

Ecology and spatial distributions of surface-sediment diatoms from 77 lakes in the subarctic Canadian treeline region

Kathleen M. Rühland, John P. Smol, and Reinhard Pienitz

Abstract: Diatom ecology and species compositional patterns across current arctic treeline can provide important paleoecological information associated with climatic and environmental change. In this paper we examine the relationships between measured environmental variables and modern diatom assemblage composition from 77 lakes across the treeline ecozones of the Central Canadian Arctic. The weighted-average optima for selected environmental variables were calculated for 74 of the most common diatoms, and photographic plates of these taxa are included. Our results indicated that both forest-tundra and arctic tundra lakes differed significantly in diatom assemblage composition from boreal forest lakes. In general, planktonic diatom taxa (e.g., *Cyclotella* species) were more common in forested lakes, which may be due to ecological conditions related to climate. Small, benthic, alkaliphilic *Fragilaria* taxa reached their highest abundances in forested lakes, likely because of the more alkaline nature of these lakes. Arctic tundra lakes were characterized by higher abundances of circumneutral to acidophilic taxa. Heavily silicified *Aulacoseira* taxa (e.g., *Aulacoseira lirata*, *Aulacoseira perglabra*) were more common in deeper tundra lakes, likely because of the less alkaline nature of these lakes and greater wind-induced turbulence in this zone. These trends provide important information on the variability of aquatic ecosystems across this climatically sensitive vegetational gradient.

Key words: arctic treeline, Canada, diatoms, paleolimnology, weighted-average optima, climate change.

Résumé : L'écologie et les patrons d'espèces présentes de part et d'autre de l'actuelle ligne arctique des arbres peuvent fournir d'importantes informations paléocéologiques associées au changement climatique et environnemental. Les auteurs examinent les relations entre les variables environnementales observées et la composition de l'assemblage moderne des diatomées, dans 77 lacs distribués dans les écozones situées de part et d'autre de la ligne des arbres, dans l'arctique canadien central. Ils ont calculé les moyennes pondérées optimales pour des variables environnementales sélectionnées, pour 74 des diatomées les plus fréquentes; les planches photographiques de ces taxons sont présentées. Les résultats indiquent que dans les lacs de la toundra forestière aussi bien que de la toundra arctique, la composition de l'assemblage des diatomées diffère significativement de celle des lacs de la forêt boréale. En général, les taxons des diatomées planctoniques (e.g., *Cyclotella* spp.) sont plus communs dans les lacs des régions forestières, ce qui pourrait être dû aux conditions écologiques liées au climat. Les taxons benthiques, alcaliphiles de *Fragilaria* de petite dimension, montrent leur abondance maximale dans les lacs bordés de forêts, vraisemblablement dû à la composition plus alcaline de ces lacs. Les lacs de la toundra arctique sont caractérisés par une plus grande abondance de taxons neutrophiles à acidiphiles. Les taxons d'*Aulacoseira*, fortement silicifiés (e. g. *Aulacoseira lirata*, *Aulacoseira perglabra*), sont plus communs dans les lacs profonds de la toundra, vraisemblablement dû à la nature moins alcaline de ces lacs et à une plus forte turbulence induite par le vent, dans cette zone. Ces tendances fournissent d'importantes informations sur la variabilité des écosystèmes aquatiques, le long de ce gradient de végétation sensible au climat.

Mots clés : ligne arctique des arbres, Canada, diatomées, paléolimnologie, optimums moyens pondérés, changement climatique.

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Introduction

Diatoms (Class Bacillariophyceae) are important indicators of past lakewater environments as they are often well preserved in sediments, have very short generation times, often have well-defined optima and tolerances to measured environmental variables, and are identifiable to species level, based on their siliceous cell walls (Stoermer and Smol 1999). Consequently, they have been widely used in paleolimnological studies to develop environmental models (transfer functions) that enable the reconstruction and interpretation of past environments including climatic change (e.g., Smol 1988; MacDonald et al. 1993; Douglas et al.

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1994; Pienitz et al. 1995; Weckström et al. 1997a; Sorvari and Korhola 1998; Fallu and Pienitz 1999; Lotter et al. 1999; Smol and Cumming 2000; Rosén et al. 2000; Fallu et al. 2002; Ponader et al. 2002; Bigler and Hall 2002). The success of diatoms as bioindicators stems from ongoing research on their autecology and the documentation of their distribution from a great variety of geographic locations and habitats. However, to date, relatively little information exists on diatoms from circumpolar treeline regions.

Similar studies in the Canadian northern treeline region are scarce. For example, Kling and Håkansson (1988) and Håkansson and Kling (1989) presented taxonomic and ecological descriptions of centric diatoms from several lakes in northern and central Canada. Moser (1996) provided ecological information on diatoms collected from the surficial sediments of 35 lakes from Wood Buffalo National Park. Fallu et al. (2000) produced a monograph on the taxonomy and ecology of diatoms from lakes in northern Quebec and Labrador. Pienitz and Smol (1993) and Pienitz et al. (1995) examined the distributions of diatoms from transects of lakes spanning the northern treeline in both the Yukon and the Northwest Territories, relating diatom variability across ecozones to temperature, dissolved organic carbon (DOC), and related variables. Diatom-based calibration studies have also been carried out in other circumpolar treeline regions including Siberia (Laing and Smol 2000), Alaska (Gregory-Eaves et al. 1999), Finland (Weckström et al. 1997a, 1997b; Weckström and Korhola 2001; Korhola et al. 2002), and northern Sweden (Rosén et al. 2000; Bigler and Hall 2002). These studies continue to furnish new information on the environmental factors that influence diatom distributions at ecotonal boundaries.

The northern treeline ecotone is expected to respond very sensitively to future climatic changes (Schlesinger and Mitchell 1987; Serreze et al. 2000). The possibility of increased temperatures at northern treeline is anticipated to have significant impacts on the vegetation through either a change in stand density (Lavoie and Payette 1994) or through the northward migration of trees (Serreze et al. 2000). Changes in the composition of diatom assemblages preserved in lake sediments from northern treeline sites provide strong evidence for climatic signals throughout the Holocene (e.g., Weckström et al. 1997a, 1997b; Sorvari and Korhola 1998; Pienitz et al. 1999; Laing et al. 1999; Rosén et al. 2000; Bigler and Hall 2002). These arctic treeline studies contribute to many other paleoecological studies of Holocene environments currently being undertaken in the Arctic (e.g., see MacDonald et al. 2000; Anderson et al. 2001; Cremer et al. 2001a, 2001b; Gajewski and Frappier 2001; Smith 2002).

The use of multivariate statistical techniques for our 77 lakes resulted in the development of diatom-based inference models (Rühland and Smol 2002) that could be used for paleolimnological reconstructions. However, to more accurately interpret these floristic changes, it is essential to define further the ecology (e.g., apparent environmental optima) of individual diatom taxa. These data are essential for generating robust and ecologically sound inference models. In this paper, we present data on the most abundant diatom taxa found in the surface sediments of 77 lakes spanning current treeline in Canada's Northwest Territories and

Nunavut. The aims of this study were to: (i) examine the trends in diatom distributions in relation to important measured environmental variables; (ii) establish the spatial trends in diatom distributions across the various ecozones (boreal forest, forest-tundra, arctic tundra); and (iii) determine whether diatom assemblage composition within each ecozone is distinct from other ecozones.

Materials and methods

Study Area

The 77 study lakes were sampled along a latitudinal transect across northern treeline from the Yellowknife area (62°32'42"N, 114°07'06"W) and then in a northeasterly direction to the Arctic Circle east of Bathurst Inlet (66°41'18"N, 104°55'54"W) in the Central Canadian Arctic (Fig. 1). The region contains a variety of vegetation zones, from boreal forest cover in the south, which gradually thins to a transitional zone (forest-tundra) until trees are no longer present in the arctic tundra zone. The dominant tree species within the boreal forest zone include *Picea mariana* (black spruce), *Picea glauca* (white spruce), *Abies balsamea* (balsam fir), and *Pinus banksiana* (jack pine) (Ritchie 1993). The conditions for tree growth deteriorate northwards where only the hardiest species exist at the northern limit. The most common tree in the transitional zone is *Picea mariana* (Timoney and Wein 1991), with fewer species associated with forest fires, such as *Populus balsamifera* (balsam poplar), *Populus tremuloides* (trembling aspen), and *Betula papyrifera* (paper birch) (Sirois 1992). The arctic tundra zone consists primarily of dwarfed shrub vegetation including *Betula glandulosa* (resin birch), *Salix* (willow) species, and various heath shrubs including *Ledum* and *Vaccinium* (Ritchie 1993).

The study region lies entirely on the Canadian Shield, and is typified by granites and granitic gneisses (Ross and Kearns 1989; Padgham and Fyson 1992). Lakes in this study were typically circumneutral to slightly acidic (mean pH = 7.4), in part owing to the absence of major limestone and gypsum deposits along this transect (Ford 1993).

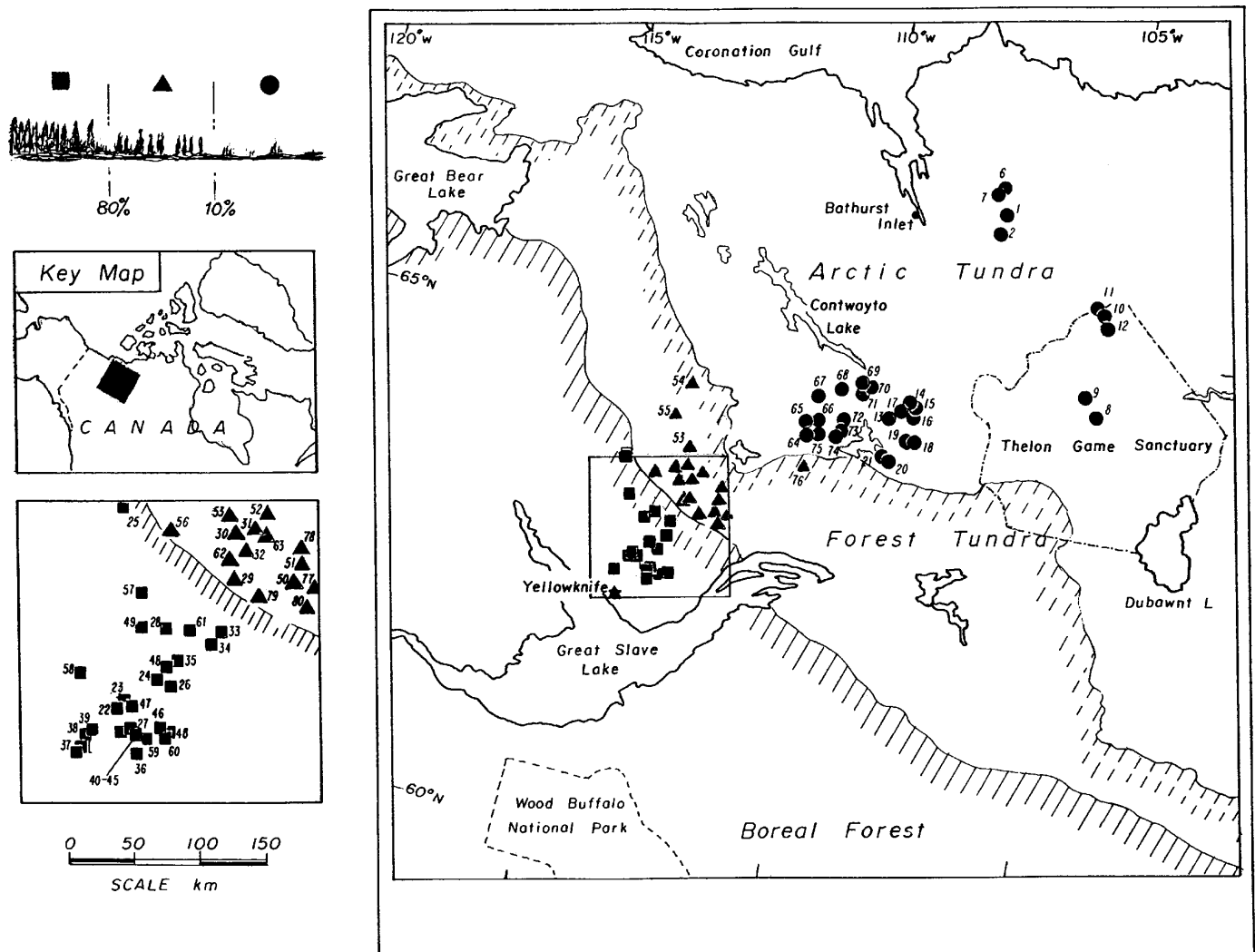
Soils consist mainly of dystric brunisols at more southerly sites, with cryic regosols to the north (Clayton et al. 1977). The region is underlain by permafrost, with the boundary between continuous and discontinuous permafrost closely following the current position of treeline.

The climate of the study region is subarctic continental characterized by long cold winters and short dry summers. The average ice-free periods for lakes in this region range from 90 days for the northernmost sites to 120 days for sites near Yellowknife (National Atlas of Canada 1991; Wedel et al. 1990). Average annual precipitation (about half occurring as snow) ranges from approximately 267 mm near Yellowknife (Environment Canada 1990; Wedel et al. 1990) to 200 mm near Coronation Gulf (Environment Canada 1990; National Atlas of Canada 1991).

Sample collection

Samples were collected between 7 and 19 August 1996 for sites TK-1 to TK-36 and between 14 and 23 August 1998 for sites TK-37 to TK-59. An additional 21 sites (RP-60 to RP-80) collected via helicopter on 12 July 1991

Fig. 1. Map showing distribution of the 77 study sites across the vegetational gradient in the central Canadian arctic treeline region.



(Pienitz and Smol 1993) were included in the training set, as these lakes were within our sampling transect. Limnological variables for all lakes were analysed at the same water chemistry laboratory (National Water Research Institute, Burlington, Ontario) and followed the same sampling and analysis protocols (International Organization for Standardization). The final training set consisted of 30 arctic tundra sites, 18 forest-tundra sites, and 29 boreal forest sites for a total of 77 lakes.

Surficial sediments were collected from the deepest part of the lake using a modified KB-type gravity corer (Glew 1991) equipped with a 4.0 cm diameter core tube. The cores were extruded on site using a Glew (1988) extruder and the upper 0.5 cm of sediment, representing recent lake conditions, was analysed for diatoms.

Diatom sample preparations and enumeration

Sediment samples were processed using standard procedures for diatom preparations, as outlined in Pienitz and Smol (1993). Briefly, approximately 0.5 g of wet sediment from each surface sample was placed into glass scintillation vials and then treated with strong acids (50:50 molar ratio of

concentrated nitric acid (H_2NO_3) to concentrated sulphuric acid (H_2SO_4) to digest the organic sediment matrix. Small aliquots of the final slurries were strewn onto glass coverslips in four different dilutions and allowed to evaporate slowly at room temperature on a slide warmer. Coverslips were mounted onto microscope slides with Naphrax[®] (refractive index of 1.74).

For each sample, a minimum of 500 diatom valves were identified and enumerated along transects on the coverslip using a Leitz Dialux 20 microscope (100× oil immersion objective lens, numerical aperture (na) = 1.32; condenser lens, na = 0.90) fitted with differential interference contrast optics. The 21 samples from Pienitz and Smol (1993) were recounted to ensure taxonomic consistency. Taxonomic identifications were made with the help of the following sources: Hustedt (1927–1966), Patrick and Reimer (1966, 1975), Foged (1981), PIRLA Diatom Iconograph (Camburn et al. 1984–1986), Krammer and Lange-Bertalot (1986–1991), Hein (1990), Cumming et al. (1995), and Lange-Bertalot and Metzeltin (1996).

A Leica DMRB light microscope (100× oil immersion; na = 1.3) equipped with a Wild Photoautomat MPS45 cam-

era system was used to obtain photomicrographs of common and difficult taxa. A reference collection of the most common diatom taxa was prepared and consisted of over 1000 photomicrographs. A portion of this photo collection is included in this paper.

Diatom identifications for this study largely followed the taxonomic scheme given by Krammer and Lange-Bertalot (1986–1991) in *Süßwasserflora von Mitteleuropa*. Although we are aware that diatom nomenclature has changed considerably since the publication of these works, we have followed this approach to maintain taxonomic consistency with other diatom-based paleolimnological studies at arctic tree-line. To aid in taxonomic comparisons among researchers, we have included photomicrographs of 74 of the most common diatom taxa present in our 77-lake study (Appendix A, Figs. A1–A4).

Taxa that occurred with a relative abundance of 1% in at least two lakes (141 taxa) were used to develop inference models for measured environmental variables that were significant in explaining the variation in the diatom assemblages. Full details for these models and the methods used to construct them are given Rühland and Smol (2002). For this paper, only those diatoms that attained a relative abundance of 2% in at least three lakes (74 taxa) were included for taxonomic references and ecological preferences. The computer program WACALIB version 3.3 (Line et al. 1994) was used to calculate the weighted-average optima of these 74 taxa for five significant environmental variables identified with the forward selection option in canonical correspondence analysis using the computer program CANOCO (ter Braak and Šmilauer 1998).

Based on the diatom assemblage composition, we used an analysis of similarity (ANOSIM), a PRIMER program (Clarke and Warwick 1994), to determine whether there were statistically significant differences among the tree-line ecozones. ANOSIM is essentially a one-way ANOVA for multivariate data (Clarke and Warwick 1994) that uses pairwise comparisons between groups of samples (e.g., boreal forest sites versus arctic tundra sites).

The relative abundances of some of the more common diatom taxa were plotted across the measured environmental gradients as well as across the three vegetation zones. To identify which diatom taxa were important in determining the differences between the zones we used the PRIMER program SIMPER (Clarke and Warwick 1994), which computes the average dissimilarity between zones and then assesses the separate contributions of each species to this dissimilarity (Clarke and Warwick 1994).

Results and discussion

Comments on diatom taxonomy

A total of 410 diatom taxa were identified from the 77 lakes. Diatom taxa that were very similar and difficult to distinguish using light microscopy were treated as a species “complex” or grouped. These included *Cyclotella stelligera* and *Cyclotella pseudostelligera* (herein referred to as the *Cyclotella stelligera* complex). Many researchers believe that the splitting of *Cyclotella stelligera* and *Cyclotella pseudostelligera* may not be feasible because when valves become extremely small, they lose much of their distin-

guishing ornamentation (see Fig. A2, #66–70). It is now believed that both *Cyclotella stelligera* and *Cyclotella pseudostelligera* display a wide range in valve size. In fact, the size of any centric diatom cell is not a good criterion for distinguishing one centric diatom species from another (Kling 1997). In the case of *Cyclotella stelligera* and *Cyclotella pseudostelligera*, smaller valves may simply be a variation on the larger *Cyclotella stelligera* individuals. Therefore, a distinct central area and a well-defined star-shaped ornamentation in the central area may simply be an artifact of valve size.

Some varieties within a given species were often difficult to distinguish under light microscopy, and because they displayed highly similar autecology, these taxa were grouped. For example, *Aulacoseira lirata* and *Aulacoseira lirata* var. *biseriata* were at times difficult to distinguish under light microscopy, especially when in valve view (Fig. A2, #82 and #86). These taxa were split during enumeration as best as possible, but subsequently grouped for purposes of numerical analyses. According to the PIRLA Iconograph (Camburn et al. 1984–1986), the development of the areolae (the morphological criterion used for distinction) may be ascribed to ecological or growth conditions.

Many species within a genus displayed highly similar trends and so were grouped in the figures for simplicity. However, for statistical analyses, these taxa (species and varieties) were kept distinct. These included small benthic *Fragilaria* taxa including *Fragilaria construens*, *Fragilaria construens* var. *venter*, *Fragilaria pseudoconstruens*, *Fragilaria pinnata*, and *Fragilaria brevistriata*.

Trends in diatom species composition across ecozones

The distributions of selected diatom taxa across vegetation zones and across environmental gradients showed distinct trends in taxonomic preferences for specific ecological zones and (or) for measured limnological conditions (Figs. 2a–2c, 3a–3e, 4a–4e, and 5a–5e). Most lakes across the vegetational gradient were rich in diatom taxa (mean of 51 taxa, minimum of 18, maximum of 94) and also showed high diatom diversity (Shannon–Weaver diversity index mean $H' = 3.04$; mean evenness $J' = 0.78$). The comparison of diatom diversity among ecozones in our study is somewhat problematic as the rates of sediment accumulation may vary across tree-line and are not known for each lake sampled. Therefore, the diversity indices cited here represent a general trend of the diversity patterns encountered in this lakeset, and comparisons among ecozones should be viewed with caution (Smol 1981). Nevertheless, it is clear that these oligotrophic lakes contain assemblages with low dominance of any taxon and high taxa numbers.

The diatom assemblages we recorded were generally characteristic of the shallow, circumneutral, and oligotrophic nature of these subarctic tree-line lakes. Benthic diatoms dominated the assemblages in most lakes, reflecting the generally shallow nature of this lakeset (mean depth = 5.35 m). The majority of these benthic diatoms consisted of small taxa belonging to the genera *Achnanthes* (24 species), *Navicula* (19 species), *Cymbella* (11 species), and *Fragilaria* (9 species) (Table 1; Figs. A1–A4). Deeper lakes (>5 m) in all ecozones were commonly dominated by small, centric, planktonic taxa belonging to the genus *Cyclotella* (Fig. A2,

Table 1. Weighted average optima of the 74 most common diatom taxa (2% in at least three lakes) encountered in the 77 study lakes for important measured environmental variables.

Taxon and authority	DIC (mg·L ⁻¹)	TN (µg·L ⁻¹)	DOC (mg·L ⁻¹)	Depth (m)	SiO ₂ (mg·L ⁻¹)	#occ	Hill's N2
<i>Achnanthes acares</i> Hohn and Hellermann	1.0	277.6	6.9	5.9	0.3	33	15.9
<i>Achnanthes altaica</i> (Portezky) Cleve-Euler	1.8	318.9	6.1	3.0	0.3	25	13.4
<i>Achnanthes conspicua</i> Mayer	22.1	878.0	21.0	4.4	0.9	8	3.5
<i>Achnanthes curtissima</i> Carter	0.7	208.4	3.2	6.4	0.3	42	23.4
<i>Achnanthes didyma</i> Hustedt	0.5	220.8	3.4	5.6	0.2	18	11.9
<i>Achnanthes lacus-vulcani</i> Lange-Bert. and Kramm.	0.9	242.2	4.1	5.9	0.3	40	22.0
<i>Achnanthes marginulata</i> Grunow	1.0	187.4	2.4	4.2	0.5	28	9.7
<i>Achnanthes minutissima</i> Kützing	4.4	621.3	17.9	3.1	0.3	69	33.7
<i>Achnanthes pusilla</i> (Grunow) De Toni	1.9	351.4	9.7	5.0	0.4	50	30.9
<i>Achnanthes rossii</i> Hustedt	1.2	232.3	5.2	4.4	0.3	19	11.2
<i>Achnanthes scotica</i> Flower	0.8	205.5	3.0	5.1	0.4	45	24.7
<i>Achnanthes suchlandtii</i> Hustedt	5.4	375.7	9.9	9.2	0.5	14	3.7
<i>Aulacoseira distans</i> var. <i>nivalis</i> (W. Smith) Haworth	0.8	250.2	5.6	5.5	0.6	33	12.4
<i>Aulacoseira distans</i> (Ehrenberg) Simonsen	2.2	420.7	18.3	3.2	0.8	19	7.8
<i>Aulacoseira lirata</i> (Ehrenberg) Ross	0.9	310.9	9.2	6.0	0.5	31	5.0
<i>Aulacoseira perglabra</i> var. <i>floriniae</i> Camburn	0.7	327.1	11.4	4.5	0.4	37	11.8
<i>Aulacoseira perglabra</i> (Oestrup) Haworth	0.6	250.2	7.7	6.4	0.3	34	16.7
<i>Aulacoseira subarctica</i> (O. Müller) Haworth	2.7	567.9	158.9	6.7	0.3	7	1.7
<i>Brachysira brebissonii</i> Ross	1.1	265.1	5.8	3.9	0.4	47	22.3
<i>Brachysira vitrea</i> (Grunow) Ross	4.3	698.8	17.1	2.8	0.2	60	16.9
<i>Cyclotella michiganiana</i> Skvortzow	15.6	882.1	23.5	4.9	0.8	16	4.6
<i>Cyclotella ocellata</i> Pantocsek	1.4	268.8	10.5	9.2	0.5	29	10.6
<i>Cyclotella radiosa</i> (Grunow) Lemmermann	2.3	313.1	28.8	8.2	0.4	11	6.4
<i>Cyclotella rossii</i> Håkansson	0.4	229.7	3.0	8.6	0.2	20	7.6
<i>Cyclotella stelligera</i> complex Cleve and Grun./Hust.	2.2	353.8	11.4	6.2	0.3	63	29.5
<i>Cyclotella tripartita</i> Håkansson	0.8	265.7	9.9	9.5	0.3	22	10.4
<i>Cymbella angustata</i> (W. Smith) Cleve	3.0	528.7	12.3	4.0	0.2	32	16.2
<i>Cymbella cesatii</i> (Rabenhorst) Grunow	4.5	653.6	14.2	3.4	0.3	37	12.7
<i>Cymbella gaeumannii</i> Meister	0.8	215.3	3.5	4.9	0.3	51	29.1
<i>Cymbella gracilis</i> (Ehrenberg) Kützing	1.7	390.7	8.6	3.8	0.2	63	34.2
<i>Cymbella hebridica</i> (Grunow) Cleve	1.5	281.5	5.2	3.6	0.4	44	25.4
<i>Cymbella microcephala</i> Grunow	5.3	687.7	16.7	3.4	0.2	43	14.9
<i>Cymbella silesiaca</i> Bleish	1.2	338.6	5.7	4.0	0.3	35	18.3
<i>Eunotia exigua</i> (Brébisson) Rabenhorst	0.9	328.6	7.9	3.3	0.2	21	8.5
<i>Eunotia faba</i> Ehrenberg	1.5	383.6	6.7	2.5	0.3	22	11.0
<i>Eunotia rhynchocephala</i> Hustedt	1.2	249.6	5.1	3.9	0.4	22	14.9
<i>Fragilaria brevistriata</i> Grunow	3.3	344.1	8.5	6.4	0.6	27	11.8
<i>Fragilaria construens</i> (Ehrenberg) Grunow	6.3	423.6	13.8	6.7	0.5	10	3.3
<i>Fragilaria construens</i> var. <i>venter</i> (Ehrenberg) Hustedt	4.5	485.4	14.4	3.5	0.4	31	9.7
<i>Fragilaria oldenburgiana</i> Hustedt	1.2	213.8	3.8	4.2	0.9	10	5.2
<i>Fragilaria pinnata</i> Ehrenberg	5.0	473.2	13.3	4.6	0.5	48	15.1
<i>Fragilaria pseudoconstruens</i> Marciniak	2.0	439.6	15.3	4.1	0.4	16	3.9
<i>Fragilaria tenera</i> (W. Smith) Lange-Bertalot	14.3	925.8	35.9	3.1	1.0	10	6.3
<i>Fragilaria virescens</i> var. <i>exigua</i> Grunow	1.1	248.5	5.2	4.1	0.4	55	23.7
<i>Frustulia rhomboides</i> var. <i>crassinervia</i> (Brébisson) Ross	1.4	286.7	6.0	3.5	0.3	40	16.0
<i>Frustulia rhomboides</i> (Ehrenberg) De Toni	0.8	222.9	3.9	5.0	0.4	30	14.0
<i>Frustulia rhomboides</i> var. <i>saxonica</i> (Raben.) De Toni	1.0	241.1	4.0	4.6	0.3	48	23.4
<i>Gomphonema parvulum</i> Kützing	4.2	465.7	11.0	2.9	0.5	35	11.0
<i>Navicula bryophila</i> Petersen	1.8	332.4	10.3	4.9	0.3	38	22.3
<i>Navicula cocconeiformis</i> Gregory ex. Greville	1.1	297.5	6.8	6.0	0.4	32	18.4
<i>Navicula cryptocephala</i> Kützing	14.7	1206.8	44.9	1.6	0.4	15	4.9
<i>Navicula cryptotenella</i> Lange-Bert.	5.6	750.6	19.8	2.8	0.3	54	15.2
<i>Navicula disjuncta</i> Hustedt	11.6	597.4	29.0	4.3	2.0	13	5.1
<i>Navicula jaagii</i> Meister	4.0	573.1	12.4	2.4	0.2	13	6.3
<i>Navicula kuelbsii</i> Lange-Bert.	2.6	356.3	12.9	5.4	0.6	34	16.1

Table 1 (concluded).

Taxon and authority	DIC (mg·L ⁻¹)	TN (µg·L ⁻¹)	DOC (mg·L ⁻¹)	Depth (m)	SiO ₂ (mg·L ⁻¹)	#occ	Hill's N2
<i>Navicula mediocris</i> Krasske	1.1	284.8	5.8	3.9	0.3	48	30.3
<i>Navicula minima</i> Grunow	5.2	513.0	11.0	3.9	0.6	33	12.4
<i>Navicula pseudoscutiformis</i> Hustedt	1.1	313.8	7.0	4.0	0.3	27	15.6
<i>Navicula pupula</i> Kützing	4.6	582.4	14.0	3.1	0.5	54	22.5
<i>Navicula radiosa</i> Kützing	10.6	1058.3	31.4	1.9	0.4	33	7.5
<i>Navicula schmassmannii</i> Hustedt	0.5	219.8	4.1	7.5	0.3	19	11.6
<i>Navicula seminulum</i> Grunow	1.7	342.6	8.3	5.2	0.4	41	23.9
<i>Navicula seminuloides</i> Hustedt	4.0	348.1	5.5	8.8	0.4	6	2.9
<i>Navicula submuralis</i> Hustedt	3.4	358.7	8.8	6.7	0.4	16	7.1
<i>Navicula subtilissima</i> Cleve	1.5	385.4	7.9	3.2	0.2	38	12.8
<i>Neidium ampliatum</i> (Ehrenberg) Krammer	1.7	330.1	6.8	3.5	0.4	49	29.6
<i>Nitzschia fonticola</i> Grunow	3.5	567.9	14.5	3.2	0.2	54	13.4
<i>Nitzschia frustulum</i> (Kützing) Grunow	2.7	455.0	10.7	3.8	0.3	49	19.9
<i>Nitzschia palea</i> (Kützing) W. Smith	6.5	791.5	20.6	2.9	0.3	34	18.4
<i>Nitzschia perminuta</i> (Grunow) M. Pergallo	1.9	387.2	7.7	3.1	0.3	64	32.1
<i>Pinnularia biceps</i> Gregory	0.3	218.3	2.8	6.9	0.2	16	10.6
<i>Pinnularia interrupta</i> W. Smith	2.3	367.1	9.2	3.6	0.4	45	24.8
<i>Stauroneis anceps</i> Ehrenberg	1.2	300.3	6.7	4.7	0.3	49	31.7
<i>Tabellaria flocculosa</i> (Roth) Kütz. (str. IV <i>sensu</i> Koppen)	1.7	388.0	10.9	4.1	0.3	58	25.7

Note: DIC, dissolved inorganic carbon; TN, total nitrogen; DOC, dissolved organic carbon; #occ, no. of occurrences; Hill's N2, diversity index as an estimate of the effective no. of occurrences of each taxon.

#54–70, Figs. 2a and 3a). Deep arctic tundra lakes had high relative abundances of heavily silicified, planktonic, centric *Aulacoseira* taxa (Fig. A2, #71–89, Figs. 2b and 4a).

To test whether lakes in the arctic tundra, forest-tundra, and boreal forest differ significantly from each other in terms of diatom assemblage composition, an analysis of similarity (ANOSIM) was used (Table 2). No significant difference was found between diatom assemblages from arctic tundra lakes and from forest-tundra lakes ($R = 0.050$, $p = 0.13$). Both forest-tundra and arctic tundra lakes differed significantly in diatom assemblage composition from boreal forest lakes ($R = 0.543$, $R = 0.273$, $p = 0.00$, respectively). The high similarity between arctic tundra and forest-tundra lakes is consistent with other treeline studies (e.g., Laing et al. 1999; Fallu et al. 2000) and reflects the greater similarity in limnological characteristics between these two ecozones.

Based on SIMPER results, diatom assemblages in boreal forest lakes were characterized by higher abundances of small benthic *Fragilaria* species (most notably *Fragilaria pinnata*, *Fragilaria construens*, *Fragilaria construens* var. *venter*, *Fragilaria pseudoconstruens*, and *Fragilaria brevistriata*), *Brachysira* species (*Brachysira vitrea*, *Brachysira brébissonii*, *Brachysira procera*, and *Brachysira styriaca*), and larger *Navicula* species (e.g., *Navicula jaagii*, *Navicula radiosa*, *Navicula cryptotenella*, *Navicula cryptocephala*). These trends likely relate to higher concentrations of dissolved inorganic carbon (DIC), DOC, and total nitrogen (TN) within these forested lakes (see below). Lakes within the arctic tundra zone were typified by higher abundances of circumneutral to acidophilic taxa such as *Fragilaria virescens* var. *exigua*, *Cymbella* taxa (most notably *Cymbella gaeumannii*), small benthic *Achnanthes* taxa (*Achnanthes curtissima*, *Achnanthes scotica*), and *Eunotia* species (e.g., *Eunotia rhynchocephala*, *Eunotia faba*, and *Eunotia praerupta*) relating to the less alkaline nature of

Table 2. Results of ANOSIM (analysis of similarity) test showing the differences between study lakes from the three vegetational zones based on diatom species assemblages.

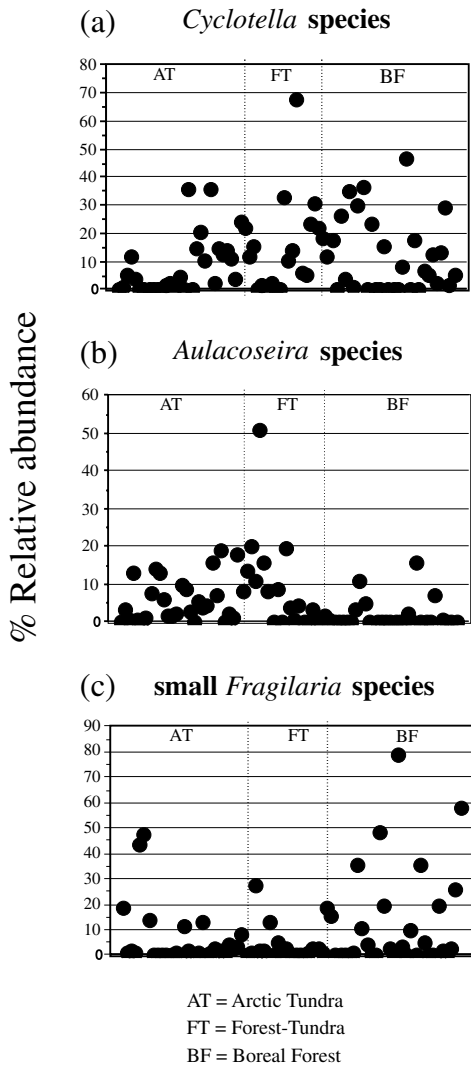
Zone comparisons	<i>R</i>	<i>p</i>
Arctic tundra vs. forest-tundra	0.050	0.13
Arctic tundra vs. boreal forest	0.542	0.0*
Forest-tundra vs. boreal forest	0.273	0.0*

*Statistical significance ($p < 0.017$).

lakes within this zone. As well, arctic tundra lakes had consistently higher abundances of *Pinnularia* species (e.g., *Pinnularia biceps*, *Pinnularia interrupta*), *Cymbella* species (e.g., *Cymbella hebridica*, *Cymbella gracilis*, *Cymbella silesiaca*), and *Frustulia* species (*Frustulia rhomboides*, *Frustulia rhomboides* var. *crassinervia*, *Frustulia rhomboides* var. *saxonica*). These larger pennates (see Figs. A3 and A4) appear to have preferences for shallower lakes that had low concentrations of DIC (<2.0 mg·L⁻¹), TN (<390 µmg·L⁻¹), DOC (<9.0 mg·L⁻¹), and SiO₂ (<0.4 mg·L⁻¹) (Table 1).

Unlike other treeline studies (e.g., Pienitz et al. 1995; Rühland 1996; Laing and Smol 2000), but similar to Pienitz and Smol (1993), small, benthic, alkaliphilous *Fragilaria* species did not show a clear preference for arctic tundra lakes and occurred in high abundances (10–80%) in both arctic tundra and boreal forest lakes (Fig. 2c). The high percentage of these small benthic taxa (e.g., *Fragilaria pinnata*, *Fragilaria construens*, *Fragilaria construens* var. *venter*, *Fragilaria brevistriata*) in arctic tundra lakes is not surprising, as they are known to be competitive in shallow, nutrient-poor, cold environments where they can thrive under short growing seasons with prolonged lake-ice cover (Pienitz 1993; Rühland 1996; Lotter and Bigler 2000). Depth

Fig. 2. Trends in the percent relative abundance of selected diatoms across treeline ecozones: (a) *Cyclotella* species; (b) *Aulacoseira* taxa; (c) small benthic *Fragilaria* taxa. AT, arctic tundra, FT, forest-tundra; BF, boreal forest.



appeared to have no major influence on these taxa, as high abundances (>20% relative abundance) were recorded in the shallowest lakes (1.4 to 3.0 m) and in the deepest lakes (5.5 to 13.0 m) (Fig. 5a). However, many of these deeper lakes had large littoral zones that may explain the high abundances of these small benthic taxa (e.g., RP-61 is a 10 m deep lake had ~60% abundance of small benthic *Fragilaria* species). As previously reported by Pienitz and Smol (1993), their strong presence in boreal forest lakes may be explained by the distinctly more alkaline nature (mean DIC = 11.34 mg·L⁻¹) of lakes found in this ecozone compared with the arctic tundra lakes (mean DIC = 1.13 mg·L⁻¹). This trend is likely more pronounced in our lakeset, as the geology along the transect of lakes is relatively uniform (i.e., no major occurrences of calcareous deposits) so that ionic trends are more likely to be a function of the differences in the ecozones. The higher alkalinity of boreal forest waters appears to have an important influence on the occurrence and abundance of these benthic, alkaliphilous *Fragilaria*

Fig. 3. Trends in the percent relative abundance of *Cyclotella* taxa (*Cyclotella stelligera*, *Cyclotella pseudostelligera*, *Cyclotella ocellata*, *Cyclotella radiosa*, *Cyclotella rossii*, *Cyclotella michiganiana*, *Cyclotella tripartita*) across measured environmental gradients: (a) depth; (b) DIC; (c) DOC; (d) TN; (e) SiO₂.

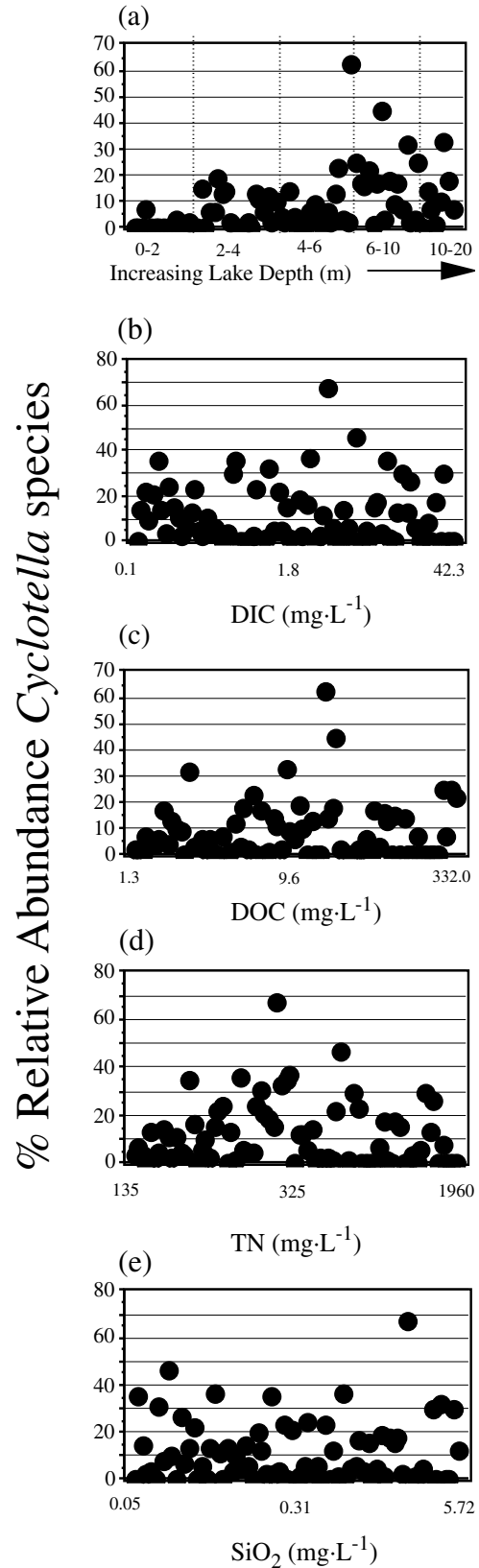
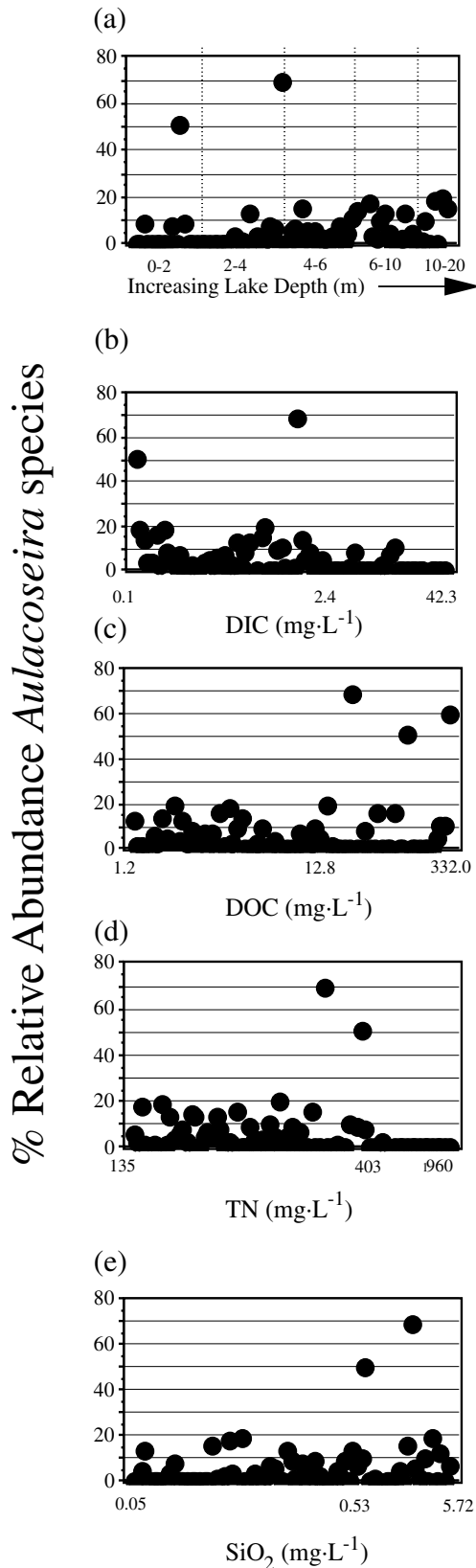


Fig. 4. Trends in the percent relative abundance of *Aulacoseira* taxa (*Aulacoseira lirata*, *Aulacoseira perglabra*, *Aulacoseira perglabra* var. *floriniae*, *Aulacoseira distans*, *Aulacoseira distans* var. *nevalis*, *Aulacoseira subarctica*) across measured environmental gradients: (a) depth; (b) DIC; (c) DOC; (d) TN; (e) SiO₂.



species, irrespective of vegetation zone and lakewater depth, with the majority of these taxa having optima in the more alkaline range (Fig. 5b, Table 1) and occurring in small numbers in lakes that are low in DIC (Fig. 6).

Similar to other treeline studies (Laing et al. 1999; Pienitz and Smol 1993; Pienitz et al. 1995; Lotter et al. 1999), planktonic diatoms were more common in forested lakes. Planktonic *Cyclotella* taxa (most notably *Cyclotella stelligera* complex) and *Fragilaria* taxa (e.g., *Fragilaria nanana*, *Fragilaria crotonensis*, *Fragilaria tenera*) reached their highest abundances in boreal forest lakes. *Cyclotella* taxa are generally known to occur in greater abundance in lakes with forested catchments, partly because of the deeper lakes found in this ecozone (Pienitz and Smol 1993). However, in this study, no clear trend in lake depth was observed across ecozones, as some of the deepest lakes (15–20 m) occurred in all three ecozones (Rühland 2001). Although results of SIMPER indicated that the *Cyclotella stelligera* complex occurred in greater abundance within forested lakes, they often reached high abundances in the arctic tundra as well (e.g., Fig. 2a). Plotting the percentages of *Cyclotella* taxa against increasing lake depth for the 77 sites, a clear pattern emerges for increasing abundances as lake depth increases (Fig. 3a).

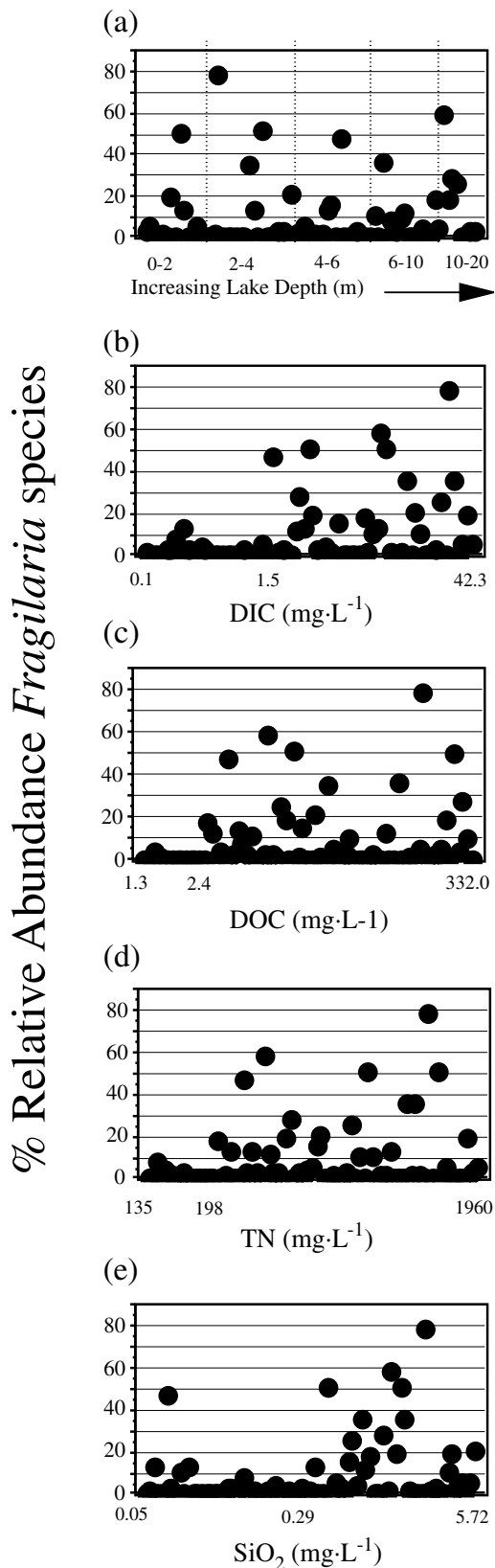
Apart from lake depth, it is difficult to decipher a clear environmental trend in the distribution of *Cyclotella stelligera* (Figs. 3b–3e), as these diatoms appear to be generalists in terms of their preference for our measured variables. The higher abundances of *Cyclotella* taxa in lakes with forested catchments may be due to ecological factors that were not measured, but are related to climate and lake depth. For example, several recent studies have reported a relative increase in *Cyclotella stelligera* (*Cyclotella pseudostelligera*, *Cyclotella glomerata*) over the past ~200 years (Sorvari and Korhola 1998; Sorvari et al. 2002; Rühland 2001; Cremer et al. 2001a, 2001b). These studies suggest that recent (19th century) climatic warming may have resulted in longer ice-free periods (longer growing season) and longer and more stable thermal stratification (particularly in deeper lakes) that would favour these planktonic diatoms.

Heavily silicified *Aulacoseira* taxa, such as *Aulacoseira lirata* and *Aulacoseira perglabra*, are believed to flourish in deeper arctic tundra lakes where the open landscape provides higher wind-induced turbulence that is required to maintain their position in the photic zone (Wilson et al. 1993; Korhola et al. 1996; Sorvari and Korhola 1998). Our results agree well with this observation, as *Aulacoseira* species tended to be more common in deeper arctic tundra lakes (Fig. 2b, Fig. 4a) that had lower DIC (Figs. 4b and 6) and higher SiO₂ (Fig. 4e).

Diatom distributions in relation to DIC, TN, and DOC gradients

The clearest trends in the distribution of diatom taxa for this study appear along the DIC, TN, and DOC gradients. For the most part, diatom distribution patterns along these three important gradients were similar, suggesting that the diatoms are responding to a combination of these and other related variables. Some notable differences between the influence of these variables on diatom distributions include a more pronounced decrease in *Achnanthes marginulata*,

Fig. 5. Trends in the percent relative abundance of *Fragilaria* taxa (*Fragilaria pinnata*, *Fragilaria construens*, *Fragilaria construens* var. *venter*, *Fragilaria pseudoconstruens*) across measured environmental gradients: (a) depth; (b) DIC; (c) DOC; (d) TN; (e) SiO₂.



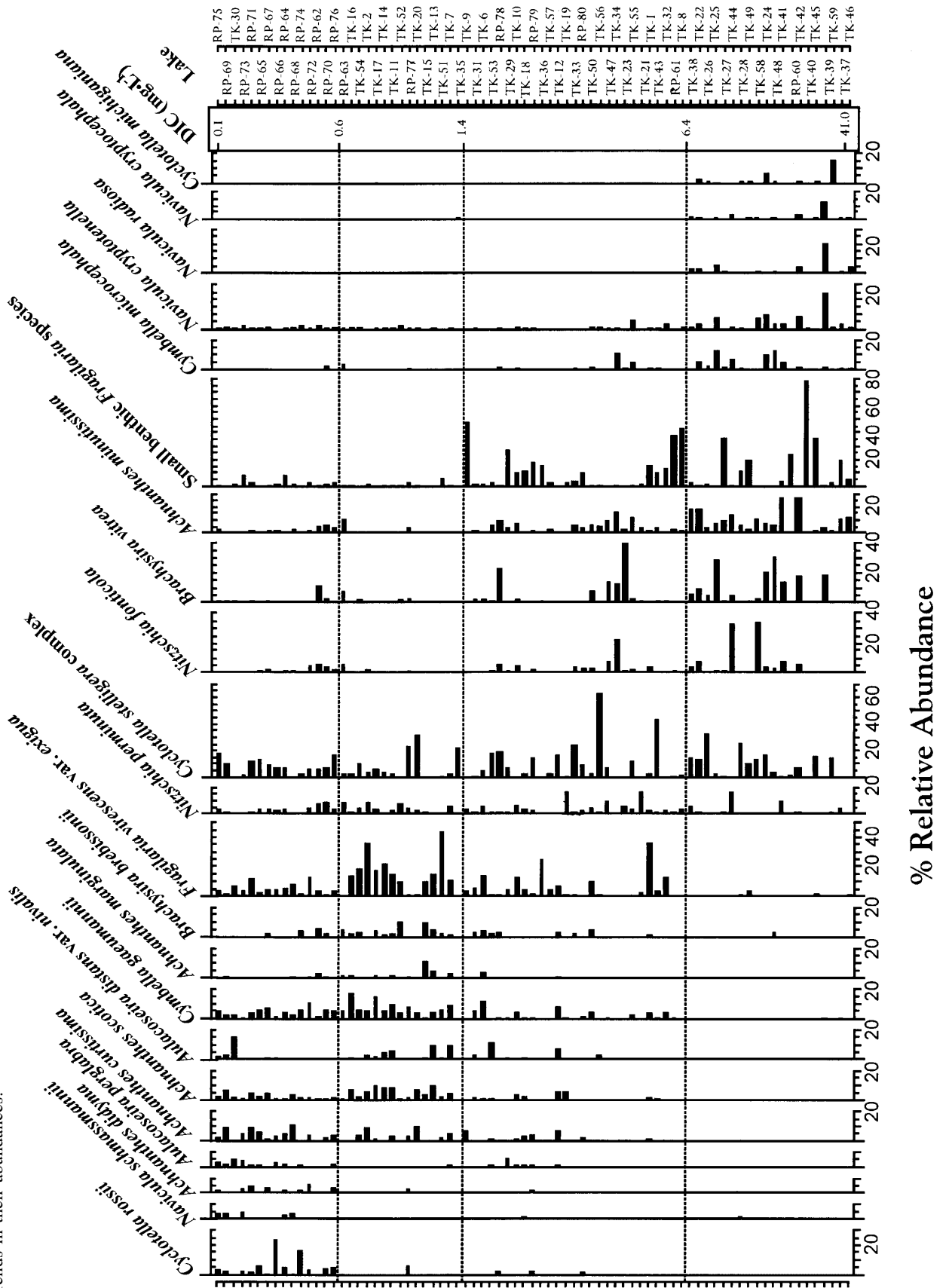
Achnanthes scotica, and *Cymbella gaeumannii* with increases in TN and DOC, than with increases in DIC (Rühland 2001). As well, *Fragilaria virescens* var. *exigua* (a common diatom in this lakeset) has a clear preference for lakes with low DIC, and is almost absent in lakes with values $> 3.5 \text{ mg}\cdot\text{L}^{-1}$ DIC (Fig. 6). No such trend was observed with respect to TN or DOC (Rühland 2001).

Figure 6 illustrates the distribution of the most common diatom taxa along a gradient of DIC, arranged from low to high weighted average optima (along the x -axis) and lakes arranged from low to high measured DIC along the y -axis. As there was a high degree of similarity in the diatom patterns, distributions of common taxa along TN and DOC gradients are not shown here but are given in Rühland (2001). Weighted average optima for ecologically important measured variables (DIC, TN, DOC, depth, and SiO₂) for common taxa are given in Table 1. Many of the diatom species showed clear optima to these measured environmental variables. For example, taxa towards the left of Fig. 6 are more common in lakes with low DIC (values $< 2.4 \text{ mg}\cdot\text{L}^{-1}$; arctic tundra lakes = 65% and forest-tundra lakes = 32%). These taxa include *Cyclotella rossii*, *Navicula schmassmannii*, *Aulacoseira perglabra*, *Achnanthes curtissima*, *Achnanthes scotica*, and *Aulacoseira distans* var. *ivalis*, which become increasingly rare in lakes with higher DIC concentrations. Diatoms that were more commonly found in lakes on the higher end of the DIC gradient ($\sim 3.5\text{--}42.3 \text{ mg}\cdot\text{L}^{-1}$; 95% in the boreal forest) included *Cyclotella michiganiana*, *Navicula cryptocephala*, *Navicula radiosa*, *Navicula cryptotenella*, *Cymbella microcephala*, and *Fragilaria pinnata*. Diatom taxa that appeared to have a broader tolerance to DIC commonly occurred along the entire range of the measured gradient including the *Cyclotella stelligera* complex, *Nitzschia perminuta*, and *Achnanthes minutissima* (Fig. 6).

The distribution of taxa in relation to TN showed a clear latitudinal trend. Diatom taxa with higher TN optima included *Navicula cryptocephala*, *Navicula radiosa*, *Navicula cryptotenella*, *Cyclotella michiganiana*, *Nitzschia palea*, *Brachysira vitrea*, *Cymbella microcephala*, and *Achnanthes minutissima*. These taxa were found in highest abundances in lakes with TN values ranging from 633 to 1960 $\mu\text{g}\cdot\text{L}^{-1}$ (95% of which were in the boreal forest). Diatom taxa that were clearly absent in lakes with higher TN concentrations had TN optima near the lower end of the gradient and included *Achnanthes marginulata*, *Achnanthes curtissima*, *Cymbella gaeumannii*, and *Cyclotella rossii*. These taxa were found in highest abundances in lakes with low TN concentrations ranging from 135 $\mu\text{g}\cdot\text{L}^{-1}$ to 300 $\mu\text{g}\cdot\text{L}^{-1}$ (80% of which were in the arctic tundra). Taxa that appeared to have no particular preference to TN included the *Cyclotella stelligera* complex and *Nitzschia perminuta*.

Boreal forest lakes generally had higher values of DOC (mean = 49.2 $\text{mg}\cdot\text{L}^{-1}$) than arctic tundra lakes (mean = 2.9 $\text{mg}\cdot\text{L}^{-1}$). Lakes with lower DOC (1.3 to 10.3 $\text{mg}\cdot\text{L}^{-1}$; 40 lakes, 70% arctic tundra, 17.5% forest-tundra, 12.5% boreal forest) were commonly dominated by *Achnanthes marginulata*, *Achnanthes scotica*, *Achnanthes curtissima*, *Achnanthes didyma*, *Achnanthes lacus-vulcani*, *Achnanthes suchlandtii*, *Cymbella gaeumannii*, *Navicula schmassmannii*, and *Fragilaria brevistriata*. Diatom taxa that had greater abundances in high DOC lakes (10.3 $\text{mg}\cdot\text{L}^{-1}$ to 80.0 $\text{mg}\cdot\text{L}^{-1}$;

Fig. 6. Distribution of the most common diatom taxa encountered in the 77 lakes, expressed as percent relative abundances along the measured gradient of dissolved inorganic carbon (DIC). Taxa were arranged in increasing order (left to right) of their estimated weighted average (WA) optima to DIC; sites were arranged in increasing order (top to bottom) for their measured DIC values. *Cyclotella stelligera* complex (*Cyclotella stelligera* and *Cyclotella pseudostelligera*) were grouped as a complex, as many were difficult to distinguish. Small, benthic *Fragilaria* species (*Fragilaria construens*, *Fragilaria construens* var. *venter*) were treated as a complex as they showed similar trends in their abundances.



2.8% arctic tundra, 28% forest tundra, 69.2% boreal forest) included *Nitzschia fonticola*, *Cymbella microcephala*, *Brachysira vitrea*, *Achnanthes minutissima*, *Navicula cryptotenella*, *Nitzschia palea*, *Cyclotella michiganiana*, *Navicula radiosa*, and *Navicula cryptocephala*. Diatom taxa that appeared to be generalists in terms of their preference for DOC included the *Cyclotella stelligera* complex and *Nitzschia perminuta*.

Conclusions

Distinct diatom assemblages characterize treeline ecozones in the Central Canadian Arctic, with significant differences between boreal forest lakes and arctic tundra and the forest tundra lakes. In general, trends in diatom distributions were similar to circumpolar treeline studies from other regions, with the following notable exceptions: (i) high abundances of small benthic *Fragilaria* taxa were not found exclusively in arctic tundra lakes; and (ii) small planktonic *Cyclotella* species were more common in boreal forest lakes, but also occurred in high abundances in deeper lakes irrespective of ecozone. These differences can best be explained by the lack of a clear trend in lake depth across ecozones together with the more alkaline nature of boreal forest lakes. As small benthic *Fragilaria* taxa tended to be more common in higher DIC lakes, they were found in higher abundances in the boreal forest. Similarly, *Cyclotella* taxa had a clear preference for deeper lakes and therefore were found in relatively high abundance in all ecozones.

Aside from these differences, diatom assemblages were similar to diatom floras recorded in other circumpolar treeline studies. For example, shifts in species composition across the treeline ecozones were closely associated with differences in the limnological characteristics (in particular, DIC, DOC, and TN). This suggests that, despite regional differences, diatom assemblage composition at circumpolar treeline is influenced by mutual environmental gradients that result in similarities in treeline diatom assemblages. These diatom-based calibration sets from different treeline regions may be similar enough to be merged. The expansion and refinement of existing diatom-based training sets will improve our understanding of diatom autecology and the relationships between measured limnological variables and modern diatom distributions, as well as increase the measured ecological gradients in which treeline diatoms occur. This has the potential for strengthening inference models and producing more reliable estimates of past environmental change from paleoecological studies in boreal and tundra ecosystems.

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Appendix on next page.

Appendix A

Fig. A1. 1–3: *Achnanthes acares*; 4–7: *Achnanthes curtissima*; 8–10: *Achnanthes carissima*; 11: *Achnanthes rossii*; 12: *Achnanthes minutissima*; 13–17: *Achnanthes lacus-vulcani*; 18–19: *Achnanthes pusilla*; 20–22: *Achnanthes marginulata*; 23–26: *Achnanthes scotica*; 27–28: *Achnanthes suchlandtii*; 29: *Tabellaria flocculosa* (str. III sensu Koppen); 30–31: *Tabellaria flocculosa* (strain IV sensu Koppen); 32: *Eunotia rhynchocephala*; 33: *Eunotia praerupta*; 34–35: *Eunotia faba*; 36–40: *Fragilaria virescens* var. *exigua*; 41–42: *Fragilaria pseudoconstruens*; 43–45: *Fragilaria brevistriata*; 46–48: *Fragilaria pinnata*; 49–53: *Fragilaria construens* var. *venter*.

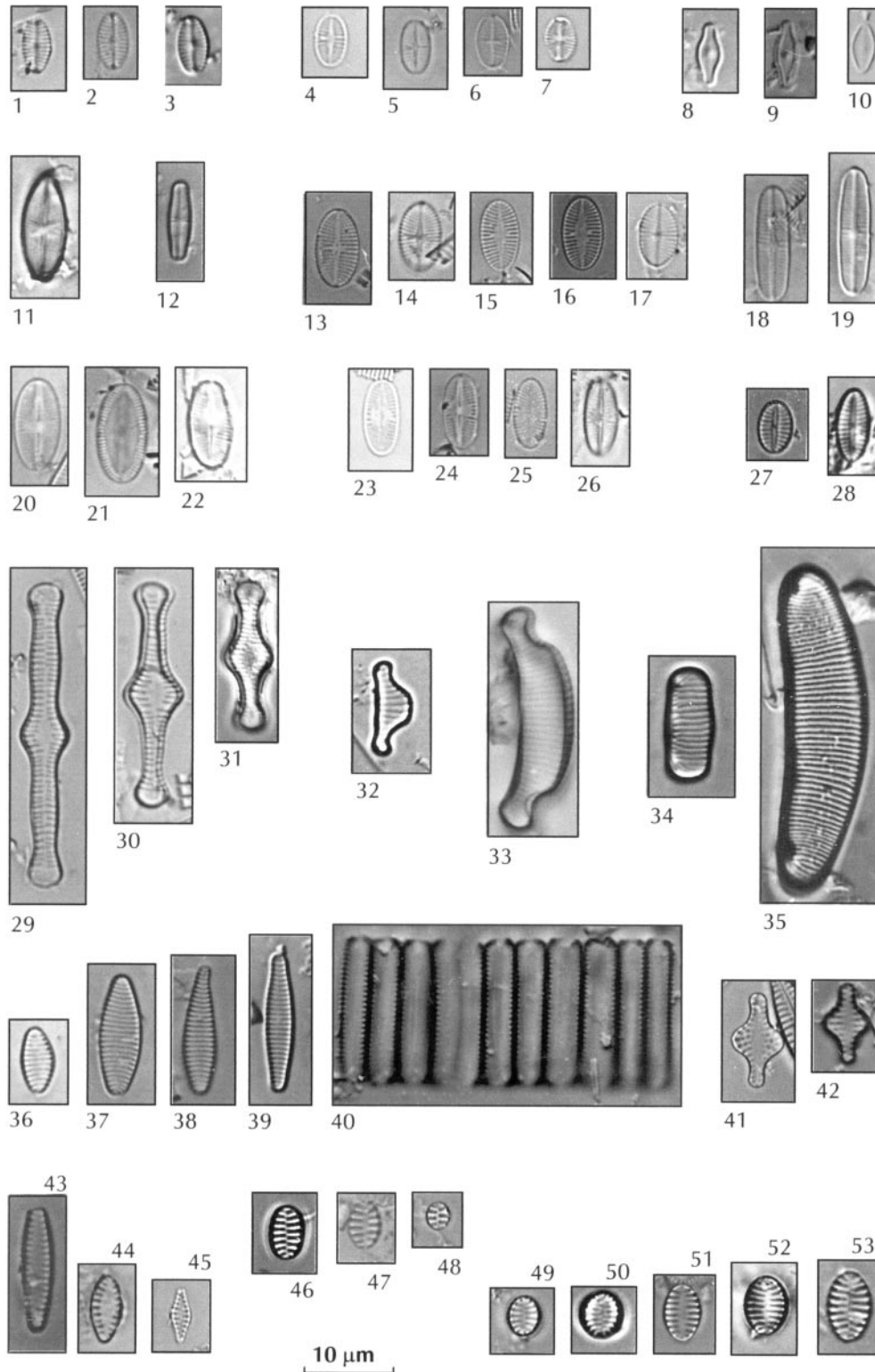


Fig. A2. 54–55: *Cyclotella rossii*; 56–59: *Cyclotella ocellata*; 60–62: *Cyclotella tripartita*; 63: *Cyclotella michiganiana*; 64–65: *Cyclotella radiosa*; 66–70: *Cyclotella stelligera* complex; 71–73: *Aulacoseira perglabra* var. *floriniae*; 74–77: *Aulacoseira distans* var. *nivalis*; 78: *Aulacoseira distans*; 79–82: *Aulacoseira lirata*; 83–86: *Aulacoseira lirata* var. *biseriata*; 87–89: *Aulacoseira perglabra*.

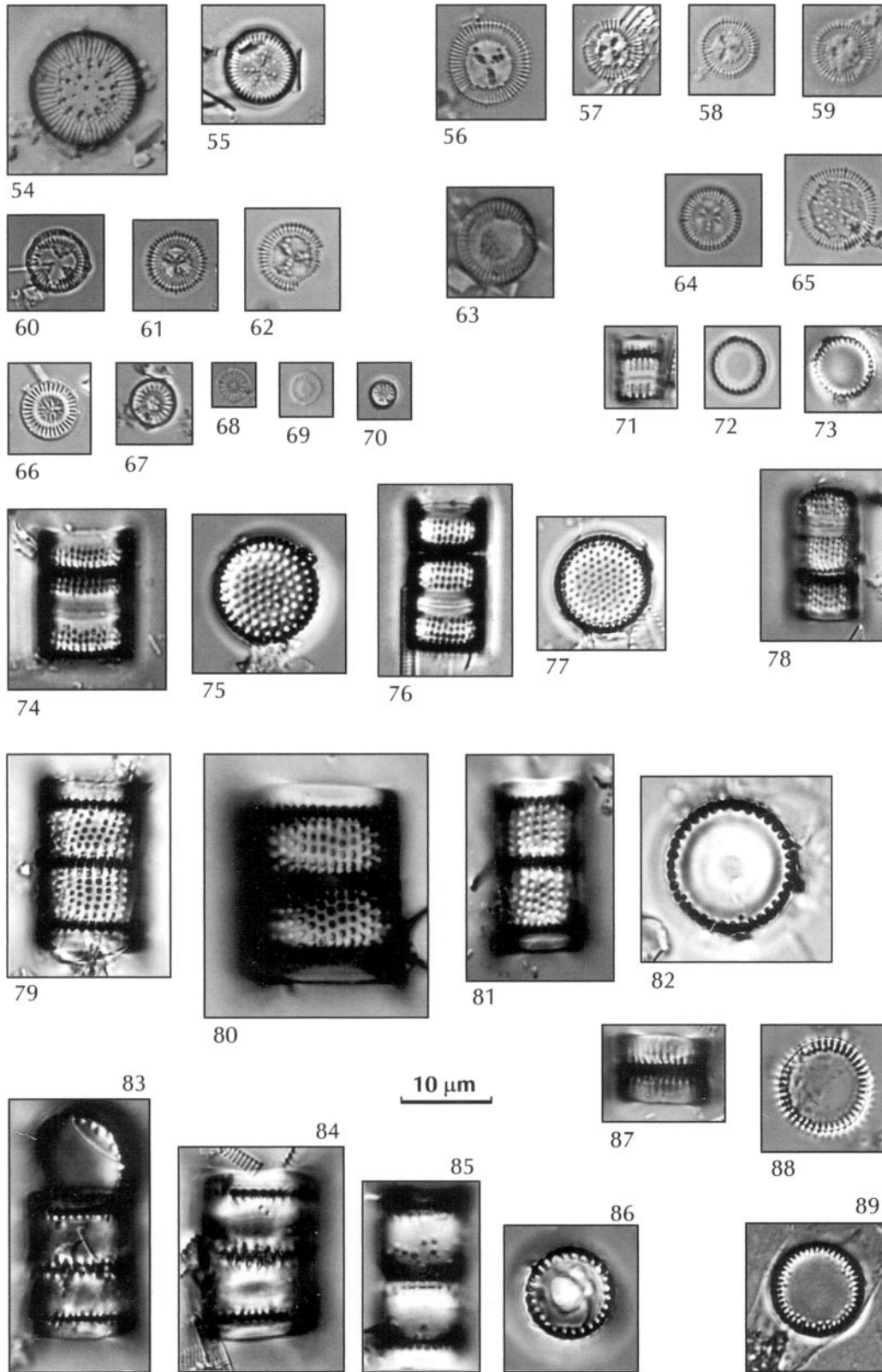


Fig. A3. 90: *Navicula jaagii*; 91: *Navicula bryophila*; 92: *Navicula subtilissima*; 93: *Navicula pseudostauron*; 94–96: *Navicula cocconeiformis*; 97–98: *Navicula pseudoscutiformis*; 99–101: *Navicula kuelbsii*; 102–105: *Navicula seminulum*; 106–108: *Navicula submuralis*; 109–111: *Navicula minima*; 112–113: *Navicula schmassmannii*; 114–115: *Navicula mediocris*; 116: *Navicula disjuncta*; 117–118: *Navicula pupula*; 119: *Neidium ampliatum*; 120–122: *Brachysira brébissonii*; 123: *Brachysira vitrea*; 124–125: *Pinnularia interrupta*; 126: *Nitzschia frustulum*; 127: *Nitzschia fonticola*; 128–129: *Nitzschia perminuta*.

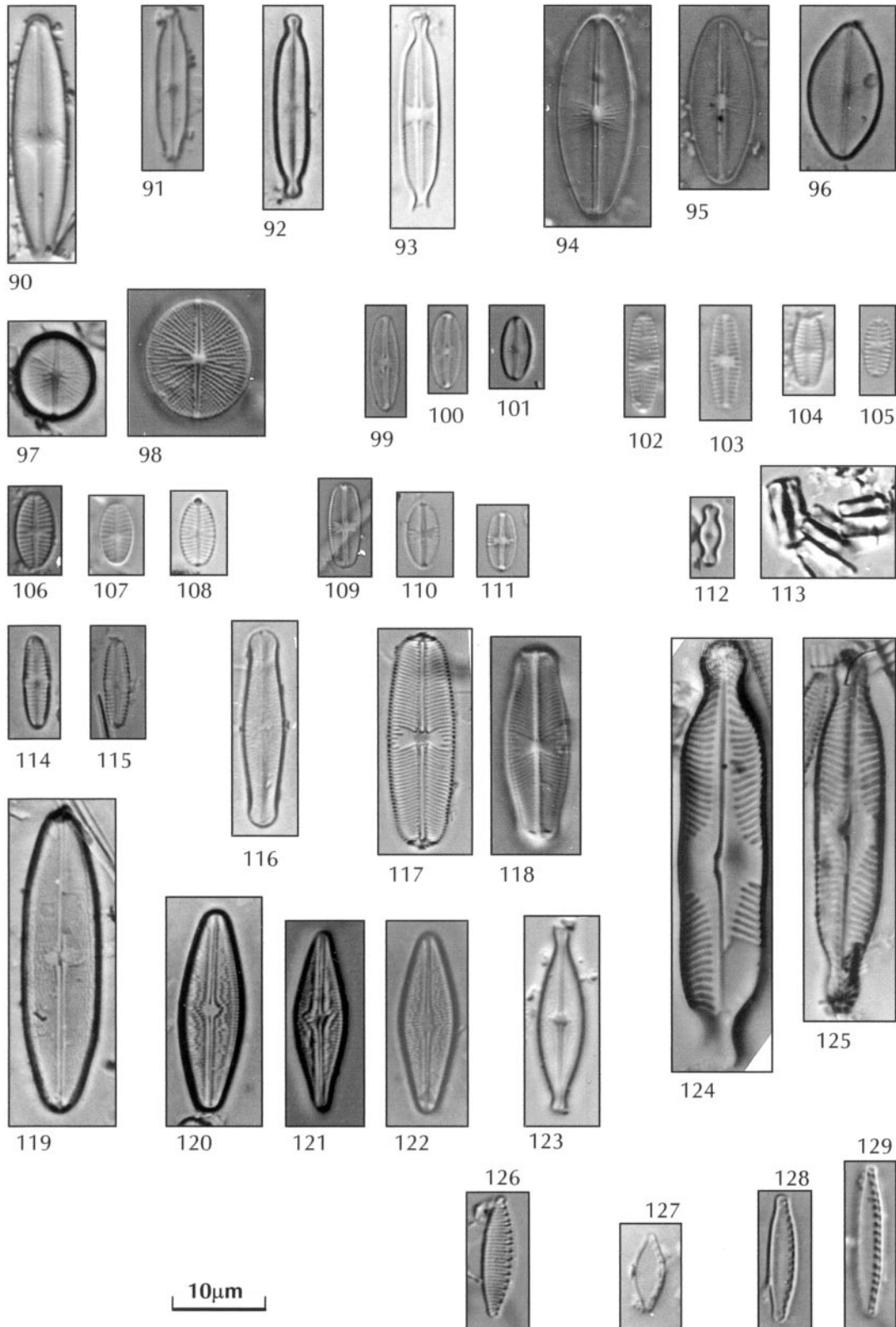


Fig. A4. 130: *Cymbella angustata*; 131: *Cymbella incerta*; 132: *Cymbella cesatii*; 133–134: *Cymbella gracilis*; 135–136: *Cymbella hebridica*; 137–138: *Cymbella silesiaca*; 139: *Cymbella microcephala*; 140–142: *Cymbella gaeumannii*; 143: *Gomphonema parvulum*; 144: *Frustulia rhomboides*; 145: *Frustulia rhomboides* var. *crassinervia*; 146: *Frustulia rhomboides* var. *saxonica*; 147: *Stauroneis anceps*.

