Pienitz and Smol 1993; Korsman and Birks 1996; Fallu and Pienitz 1999). Diatom-based inference models for DOC have been developed for freshwater lakes in temperate North America (Kingston and Birks 1990; Dixit et al. 1993), Europe (Stevenson et al. 1991; Korsman and Birks 1996), and subarctic regions of the Northwest Ter-

Table 4. Potential indicator diatom taxa for water colour (CLR) and alkalinity (ALK).

<i>N</i>	Code	Species	Optima	Tolerance	% Variance explained	Number of occurrences
Colour (Pt units)						
40	CYMLAPP	<i>Cymbella lapponica</i> Grunow in Cleve & Möller	8	2.0	11.1	13
47	CYMMINU	<i>Cymbella minuta</i> Hilse ex Rabenhorst	8	1.8	12.7	15
122	NITFONT	<i>Nitzschia</i> sp. [cf. <i>fonticola</i> Grunow in Van Heurck]	9	1.8	20.9	29
4	ACHCURT	<i>Achnanthes</i> sp. [cf. <i>curtissima</i> Carter]	9	2.2	26.0	36
29	AULDITE	<i>Aulacoseira distans</i> var. <i>tenella</i> (Nygaard) Florin	43	2.3	21.2	18
24	ASTRAAM	<i>Asterionella ralfsii</i> var. <i>americana</i> Körner	53	2.1	27.6	16
60	EUNINCI	<i>Eunotia incisa</i> Gregory	53	1.9	40.9	20
81	FRAPILA	<i>Fragilaria pinnata</i> var. <i>lancettula</i> (Schumann) Hustedt in Schmidt et al.	62	2.2	21.3	11
94	NAVARVE	<i>Navicula arvensis</i> Hustedt	68	1.7	36.5	19
Alkalinity ($\mu\text{eq}\cdot\text{L}^{-1}$)						
24	ASTRAAM	<i>Asterionella ralfsii</i> var. <i>americana</i> Körner	17	1.8	19.6	16
117	NAVTEU	<i>Navicula tenuicephala</i> Hustedt	17	1.7	11.4	12
67	EUNSUBA	<i>Eunotia subarcuatoidea</i> Alles, Nörpel & Lange-Bertalot	18	1.9	19.0	15
76	FRAONA	<i>Fragilaria constricta</i> Ehrenberg	18	2.1	20.1	18
79	FRAOLDE	<i>Fragilaria oldenburgiana</i> Hustedt	18	1.8	16.1	15
78	FRALATA	<i>Fragilaria lata</i> (Cleve-Euler) Renberg	18	2.0	18.3	17
59	EUNHEMI	<i>Eunotia hemicyclus</i> (Ehrenberg) Ralfs in Pritchard	19	1.9	15.8	14
48	CYMSCHU	<i>Cymbella</i> sp. [cf. <i>schubartii</i> Hustedt]	19	2.1	18.2	16
96	NAVBRM	<i>Navicula bremensis</i> Hustedt	21	2.0	11.5	16
88	FRURHOM	<i>Frustulia rhomboides</i> (Ehrenberg) De Toni	22	2.0	26.5	35
27	AULDINI	<i>Aulacoseira distans</i> var. <i>nivalis</i> (W. Smith) Haworth	24	1.9	20.3	36
58	EUNFABA	<i>Eunotia faba</i> Ehrenberg	24	2.1	10.4	21
44	CYMHEBR	<i>Cymbella hebridica</i> (Grunow) Cleve	25	2.2	22.4	37
116	NAVPARA	<i>Navicula parasubtilissima</i> Kobayasi and Nagumo	27	2.0	11.6	35
89	FRURHSA	<i>Frustulia rhomboides</i> var. <i>saxonica</i> (Rabenhorst) De Toni	27	2.1	20.7	49
37	AULPEFL	<i>Aulacoseira perglabra</i> var. <i>floriniae</i> (Camburn) Haworth	28	2.1	16.0	46
103	NAVKRAS	<i>Navicula krasskei</i> Hustedt	31	1.7	10.3	13
7	ACHDIDY	<i>Achnanthes didyma</i> Hustedt	71	2.2	22.5	23
23	ASTFORM	<i>Asterionella formosa</i> Hassal	82	2.0	11.7	14

Note: The taxa are presented with their optimum and tolerance, the percent of their variance explained by the variable of interest in a constrained CCA, and their number of occurrences. Numbers (*N*) for taxa refer to those used in Fig. 4. Codes for names are used in Appendix A with illustrations of WA optimum and tolerance ranges.

ritories (Pienitz and Smol 1993) and northwestern Québec (Fallu and Pienitz 1999). Basin hydrology and the nature of the catchment vegetation and soils are important factors controlling the concentration of humic compounds in surface waters (Curtis and Schindler 1997; D'Arcy and Carignan 1997; Gibson et al. 2001). In Labrador, the water colour (DOC) gradient showed an inverse correlation with latitude. The influence of water colour seems to be attenuated in lichen woodland, forest-tundra, and tundra sites, as a dramatic change in the mean water colour could be observed,

from 89 Pt units in wetland forest lakes and 50 Pt units in spruce/fir forest lakes to 14 Pt units in forest-tundra, 8 Pt units in lichen woodland, and 6 Pt units in tundra lakes. In the forested zone of the Subarctic in Québec and Labrador, the soils are often composed of peat because litter production is much higher than decomposition. The water run-off occurs mainly as surface flow and enters these lakes with rich-coloured humic acid contents because the acids have not been filtered by mineral soils (Engstrom 1987). As the vegetation becomes more patchy, the humic acid obtained

by decomposition percolates through mineral soils and is mineralized, leading to surface water carrying less coloured humic compounds. In the tundra, the sparse vegetation cover results in clear-water lakes with extremely low humic acid inputs (Engstrom 1987). In this study, other environmental variables were also associated with the water colour (DOC) gradient, such as water transparency and surface water temperature, as well as the concentrations of total phosphorus and iron.

The WA-PLS calibration models may be used to infer past lake water alkalinity and water colour from fossil diatom assemblages preserved in the sediments of Labrador lakes within the alkalinity range of 3–463 $\mu\text{eq}\cdot\text{L}^{-1}$ and the water colour range of 5–130 Pt units. Because they tend to slightly overestimate the values at the lower end of the gradient and underestimate them at the higher end, these models would perform best on a site from the central part of the gradient. The water colour and alkalinity inferences are based on the optima and tolerances of 132 diatom species common in Labrador. As discussed above, colour is a suitable variable to reconstruct past optical conditions in lakes that are related to shifts in catchment vegetation and DOC concentrations. Studies using similar models commonly showed progressive loss of alkalinity over time, abrupt increases in water colour that coincides with the arrival of trees (Saulnier-Talbot and Pienitz 2002), and subsequent shifts that are closely correlated with vegetation and soil changes in the catchment (Engstrom et al. 2000; Pienitz and Vincent 2000).

The ecological preferences estimated by the WA calibration models show good correspondence with those of other studies. When compared with Fallu and Pienitz (1999), the water colour model shows several similarities. For example, *Actinella punctata*, *Eunotia incisa*, *Fragilaria lata*, and *Melosira arentii* tended to have higher water colour and DOC optima in both northern Québec and Labrador. Optima that are below average were inferred in both regions for *Achnanthes curtissima*, *A. levanderi*, *A. suchlandtii*, *Cyclotella ocellata*, *Cymbella gaeumannii*, *C. lapponica*, *Fragilaria pseudoconstruens*, *Navicula jaernefeltii*, *N. krasskei*, and *Nitzschia* sp. [cf. *fonticola*]. The water colour optima for selected indicator species in this study are comparable with the potential DOC indicator species identified by Fallu and Pienitz (1999). One taxon seems to be a particularly good indicator of low DOC concentrations (or low Pt units): *Nitzschia* sp. [cf. *fonticola*] with a DOC optimum of 5.13 $\text{mg}\cdot\text{L}^{-1}$ (Fallu and Pienitz 1999) and a water colour optimum of 9 Pt units. Good correspondence to other studies also exists with respect to alkalinity preferences. The taxon *Cyclotella michiganiana* is known to prefer highly alkaline conditions (Stevenson et al. 1991; Rühland 1996). The optima of many taxa in Labrador show values close to the optima reported from Sweden and the Northwest Territories (N.W.T.) (Korsman and Birks 1996; Rühland 1996; this study). However, though the ecological optima inferred for taxa in the N.W.T. and Labrador follow similar trends, a few differences could also be observed. The alkalinity optima inferred for N.W.T. taxa seem to be generally higher than those inferred for Labrador species. Also, the taxa representing the lower alkalinity range in Labrador are not listed among the 116 most common diatom taxa in the N.W.T. (e.g., *Eunotia paludosa* var. *trinacria*, *Fragilaria acido-*

biontica). This is likely due to the generally higher alkalinity of lakes in the Slave and Bear provinces of the N.W.T. (alkalinity values $\sim 4 \mu\text{eq}\cdot\text{L}^{-1}$ to $\sim 1998 \mu\text{eq}\cdot\text{L}^{-1}$ vs. $8.9 \mu\text{eq}\cdot\text{L}^{-1}$ to $306.5 \mu\text{eq}\cdot\text{L}^{-1}$ in Labrador). Major differences can be found in the optima of the two small taxa *Navicula minuscula* and *Navicula seminuloides*, which may be due to taxonomic uncertainties.

In conclusion, the final CCA of the Labrador lake set demonstrated that water colour and alkalinity were significantly correlated with diatom community composition ($P \leq 0.005$). Based on this observation, it was assumed that the relationship between water colour and diatoms, and between alkalinity and diatoms, was sufficiently robust to produce reliable inference models for the reconstruction of these environmental variables from fossil diatom assemblages. However, even though water colour and alkalinity fulfilled the requirements for developing inference models, it should be kept in mind that other unmeasured variables not included in the Labrador data set may also exert a strong influence, such as physical mixing, day-length effects, grazing, parasitism, and availability of microhabitats. Information about these environmental variables could improve the ordination, but they were not available for the Labrador calibration set.

The species–environment relationships revealed by the Labrador data confirm observations that alkalinity–pH–DIC and water colour – DOC gradients strongly impact diatom distributions across broad geographic regions in the Subarctic (reviewed in Lotter et al. 1999). They also suggest that lake water colour and alkalinity are variables of particular ecological importance, especially in electrolyte-poor, oligotrophic freshwater ecosystems. Changes in wetland patterns and vegetation cover in the catchment associated with climate warming will modify water colour (transparency) and DOC concentrations in the recipient lakes (Forsberg 1992; Vincent and Pienitz 1996), which will likely result in marked shifts in diatom assemblage composition and aquatic community structure (Seppä and Weckström 1999; Weckström and Korhola 2001). Although these kinds of shifts have been observed in other studies, our results may help detect more subtle changes within the boreal forest zone (spruce/fir forest and wetland forest). Quantitative estimates of past lake water colour and alkalinity will therefore provide important information concerning the changes in physical (e.g., underwater light regime) and chemical conditions of northern lakes driven by climatic change and (or) successional changes in catchment vegetation and soils. Future studies should aim to achieve a finer resolution of catchment properties, such as the degree of paludification, forest density, and the species composition of forest cover, and thereby further enhance the value of diatoms as proxies for change in the terrestrial environment surrounding study lakes.

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(Appendices A and B follow.)

Appendix A

Graphic illustration of weighted-averaging (WA) optimum and tolerance range of diatom indicator taxa for colour (CLR, Fig. A1) and alkalinity (ALK, Fig. A2). The estimated WA optimum of each taxon is shown as a vertical line at the top of each plot, as well as the fitted Gaussian logit curves. Taxon names are presented in Table 4.

Fig. A1. Weighted-averaging optimum and tolerance range of diatom indicator taxa for water colour.

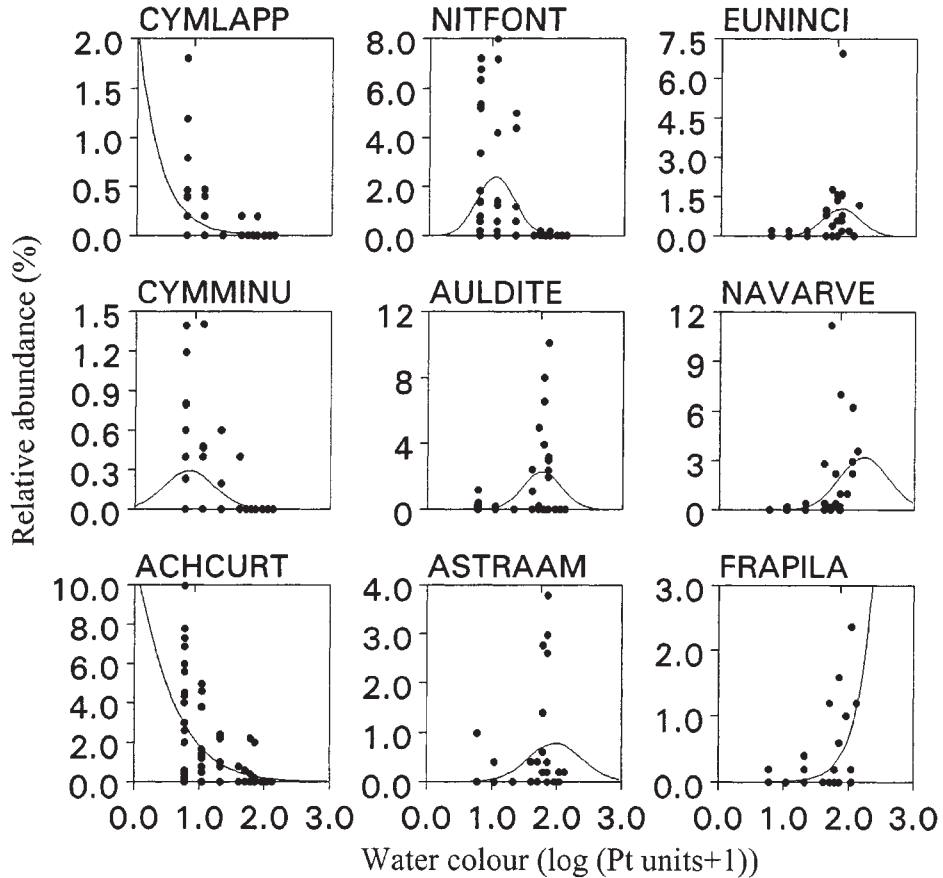
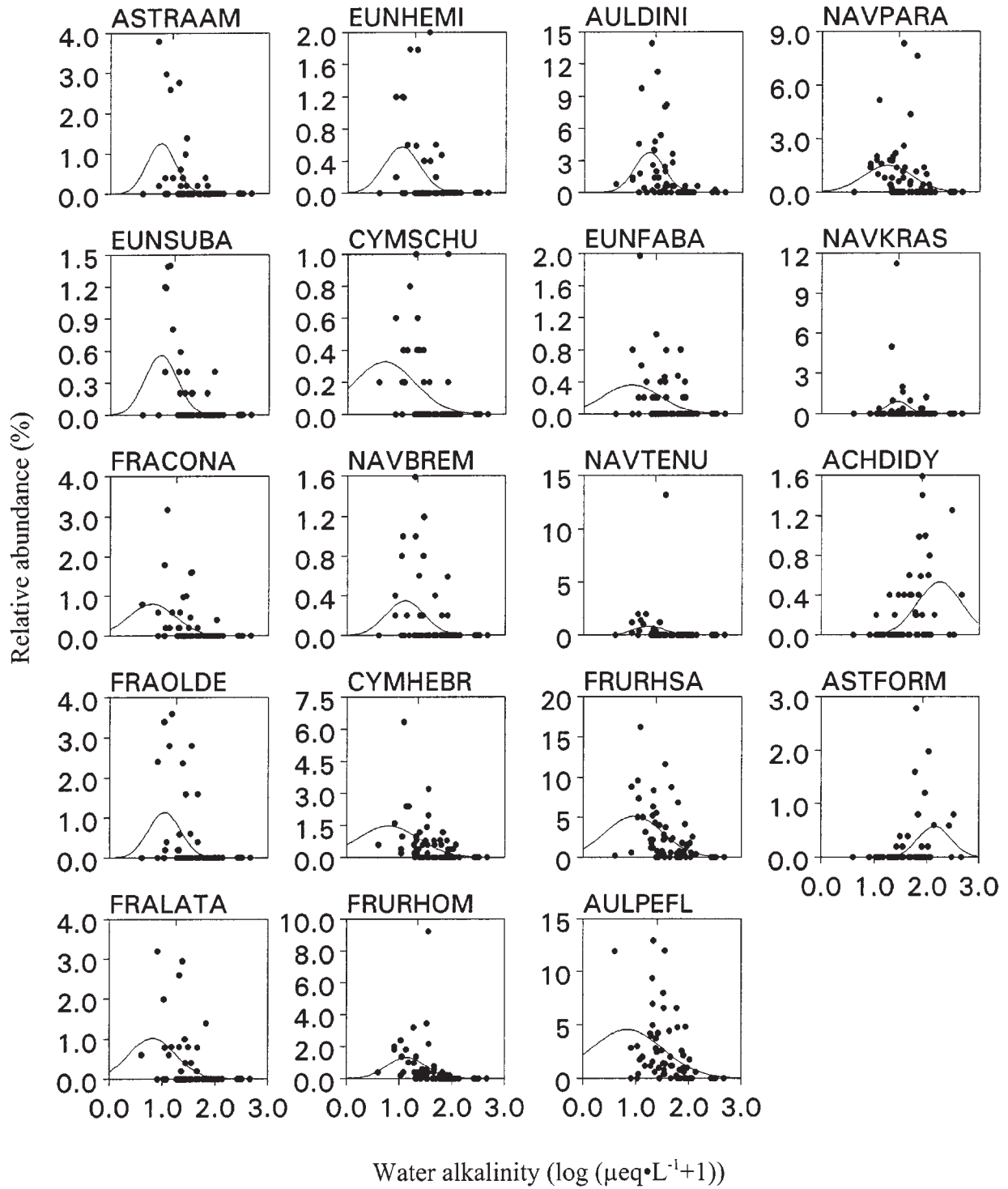


Fig. A2. Weighted-averaging optimum and tolerance range of diatom indicator taxa for water alkalinity.



Appendix B

Table B1. Weighted-averaging optima and tolerances for water colour (CLR, Pt units) and alkalinity (ALK, $\mu\text{eq}\cdot\text{L}^{-1}$), number of occurrences, and effective number of occurrences (N_2 , Hill 1973) of the 132 screened taxa.

	Taxon name	CLR optimum	CLR tolerance	ALK optimum	ALK tolerance	Occurrences	Hill's N_2
1	<i>Achnanthes altaica</i> (Poretzky) Cleve-Euler	22	3.0	37	2.3	38	33.0
2	<i>Achnanthes bicapitata</i> Hustedt	46	2.7	53	1.5	8	6.7
3	<i>Achnanthes carissima</i> Lange-Bertalot in Lange-Bertalot & Krammer	7	1.6	37	3.0	6	4.7
4	<i>Achnanthes</i> sp. [cf. <i>curtissima</i> Carter]	9	2.2	43	2.2	36	29.0
5	<i>Achnanthes subatomoides</i> (Hustedt) Lange-Bertalot & Archibald in K. & L.-B.	30	2.9	41	2.3	34	26.0
6	<i>Achnanthes</i> sp. 1	8	2.2	77	2.9	9	7.7
7	<i>Achnanthes didyma</i> Hustedt	14	2.4	71	2.2	23	20.5
8	<i>Achnanthes flexella</i> (Kützing) Brun	13	2.7	45	2.8	12	10.6
9	<i>Achnanthes chlidanos</i> Hohn & Hellerman	18	3.0	38	2.6	29	26.4
10	<i>Achnanthes kuelbsii</i> Lange-Bertalot in Lange-Bertalot & Krammer	8	2.2	42	2.5	12	9.5
11	<i>Achnanthes laterostrata</i> Hustedt	17	2.3	150	2.7	3	2.4
12	<i>Achnanthes levanderi</i> Hustedt	11	2.4	54	2.4	39	29.9
13	<i>Achnanthes peterseii</i> Hustedt	12	2.3	67	2.3	19	16.4
14	<i>Achnanthes marginulata</i> Grunow in Cleve & Grunow	9	2.3	34	2.1	55	37.7
15	<i>Achnanthes minutissima</i> Kützing	9	2.0	59	2.5	40	28.8
16	<i>Achnanthes pusilla</i> Grunow in Cleve & Grunow	15	2.5	68	2.6	29	23.7
17	<i>Achnanthes suchlandtii</i> Hustedt	13	2.4	134	2.6	17	13.0
18	<i>Actinella punctata</i> Lewis	46	2.5	12	1.8	8	6.3
19	<i>Nupela paludigena</i> (Scherer) Lange-Bertalot	70	1.3	12	1.2	1	1.0
20	<i>Anomoeoneis brachysira</i> (Brébisson in Rabenhorst) Grunow in Cleve	17	2.9	30	2.3	50	40.2
21	<i>Brachysira styriaca</i> (Grunow in Van Heurck) Ross in Hartley	64	1.3	12	1.5	8	7.1
22	<i>Brachysira neoexilis</i> Lange-Bertalot in Lange-Bertalot & Moser	10	2.5	37	2.3	36	25.9
23	<i>Asterionella formosa</i> Hassal	20	2.7	82	2.0	14	11.7
24	<i>Asterionella ralfsii</i> var. <i>americana</i> Körner	53	2.1	17	1.8	16	12.1
25	<i>Aulacoseira ambigua</i> (Grunow) Simonsen	32	2.8	55	2.2	20	17.1
26	<i>Aulacoseira distans</i> var. <i>humilis</i> Cleve-Euler	14	1.5	119	2.4	3	2.6
27	<i>Aulacoseira distans</i> var. <i>nivalis</i> (W. Smith) Haworth	14	3.0	24	1.9	36	26.3
28	<i>Aulacoseira distans</i> var. <i>nivaloides</i> (Camburn in Camburn & Kingston) Haworth	11	2.7	27	1.9	25	7.3
29	<i>Aulacoseira distans</i> var. <i>tenella</i> (Nygaard) Florin	43	2.3	26	2.1	18	13.4
30	<i>Aulacoseira distans</i> (Ehrenberg) Simonsen	23	3.2	36	2.2	48	35
31	<i>Melosira</i> sp.[cf. <i>goetzeana</i> O. Müller]	78	1.4	12	1.7	5	3.7
32	<i>Aulacoseira subarctica</i> (O. Müller) Haworth	16	2.3	82	2.2	13	7.0
33	<i>Aulacoseira lirata</i> (Ehrenberg) Kützing	29	3.0	30	2.6	39	30.0
34	<i>Aulacoseira lirata</i> f. <i>biseriata</i> (Grunow) Camburn	9	2.9	50	5.9	5	4.3
35	<i>Aulacoseira</i> sp. [cf. <i>nygaardii</i> (Camburn) Camburn in Camburn & Charles 1986]	17	3.3	31	1.8	17	15.4
36	<i>Aulacoseira perglabra</i> (Østrup) Haworth	18	3.2	30	2.1	45	34.4
37	<i>Aulacoseira perglabra</i> var. <i>floriniae</i> (Camburn) Haworth	18	3.0	28	2.1	46	37.1
38	<i>Cocconeis neothumensis</i> Krammer	5	1.3	228	4.0	2	1.9
39	<i>Cymbella</i> sp. [cf. <i>aequalis</i> W. Smith in Greville]	7	1.7	53	3.3	6	5.1

Table B1 (continued).

	Taxon name	CLR optimum	CLR tolerance	ALK optimum	ALK tolerance	Occurrences	Hill's <i>N2</i>
40	<i>Cymbella lapponica</i> Grunow in Cleve & Möller	8	2.0	36	2.0	13	11.3
41	<i>Cymbella descripta</i> (Hustedt) Krammer & Lange-Bertalot	10	1.7	144	2.5	12	11.0
42	<i>Cymbella gracilis</i> (Ehrenberg) Kützing	18	2.8	35	2.5	43	35.7
43	<i>Cymbella gaeumannii</i> Meister	10	2.4	35	2.1	50	39.3
44	<i>Cymbella hebridica</i> (Grunow) Cleve	17	3.1	25	2.2	37	30.7
45	<i>Cymbella microcephala</i> Grunow in Van Heurck	10	1.9	61	2.2	17	15.1
46	<i>Cymbella silesiaca</i> Bleisch in Rabenhorst	12	2.4	41	2.5	14	12.7
47	<i>Cymbella minuta</i> Hilse ex Rabenhorst	8	1.8	59	2.8	15	13.8
48	<i>Cymbella</i> sp. [cf. <i>schubartii</i> Hustedt]	44	2.5	19	2.1	16	14.7
49	<i>Cyclotella rossii</i> Håkansson	9	2.1	59	2.3	23	14.2
50	<i>Cyclotella tripartita</i> Håkansson	8	1.9	50	2.9	7	5.9
51	<i>Cyclotella kuetzingiana</i> Thwaites	11	2.1	78	2.8	16	14.0
52	<i>Cyclotella michiganiana</i> Skvortzow	7	1.4	287	1.6	5	4.1
53	<i>Cyclotella ocellata</i> Pantocsek	15	2.2	73	2.5	5	4.1
54	<i>Cyclotella stelligera</i> (Cleve & Grunow) Van Heurck	14	2.6	53	2.5	50	33.4
55	<i>Cyclotella bodanica</i> var. <i>lemanica</i> (O. Müller ex Schröter) Bachman	11	2.1	59	2.1	26	20.1
56	<i>Eunotia bilunaris</i> (Ehrenberg) Mills	26	3.0	28	2.2	29	24.6
57	<i>Eunotia exigua</i> (Brébisson ex Kützing) Rabenhorst	12	2.6	29	2.0	21	18.7
58	<i>Eunotia faba</i> Ehrenberg	21	3.2	24	2.1	21	18.4
59	<i>Eunotia hemicyclus</i> (Ehrenberg) Ralfs in Pritchard	34	2.6	19	1.9	14	12.4
60	<i>Eunotia incisa</i> Gregory	53	1.9	21	2.4	20	15.4
61	<i>Eunotia intermedia</i> (Krasske ex Hustedt) Nörpel & Lange-Bertalot	29	3.1	18	2.0	10	8.0
62	<i>Eunotia</i> sp. 16	39	2.1	22	1.6	4	3.3
63	<i>Eunotia major</i> (W. Smith) Rabenhorst	53	2.1	15	2.3	9	7.1
64	<i>Eunotia pectinalis</i> (Dillwyn) Rabenhorst	47	2.3	19	2.5	9	5.6
65	<i>Eunotia rhynchocephala</i> Hustedt	29	2.8	24	2.5	25	22.1
66	<i>Eunotia satelles</i> (Nörpel & Lange-Bertalot) Nörpel & Lange-Bertalot	27	2.9	22	2.7	18	15.3
67	<i>Eunotia subarcuatooides</i> Alles, Nörpel & Lange-Bertalot	28	3.0	18	1.9	15	13.1
68	<i>Eunotia paludosa</i> var. <i>trinacria</i> (Krasske) Nörpel in Lange-Bertalot & Nörpel	64	1.5	8	1.7	5	4.4
69	<i>Fragilaria capucina</i> Desmazières	12	2.1	88	2.3	7	6.2
70	<i>Fragilaria acidobiontica</i> Charles	58	1.6	11	1.5	8	5.8
71	<i>Fragilaria brevistriata</i> Grunow in Van Heurck	15	2.4	88	2.5	25	16.9
72	<i>Fragilaria construens</i> var. <i>binodis</i> (Ehrenberg) Grunow	58	2.4	36	2.8	10	8.4
73	<i>Fragilaria</i> sp. [cf. <i>construens</i> var. <i>pumila</i> Grunow in Van Heurck]	39	3.0	47	2.2	16	11.3
74	<i>Fragilaria construens</i> (Ehrenberg) Grunow	11	1.9	92	2.7	23	15.7
75	<i>Fragilaria construens</i> var. <i>venter</i> (Ehrenberg) Grunow in Van Heurck	30	2.9	48	2.4	24	16.6
76	<i>Fragilaria constricta</i> Ehrenberg	24	3.0	18	2.1	18	14.9
77	<i>Fragilaria lapponica</i> Grunow (in Van Heurck)	8	1.8	134	3.2	7	6.4
78	<i>Fragilaria lata</i> (Cleve-Euler) Renberg	47	2.5	18	2.0	17	14.6
79	<i>Fragilaria oldenburgiana</i> Hustedt	28	2.8	18	1.8	15	12.3
80	<i>Fragilaria pinnata</i> var. <i>acuminata</i> A. Mayer	37	2.7	48	2.5	18	14.7
81	<i>Fragilaria pinnata</i> var. <i>lancettula</i> (Schumann) Hustedt in Schmidt et al.	62	2.2	40	2.4	11	9.2

Table B1 (continued).

	Taxon name	CLR optimum	CLR tolerance	ALK optimum	ALK tolerance	Occurrences	Hill's <i>N</i> ₂
82	<i>Fragilaria pinnata</i> Ehrenberg	18	2.9	68	2.7	39	29.2
83	<i>Fragilaria polygonata</i> Cleve-Euler	83	1.3	8	1.8	4	3.3
84	<i>Fragilaria pseudoconstruens</i> Marciniak	8	1.7	125	3.7	7	4.9
85	<i>Fragilaria vaucheriae</i> (Kützing) Petersen	16	1.6	97	2.2	2	1.7
86	<i>Fragilaria virescens</i> var. <i>exigua</i> Grunow in Van Heurck	23	3.1	34	2.3	52	42.9
87	<i>Frustulia</i> sp. [cf. <i>magaliesmontana</i> Cholnoky]	64	1.3	9	1.3	3	2.7
88	<i>Frustulia rhomboides</i> (Ehrenberg) De Toni	18	3.3	22	2.0	35	25.5
89	<i>Frustulia rhomboides</i> var. <i>saxonica</i> (Rabenhorst) De Toni	15	2.9	27	2.1	49	38.1
90	<i>Gomphonema parvulum</i> (Kützing) Kützing	20	2.7	48	2.2	10	8.7
91	<i>Melosira arentii</i> (Kolbe) Nagumo & Kobayasi	55	1.7	17	1.9	9	7.8
92	<i>Navicula absoluta</i> Hustedt	5	1.3	467	1.2	1	1.0
93	<i>Navicula agrestis</i> Hustedt	5	1.3	41	4.3	3	2.3
94	<i>Navicula arvensis</i> Hustedt	68	1.7	28	2.0	19	12.8
95	<i>Navicula</i> sp. [cf. <i>begerii</i> (Krasske) Krasske]	17	3.3	18	1.8	4	3.5
96	<i>Navicula bremensis</i> Hustedt	29	3.2	21	2.0	16	14.1
97	<i>Navicula bryophila</i> Petersen	11	2.0	64	1.9	15	12.7
98	<i>Navicula cocconeiformis</i> Gregory ex Greville	28	3.0	29	3.2	28	22.4
99	<i>Navicula disjuncta</i> Hustedt	34	2.5	34	2.8	9	8.1
100	<i>Navicula submolesta</i> Hustedt	5	1.3	39	1.7	4	3.4
101	<i>Navicula leptostriata</i> Jørgensen	18	3.0	34	2.5	48	43.0
102	<i>Navicula jaernefeltii</i> Hustedt	10	1.3	45	1.2	1	1.0
103	<i>Navicula krasskei</i> Hustedt	8	2.3	31	1.7	13	8.7
104	<i>Navicula kuelbsii</i> Lange-Bertalot in Lange- Bertalot & Krammer	8	1.5	42	1.2	2	1.7
105	<i>Navicula laevissima</i> Kützing	26	3.1	46	2.6	14	13.1
106	<i>Navicula digitulus</i> Hustedt	19	3.1	19	1.6	9	7.5
107	<i>Navicula mediocris</i> Krasske	17	2.9	30	2.2	41	35.8
108	<i>Navicula pseudoscutiformis</i> Hustedt	19	2.7	61	2.7	28	25.5
109	<i>Navicula pseudoventralis</i> Hustedt	46	8.9	45	2.5	2	1.8
110	<i>Navicula pupula</i> Kützing	19	3.1	38	3.0	24	21.1
111	<i>Navicula schmassmannii</i> Hustedt	22	3.2	31	2.4	28	23.7
112	<i>Navicula seminuloides</i> Hustedt	16	3.1	122	1.9	7	6.2
113	<i>Navicula seminulum</i> Grunow	7	1.6	51	2.8	9	8.1
114	<i>Navicula soehrensii</i> var. <i>hassiacae</i> (Krasske) Lange-Bertalot	41	2.7	16	2.4	15	12.6
115	<i>Navicula</i> sp. [cf. <i>submuralis</i> Hustedt]	8	1.9	294	2.3	3	2.5
116	<i>Navicula parasubtilissima</i> Kobayasi & Nagumo	11	2.8	27	2.0	35	28.2
117	<i>Navicula tenuicephala</i> Hustedt	31	2.7	17	1.7	12	8.0
118	<i>Navicula ventralis</i> Krasske	23	4.3	16	2.5	5	4.7
119	<i>Navicula vitiosa</i> Schimanski	18	2.9	75	2.3	32	25.7
120	<i>Nitzschia liebetruthii</i> Rabenhorst	9	1.9	84	2.7	7	6.7
121	<i>Nitzschia amphibia</i> Grunow	10	1.8	42	2.9	5	4.6
122	<i>Nitzschia</i> sp. [cf. <i>fonticola</i> Grunow in Van Heurck]	9	1.8	62	2.3	29	22.0
123	<i>Nitzschia hantzschiana</i> Rabenhorst	5	1.3	65	1.2	1	1.0
124	<i>Nitzschia perminuta</i> (Grunow) M. Peragallo	14	3.0	37	2.3	27	24.8
125	<i>Pinnularia</i> sp. [cf. <i>braunii</i> var. <i>amphicephala</i> (Grunow) Cleve]	14	3.1	18	1.9	8	7.1
126	<i>Pinnularia mesolepta</i> (Ehrenberg) W. Smith Morphotyp 3 sensu Krammer	11	2.5	40	2.2	44	34.4
127	<i>Pinnularia microstauron</i> (Ehrenberg) Cleve	10	2.4	39	2.4	23	19.7
128	<i>Pinnularia rupestris</i> Hantzsch in Rabenhorst	7	2.4	33	1.9	5	3.8
129	<i>Stauroneis anceps</i> Ehrenberg	19	2.9	33	2.3	34	31.0

Table B1 (concluded).

	Taxon name	CLR optimum	CLR tolerance	ALK optimum	ALK tolerance	Occurrences	Hill's <i>N2</i>
130	<i>Stenopterobia delicatissima</i> (Lewis) Brébisson ex Van Heurck	25	2.9	25	2.5	16	13.6
131	<i>Tabellaria flocculosa</i> (Roth) Kützing	18	2.8	37	2.5	55	41.6
132	<i>Tabellaria quadrisepitata</i> Knudson	62	1.3	9	1.2	3	2.8