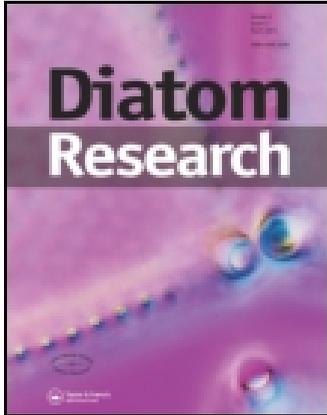


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# FRESHWATER DIATOM ASSEMBLAGES FROM 23 LAKES LOCATED NEAR NORILSK, SIBERIA: A COMPARISON WITH ASSEMBLAGES FROM OTHER CIRCUMPOLAR TREELINE REGIONS

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Knowledge of the composition and ecological preferences of diatom assemblages in northern regions is important for paleoenvironmental reconstructions of variables related to climate and/or anthropogenic disturbances. Relatively little is presently known about diatoms from circumpolar treeline areas, especially for lakes located in northern Russia. Our study set included lakes in the Siberian tundra, forest-tundra, and boreal forest regions close to Norilsk, of which nine sites were subject to anthropogenic disturbances, such as mining and housing developments. We enumerated surficial sediment diatom assemblages and used multivariate statistical techniques to investigate which environmental variables were important in explaining the variation in diatom assemblages within our lake set. Deeper lakes were associated with higher abundances of planktonic centric taxa, such as *Cyclotella* Kützing species. Warmer, higher conductivity forested lakes were associated with higher abundances of planktonic pennate taxa, such as *Fragilaria nanana* Lange-Bertalot. Diatom assemblages in the colder tundra lakes were significantly different from those in forested regions, and were dominated by small benthic *Fragilaria* Lyngbye species. Disturbed lakes near the Norilsk smelters exhibited slightly higher metal (Cu) concentrations and conductivities, and were associated with pollution-tolerant *Nitzschia* Hassall taxa, as well as species associated with higher electrolyte concentrations, such as *Navicula capitata* Ehrenberg. However, in comparison with diatom assemblages from other regions of intense mining (e.g. Sudbury, Canada), the assemblages appear relatively unaffected by mining activities, most likely reflecting the suppression of aqueous metal concentrations due to the alkaline nature of these lakes. Overall, diatom assemblages were very similar to those found in northern Canadian and Fennoscandian lakes, suggesting that the Siberian taxa are representative of a circumpolar arctic diatom flora.

## INTRODUCTION

Knowledge of the floristic diversity of aquatic ecosystems in circumpolar treeline regions is important as baseline data in light of the significant temperature changes predicted for these regions

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under global warming scenarios (Kattenberg *et al.* 1996). Furthermore, little is known about aquatic ecology in Siberia, in part because of the difficulties associated with collecting samples in these remote northern regions (Foged 1993). Most of the limnological research in Siberia has focussed on Lake Baikal, a deep rift valley lake in central Siberia, which is characterized by a high abundance of endemic planktonic diatom species (e.g. Skvortzow 1937, Nikiteeva & Likhoshway 1994, Edlund *et al.* 1995, Flower *et al.* 1995, Stoermer *et al.* 1995, Likhoshway 1996, Julius *et al.* 1997). However, it remains uncertain if diatom assemblages in different areas of Siberia, such as in lakes within the northern treeline region, are distinct from aquatic assemblages reported from other circumpolar regions. In this study, we present the most abundant diatom taxa found in a set of lakes within the treeline region near Norilsk, Siberia, and compare our species assemblages to those found in other treeline calibration sets from northern Canada and Fennoscandia.

The circumpolar treeline region is an important area in which to study the relationship between climatic change and ecosystem response, as climatic gradients are particularly steep here and vegetation growth is closely tied to climatic factors, such as temperature and precipitation (Timoney *et al.* 1992). Lakes within the northern treeline region display a gradient in environmental variables related directly to climate, such as temperature (Pienitz *et al.* 1995a, Weckström *et al.* 1997a), and indirectly to climate, such as dissolved organic carbon (DOC) (Pienitz & Smol 1993), which appears to be primarily derived from catchment vegetation in these study regions. Previous studies have shown that diatom communities respond to these climatic factors, and thus past climatic changes can be tracked through analysing changes in diatom assemblages (Smol *et al.* 1991, 1995, MacDonald *et al.* 1993, Pienitz & Smol 1993, Pienitz *et al.* 1995a,b). Such applications require an estimation of the environmental optima and tolerances of taxa, so that accurate reconstructions of past environments will be possible.

Lakes in our study region are also affected by factors other than climate. Norilsk is a major mining and smelting centre, and has recently been identified as the largest point source of pollution in the world (Bouillon 1995). Consequently, there is considerable interest to determine if lakes in this area have undergone environmental degradation. Paleolimnological studies in other areas affected by mining activities indicate that diatom assemblages respond to changes in water quality associated with the transport and deposition of airborne pollutants, resulting in heavy metal contamination and lake acidification (Dixit *et al.* 1987, 1991, 1992). An additional objective of our study was to identify diatom species in our sample lakes that may be potential indicators of anthropogenic disturbances.

The focus of this paper, therefore, is threefold. First, are the diatom assemblages in the Norilsk lakes similar to assemblages collected in other circumpolar treeline regions? To answer this question, we present a floristic comparison of the most common diatom taxa found in a set of lakes within the treeline region near Norilsk, Siberia and their counterparts collected in Scandinavia and northern Canada. Second, are diatom assemblages in lakes within contrasting vegetational zones (e.g. forest vs. tundra) significantly different, and if so, which variables influence the distribution of the assemblages within the treeline region near Norilsk? We use multivariate statistical techniques to evaluate the relationship between measured environmental variables and surficial sediment diatom assemblages. Third, are diatom assemblages in lakes close to Norilsk influenced by mining and smelting activities? We compare our species assemblages with those found in other regions of intense mining (e.g. Sudbury, Canada).

### Previous taxonomic work in Russia

Skvortzow (1929, 1937, 1938a–c) published floristic papers from a variety of Russian sites, ranging from Vladivostok in the far southeast, to Lake Baikal in central Siberia. For each taxon, he provided measurements, frequency of occurrence, and locations in which species were found.

Skvortzow & Meyer (1928) also published a list of diatom species found from Lake Baikal, documenting many benthic taxa that they classified as endemics.

Sabelina *et al.* (1951) published an extensive review of freshwater diatoms from the former USSR. Descriptions included some details on the distribution of diatoms, as well as ecological information and line drawings for each taxon.

Loseva (1982, 1992) has published two atlases focussing mostly on freshwater (1982) and marine (1992) diatom assemblages of northeastern European regions. Taxonomic descriptions, photographic plates, and some distributional and autecological information were included for each taxon. In addition, she has published several papers documenting the Russian diatom flora from the Pleistocene, such as Loseva (1997), which provides plates of the characteristic diatoms from freshwater Pleistocene deposits in northeastern Europe, and Loseva (1983), which provided a record of diatom assemblages from Upper Pleistocene deposits from the Shapkina River.

Foged (1993) collected diatoms from 11 sites during a tour along the Transiberian Railway, which included the Lake Baikal region. Ecological information for each taxon was classified according to Hustedt's (1927–1966) pH categories and the halobian spectrum.

Recent taxonomic work has focussed on the revision and description of unique Lake Baikal planktonic diatom species (e.g. Flower 1993, Edlund *et al.* 1996). Other publications of interest include Proschkina-Lavrenko *et al.* (1974) and Makarova *et al.* (1988), both of which focussed on recent and fossil diatoms of the former USSR.

### Study sites

Norilsk (69°N, 88°E) is located on the southern portion of the Taymyr Peninsula, central northern Siberia, Russia (Fig. 1). Climate in the Norilsk region is continental, reflected in the large differences between mean January (–28 to –36°C) and mean July (8 to 12°C) temperatures (World Meteorological Organization 1981). The duration of the ice-free season for lakes near Norilsk is poorly documented, but most likely comparable to similar climatic regions in northern Canada where forested lakes remain ice-free for approximately 4 months and tundra lakes approximately 2–3 months (Pienitz *et al.* 1997). Annual precipitation is relatively low, ranging from 20 to 40 cm. The sample lakes in the Norilsk region are located on the Siberian platform. The surficial geology is primarily dominated by shallow-water carbonate and terrigenous sedimentary rocks (Kunilov 1994), as well as glaciofluvial sediments deposited during the late Pleistocene (Zarkhidze *et al.* 1991). Soils range from gleysols in the tundra zone to podzols in the northern boreal forest (Symons *et al.* 1983). The vegetation is characteristic of a low arctic shrub tundra, composed mostly of heaths, sedges, herbs, and dwarf trees such as alder (*Alnus crispa* = *Alnaster fruticosa*), dwarf birch (*Betula nana*) and shrub willow (*Salix arctica*) (Clayden *et al.* 1996). Forest-tundra sites are characterized by scattered larch trees (*Larix sibirica*) and *B. nana*, with rare occurrences of spruce (*Picea obovata*) and tree birch (*B. pubescens*). The northern boreal forest is dominated by *L. sibirica*, with some *P. obovata* and *B. pubescens*.

Our sample set of 23 lakes was chosen to include lakes in three ecoclimatic (vegetational) zones within the treeline region (defined as the boundary between the forest-tundra and tundra zones, *sensu* Payette 1983). Seven lakes (TS 1–3, 20–23) were located in the tundra region, 8 lakes (TS 4–11) were located in the forest-tundra zone, and an additional 8 lakes (TS 12–19) were located in the boreal forest region. The transitional zone from boreal forest to tundra is relatively narrow in the Norilsk area (20 to 60 km in width), and the sampled lakes were located between 68°09.9' and 70°22.6'N, and between 86°33.4' and 88°26.7'E.

Limnological characteristics of the sample lakes are described in detail elsewhere (Duff *et al.* 1999), and are summarized in Table 1. Lakes in our sample set are generally oligotrophic, dilute,

relatively shallow (mean depth = 4.8 m), and alkaline (mean pH = 8.0). Forest lakes typically were characterized by higher temperatures, DOC and DIC (dissolved organic and inorganic carbon), and conductivity values compared to tundra lakes. Nine of the sites (five forest and four tundra lakes) were located close to mining and housing developments near Norilsk, and were classified as “disturbed”. These lakes commonly had higher conductivity values and metal concentrations (e.g. Fe, Mn) in comparison with other lakes in the data set.

Table 1. Selected limnological variables for the 23 lakes sampled near Norilsk, Russia between 28 July and 5 August 1993. Measurements represent single-point samples taken during the ice-free season for each lake.

Variable	Tundra		Forest-tundra		Forest	
	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD
Temp ( $^{\circ}$ C)	8.0–12.7	10.4 $\pm$ 1.6	9.2–13.5	11.0 $\pm$ 1.3	13.7–15.2	14.7 $\pm$ 0.5
Depth (m)	2.8–11.5	5.1 $\pm$ 2.7	3.0–11.0	6.7 $\pm$ 2.5	2.2–13.0	5.4 $\pm$ 3.3
Cu ( $\mu$ g L $^{-1}$ )	3.0–4.0	3.1 $\pm$ 0.4	2.0–6.0	2.5 $\pm$ 1.3	1.0–23.0	8.9 $\pm$ 6.9
pH	7.7–9.2	8.3 $\pm$ 0.6	7.5–8.2	7.8 $\pm$ 0.2	7.7–8.6	8.2 $\pm$ 0.3
Conductivity ( $\mu$ S cm $^{-1}$ )	20–91	41.6 $\pm$ 24.2	18–38	30.5 $\pm$ 5.9	35–210	92.9 $\pm$ 56.9
Secchi (m)	0.3–3.0	1.7 $\pm$ 0.8	1.4–3.5	2.6 $\pm$ 0.6	2.0–3.5	5.4 $\pm$ 3.3
Chlorophyll <i>a</i> ( $\mu$ g L $^{-1}$ )	0.7–14.4	4.1 $\pm$ 4.5	0.2–1.8	0.9 $\pm$ 0.6	0.3–5.6	1.5 $\pm$ 1.6
Dissolved TP ( $\mu$ g L $^{-1}$ )	4.1–19.9	8.8 $\pm$ 5.1	2.8–9.3	5.3 $\pm$ 1.8	3.1–8.7	5.2 $\pm$ 1.9
POC (mg L $^{-1}$ )	0.2–1.1	0.5 $\pm$ 0.27	0.2–0.3	0.2 $\pm$ 0.05	0.2–0.4	0.3 $\pm$ 0.08
PON ( $\mu$ g L $^{-1}$ )	46–171	82 $\pm$ 42	34–54	41 $\pm$ 7.1	36–76	50 $\pm$ 12
SiO $_2$ (mg L $^{-1}$ )	0.2–2.2	1.1 $\pm$ 0.6	0.9–2.0	1.4 $\pm$ 0.3	0.4–3.1	1.3 $\pm$ 0.9
DOC (mg L $^{-1}$ )	2.3–6.9	4.2 $\pm$ 1.5	2.1–4.0	3.7 $\pm$ 0.8	2.5–7.9	5.5 $\pm$ 1.7
DIC (mg L $^{-1}$ )	2.6–11.4	5.2 $\pm$ 3.0	3.4–6.5	5.1 $\pm$ 1.1	4.8–15.6	11.1 $\pm$ 4.6
SO $_4$ (mg L $^{-1}$ )	2.5–6.3	4.2 $\pm$ 1.3	1.6–3.9	3.2 $\pm$ 0.7	3.2–34.9	13.3 $\pm$ 12.2
Ca (mg L $^{-1}$ )	3.0–6.2	4.6 $\pm$ 1.4	3.5–8.8	6.4 $\pm$ 1.6	6.3–35.1	17.1 $\pm$ 9.5
Cl (mg L $^{-1}$ )	0.2–1.2	0.4 $\pm$ 0.3	0.1–0.5	0.3 $\pm$ 0.1	0.4–3.1	1.2 $\pm$ 1.0
Fe ( $\mu$ g L $^{-1}$ )	48–1800	363 $\pm$ 591	39–247	82 $\pm$ 66	17–198	83 $\pm$ 61
Mg (mg L $^{-1}$ )	1.2–2.4	1.7 $\pm$ 0.4	1.0–2.2	1.8 $\pm$ 0.4	1.9–7.6	4.3 $\pm$ 2.1
Mn ( $\mu$ g L $^{-1}$ )	7.6–43.5	17.4 $\pm$ 12.3	2.5–24.9	9.1 $\pm$ 6.8	1.1–24.5	10.2 $\pm$ 7.4
Na (mg L $^{-1}$ )	0.4–1.7	1.0 $\pm$ 0.5	0.3–0.7	0.5 $\pm$ 0.1	0.8–9.1	3.1 $\pm$ 3.2
Sr ( $\mu$ g L $^{-1}$ )	8.0–17.7	12.2 $\pm$ 2.9	6.9–17.2	12.8 $\pm$ 3.3	19.1–156	73.0 $\pm$ 52.5

## MATERIALS AND METHODS

### Sampling strategy

Samples from the 23 lakes were collected between 28 July and 5 August 1993 (Fig. 1). A complete description of the methods used for limnological and chemical analyses is outlined in Duff *et al.* (1999). In brief, limnological variables for each lake included surface water temperature, pH, Secchi depth, conductivity, and water depth measured at the lake centre. Samples for water chemistry analyses (e.g. nutrients, major ion and trace metal concentrations) were also collected at the centre of each lake, and treated in the field according to procedures outlined in the Analytical Methods Manual (Environment Canada 1994a,b). Surface sediment samples were collected from the deepest part of each lake using a gravity corer (Glew 1991). The upper 0.5 cm of sediment was analysed for diatoms.

### Diatom counts

Diatom sample preparation followed techniques outlined in Wilson *et al.* (1996). A sub-sample of wet sediment (about 0.2 g) was boiled in a 50:50 mixture of  $\text{HNO}_3$  :  $\text{H}_2\text{SO}_4$  to digest the organic material, and then rinsed several times to remove the acid residue. An aliquot of the resulting sediment slurry was resuspended in distilled water, evaporated onto coverslips, and mounted onto slides using Naphrax<sup>®</sup> mounting medium (R.I. = 1.74).

Diatom assemblages on each slide were analysed following counting procedures detailed in Kingston (1986). Every diatom within a field of view was identified and counted along random transects across the slide. At least 300 diatom valves were identified per sample, and the results were expressed as relative abundances (%). To aid in identifications, a large number of light micrographs were taken using a Wild Photoautomat MPS45 camera system attached to a Leica DMRB light microscope under a 100X oil immersion lens (N.A. = 1.3).

### Statistical analyses

Multivariate statistical analyses, performed by the computer program CANOCO version 3.12 (ter Braak 1988, 1990), were used to identify relationships between the measured environmental variables and the species assemblages found in the 23 lakes. Our calibration model included a total of 118 diatom taxa, using a cut-off criterion of  $\geq 1\%$  relative abundance in at least one lake. Because of space constraints and the limitations of inferring ecological preferences for rare taxa, we present here information for only the 52 most abundant diatom taxa (i.e. taxa with a relative abundance  $\geq 2\%$  in at least one lake).

A Detrended Correspondence Analysis (DCA) indicated that the gradient length for Axis 1 was 2.45. Gradient lengths of this value fall into the grey area between linear-based models (gradient length  $< 2$ ) and unimodal-based models (gradient length  $> 4$ ; ter Braak 1995). We compared the strength of both types of models by examining the percent of variation in species assemblages explained using linear models (Redundancy Analysis, RDA) and unimodal models (Canonical Correspondence Analysis, CCA). As CCA explained more of the variation in the species assemblage data (Axis 1 :  $\lambda = 0.24$ , total inertia = 2.18, variance explained = 11.1%) compared to RDA (Axis 1 :  $\lambda = 0.10$ , total inertia = 1.00, variance explained = 10.1%), we chose unimodal models. In addition, a comparison of species abundance curves in relation to the strongest gradient (depth) revealed that the majority of the diatom taxa showed a unimodal response curve, indicating this procedure was most appropriate for ordination (data not shown).

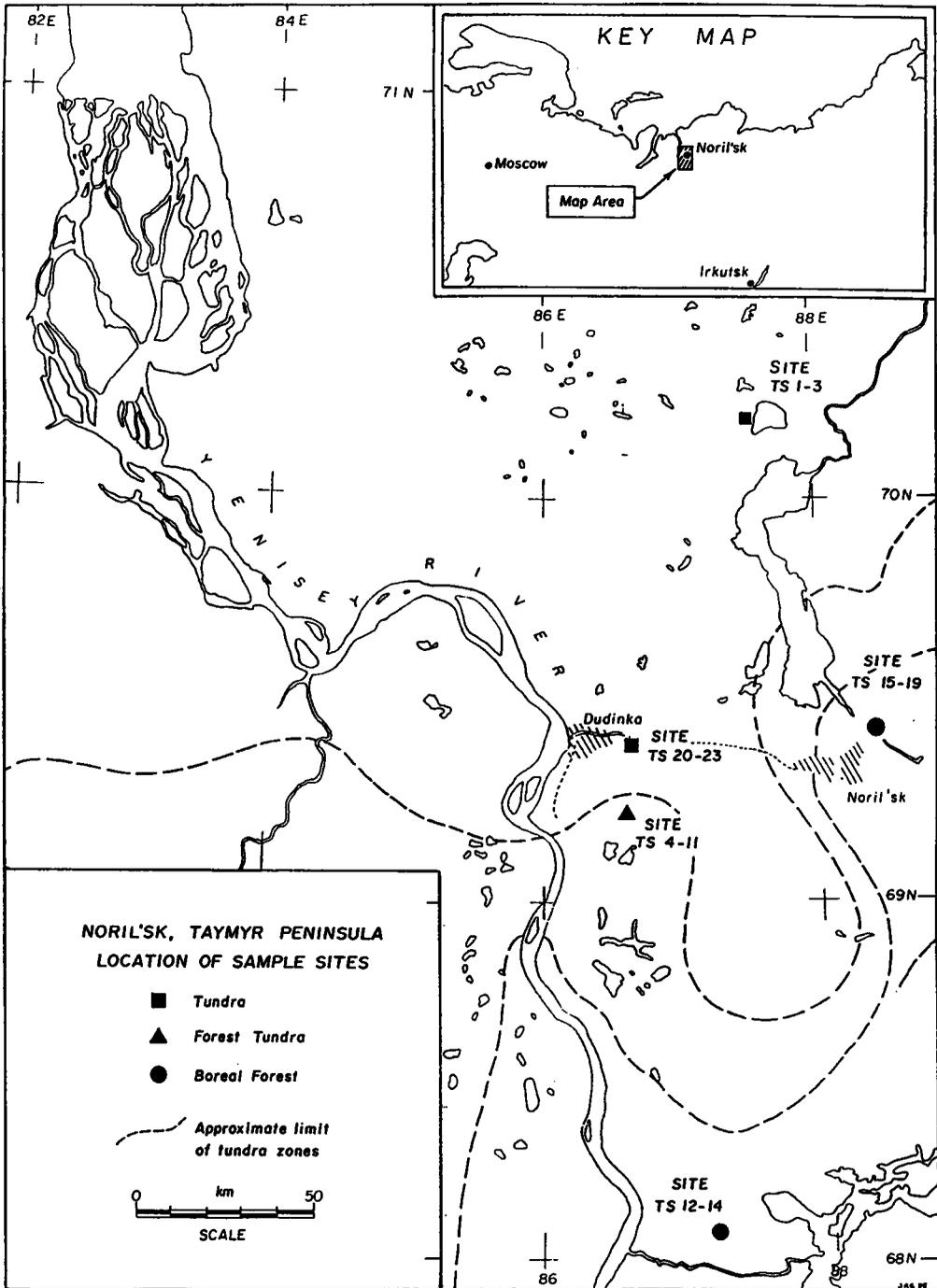


Fig. 1. Map showing location of 23 lakes sampled near Norilsk, Russia.

Canonical Correspondence Analysis (CCA), using forward selection and Monte Carlo permutation tests, was then used to identify variables which were significant in explaining the variation in the diatom assemblages (ter Braak & Verdonschot 1995). Species data were square-root transformed and rare taxa were down-weighted in order to maximize the signal:noise ratio within the data set. Centroids of site scores for the forest, forest-tundra, and tundra lakes were plotted to identify which species assemblages were common in each vegetation category. The computer program WACALIB version 3.3 (Line *et al.* 1994) was used to calculate abundance-weighted means (AWMs) for the 52 most abundant diatom taxa for significant variables identified by forward selection. We also calculated AWMs for conductivity, an ecologically important variable that explained a significant proportion of the diatom species assemblage variability in a CCA constrained to a single variable, but was not forward selected. Due to the small number of lakes ( $n = 23$ ), AWM values should be considered as approximate estimates of environmental optima.

We also used the computer program PRIMER (Clarke & Warwick 1994) to test whether diatom assemblages in each vegetational zone were significantly different from each other using analysis of similarity (ANOSIM), a non-parametric permutation test. ANOSIM functions as a multivariate equivalent of a one-way ANOVA (Clarke & Warwick 1994), and is based on comparisons of rank similarities between and within sample groups. By using pair-wise comparisons of different groups of samples (e.g. forest sites vs. tundra sites), the degree of separation of groups (the R statistic) can be calculated (Clarke & Warwick 1994). The significance of the R statistic can be tested using permutation tests, with an R value significantly greater than zero indicating that the similarities within groups are greater than those between groups. We compared our p-values for each comparison against a Bonferroni-adjusted critical probability to account for the multiplication of Type I errors when using multiple pair-wise comparisons (Sokal & Rohlf 1995). We then identified which diatom taxa were important in determining inter-group differences using the PRIMER program SIMPER, which computes the average dissimilarity between inter-group samples, then assesses the separate contributions to this dissimilarity for each species (Clarke & Warwick 1994).

## RESULTS

### Descriptions of problematic taxa

In order to maintain taxonomic consistency with previous studies and facilitate comparisons with diatom assemblages from other circumpolar treeline calibration sets, we have mainly followed the taxonomic scheme outlined in the “Süßwasserflora von Mitteleuropa” series (Krammer & Lange-Bertalot 1986–1991). Consistent taxonomy is essential for accurate inter-regional comparisons and use of species autecological information obtained from other studies. For validation of our species designations and to aid in comparisons with other work, we have included light micrographs of the 52 most abundant diatom taxa (see references to plates in Table 2). Taxonomic descriptions are only included for the 4 taxa that differed from published descriptions, or, to our knowledge, have not been previously described elsewhere.

#### *Amphora* sp. 1

Pl. 2, Figs 66, 67

This taxon appears similar to *Amphora staurosiioides* Loseva, reported from north-western Russia by Loseva (1997, figs 53, 54). However, we were unable to verify our specimens against the original taxonomic description for *A. staurosiioides*. *Amphora* sp. 1 has very fine striae which are

Table 2. Names, authorities and figure references for the 52 most abundant diatom taxa (relative abundance greater than 2% in at least one lake) in the Norilsk set of lakes, including a list of locations of other treeline calibration sets where each taxon has been previously recorded.

No	Taxon	Plate refs	Reports from other circumpolar regions *
1	<i>Achnanthes laterostrata</i> Hustedt	P1: 1, 2	AK, FE, FI, YE, YK
2	<i>Achnanthes minutissima</i> Kützing	P1: 3, 4	AK, FE, FI, LB, NT, WB, YE, YK
3	<i>Achnanthes pusilla</i> Grunow in Cleve & Grunow	P1: 5, 6	AK, FE, LB, NT, WB, YE, YK
4	<i>Achnanthes suchlandtii</i> Hustedt	P1: 7, 8	AK, FE, LB, NT, YE, YK
5	<i>Amphora inariensis</i> Krammer	P1: 9–11	AK, NT, YK
6	<i>Amphora</i> sp. 1	P2: 66, 67	
7	<i>Asterionella formosa</i> Hassall	P1: 12, 13	AK, FE, FI, LB, WB, YE, YK
8	<i>Caloneis bacillum</i> (Grunow) Cleve	P1: 14, 15	YK
9	<i>Cyclotella comensis</i> Grunow in Van Heurck	P1: 16, 17	AK
10	<i>Cyclotella stelligera</i> Cleve & Grunow in Van Heurck	P1: 18, 19	AK, FE, FI, LB, NT, WB, YE, YK
11	<i>Cyclotella tripartita</i> Håkansson	P1: 21, 22	AK, LB, YE, YK
12	<i>Cyclotella</i> sp. 1	P1: 20	
13	<i>Cymbella minuta</i> Hilse ex Rabenhorst	P1: 23, 24	FI, LB, NT, WB, YE, YK
14	<i>Fragilaria brevistriata</i> Grunow in Van Heurck	P1: 25–27	AK, FE, FI, LB, NT, WB, YE, YK
15	<i>Fragilaria brevistriata</i> var. <i>inflata</i> (Pantocsek) Hustedt	P1: 28, 29	AK, WB
16	<i>Fragilaria capucina</i> var. <i>gracilis</i> (Østrup) Hustedt	P1: 43	AK, FE, WB
17	<i>Fragilaria capucina</i> var. <i>vaucheriae</i> (Kützing) Lange-Bertalot	P1: 30, 31	AK, YE, YK
18	<i>Fragilaria construens</i> (Ehrenberg) Grunow	P1: 32, 33	AK, FE, FI, LB, NT, WB, YK
19	<i>Fragilaria construens</i> var. <i>venter</i> (Ehrenberg) Grunow in Van Heurck	P1: 34	AK, FE, LB, NT, WB, YE, YK
20	<i>Fragilaria delicatissima</i> (W. Smith) Lange-Bertalot	P1: 45	AK, WB, YE
21	<i>Fragilaria lapponica</i> Grunow in Van Heurck	P1: 40	LB, YK
22	<i>Fragilaria nanana</i> Lange-Bertalot	P1: 46	AK, FE, NT, WB
23	<i>Fragilaria parasitica</i> (W. Smith) Grunow in Van Heurck	P1: 41	FE, NT, WB, YK
24	<i>Fragilaria pinnata</i> Ehrenberg	P1: 35–37	AK, FE, FI, LB, NT, WB, YE, YK
25	<i>Fragilaria pinnata</i> var. <i>intercedens</i> (Grunow) Hustedt	P1: 38, 39	AK, NT, YK
26	<i>Fragilaria pseudoconstruens</i> Marciniak	P1: 42	FE, NT, YE, YK
27	<i>Fragilaria tenera</i> (W. Smith) Lange-Bertalot	P1: 44	AK, NT, WB
28	<i>Navicula</i> cf. <i>absoluta</i> Hustedt	P2: 47	
29	<i>Navicula agrestis</i> Hustedt	P2: 48	NT
30	<i>Navicula capitata</i> Ehrenberg	P2: 49	YK
31	<i>Navicula cryptocephala</i> Kützing	P2: 57	AK, FE, FI, NT, WB, YE, YK
32	<i>Navicula detenta</i> Hustedt	P2: 50	
33	<i>Navicula laevisissima</i> Kützing	P2: 58	LB, WB, YK
34	<i>Navicula libonensis</i> Schoeman	P2: 60	
35	<i>Navicula minuscula</i> Grunow in Van Heurck	P2: 51	AK, LB, NT, WB, YE, YK
36	<i>Navicula seminulum</i> Grunow	P2: 52, 53	AK, FE, LB, NT, YE, YK
37	<i>Navicula vitiosa</i> Schimanski	P2: 55, 56	AK, FE, LB, YE, YK
38	<i>Navicula</i> sp. 1	P2: 54	
39	<i>Nitzschia acicularis</i> (Kützing) W. Smith	P2: 70	YK
40	<i>Nitzschia dissipata</i> (Kützing) Grunow	P2: 71	WB, YK
41	<i>Nitzschia gracilis</i> Hantzsch	P2: 72	AK, WB
42	<i>Nitzschia palea</i> (Kützing) W. Smith	P2: 73, 74	AK, FE, FI, NT, WB
43	<i>Nitzschia paleacea</i> (Grunow) Grunow in Van Heurck	P2: 75, 76	FE, WB
44	<i>Nitzschia perminuta</i> (Grunow) M. Peragallo	P2: 77, 78	AK, FE, LB, NT, WB, YE, YK
45	<i>Nitzschia pura</i> Hustedt	P2: 79, 80	WB, YE, YK
46	<i>Pinnularia balfouriana</i> Grunow ex Cleve	P2: 63, 64	FE, YE, YK
47	<i>Pinnularia interrupta</i> W. Smith	P2: 59	AK, FE, FI, LB, NT, WB, YE, YK
48	<i>Stauroneis anceps</i> Ehrenberg	P2: 61	FE, FI, LB, NT, YE, YK
49	<i>Stephanodiscus minutulus</i> (Kützing) Round	P2: 68	AK
50	<i>Tabellaria flocculosa</i> (Roth) Kützing Strain IIIp <i>sensu</i> Koppen	P2: 62	AK, FE, FI, LB, YK
51	<i>Tabellaria flocculosa</i> (Roth) Kützing Strain IV <i>sensu</i> Koppen	P2: 65	NT, YE
52	<i>Thalassiosira pseudonana</i> Hasle & Heimdal	P2: 69	

\*Abbreviations with references are as follows: (boreal forest) FI = southern and central Finland (Huttunen & Turkia 1990); WB = Wood Buffalo National Park, Canada (Moser 1996); (circumpolar treeline) AK = Alaska (Gregory-Eaves 1998); FE = Fennoscandia (Weckström *et al.* 1997a,b); LB = Labrador, Canada (Allaire 1997); NT = Northwest Territories, Canada (Rühland 1996); YE = Yellowknife region, Canada (Pienitz & Smol 1993); YK = Yukon, Canada (Pienitz *et al.* 1995b). Comparisons are based on diatom taxa included in calibration set models (generally those taxa with a relative abundance  $\geq 1\%$  in one lake and present in 3 lakes; see individual references for details on cut-off criteria).

indistinguishable under the light microscope, and a central siliceous rib reminiscent of *Stauroneis* on the dorsal part of the valve. Length 15–19 µm; valve width *ca.* 3.5 µm.

*Cyclotella* sp. 1

Pl. 1, Fig. 20

This taxon appears to belong to the group formerly known as the *Cyclotella bodanica/compta* complex (Håkansson 1988). Although several morphologically different groups within this complex have been identified recently (Håkansson 1988, Håkansson & Carter 1990, Krammer & Lange-Bertalot 1991), we were unable to find a description of this diatom in the literature. Our taxon is most similar to pl. 60, figs 1–5 in Krammer & Lange-Bertalot (1991), which they listed as *C.* species (aff. *quadrijuncta*?); no taxonomic description was provided. However, our form differs from the published description of *C. quadrijuncta* (Schröter) von Keissler, as the latter has a larger diameter (20–40 µm) and coarser striae density (16 in 10 µm).

*Navicula* cf. *absoluta* Hustedt

Pl. 2, Fig. 47

This taxon differs from Hustedt's (1950) description of *N. absoluta* in that the central area appears to be more characteristic of *N. disjuncta* Hustedt in the arrangement and orientation of the central striae. However, the length (20 µm), width (6 µm), and striae density (18 in 10 µm) are all within the range of values published for *N. absoluta* by Krammer & Lange-Bertalot (1986). The apices of *N. cf. absoluta* also appear to be slightly less capitate than those figured by Hustedt (1950, pl. 38, figs 80–85) and Krammer & Lange-Bertalot (1986, pl. 71, figs 15–21).

*Navicula* sp. 1

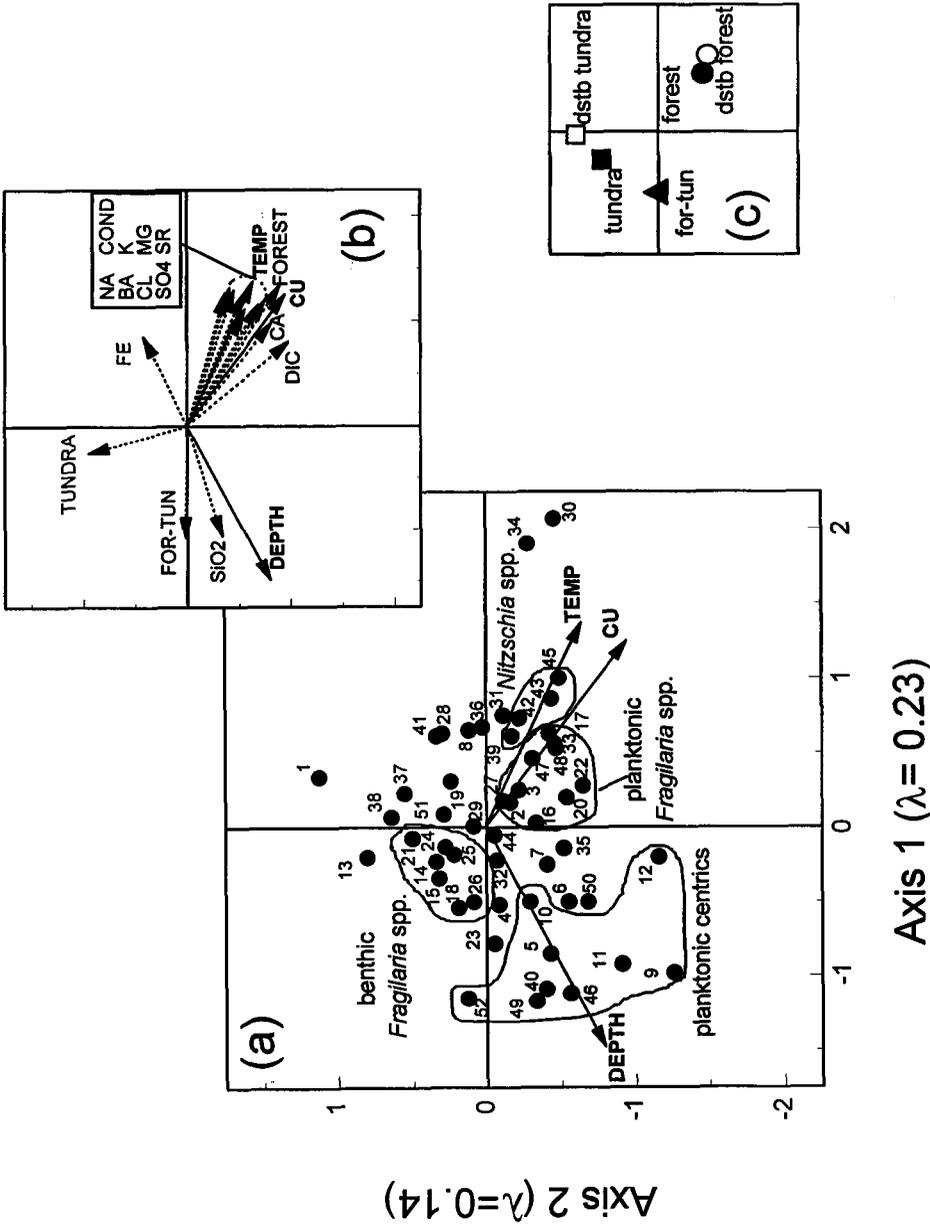
Pl. 2, Fig. 54

This form is small (length = 6 µm, width = 3–4 µm) with fine striae that are indistinguishable under the light microscope. The valve shape is elliptical, and the raphe is distinct. *Navicula* sp. 1 appears most similar to *Navicula indifferens* Hustedt; however, the latter appears to have slightly rostrate ends which are lacking in the Siberian taxon.

**Statistical analyses**

CCA with forward-selection identified three environmental variables as explaining a significant and additional proportion of the variation in diatom assemblages: depth (DEPTH), temperature (TEMP), and copper concentrations (CU) (Fig. 2a,b). All three variables were significantly correlated with both Axis 1 and 2. Depth was the strongest variable influencing the diatom assemblages, with deeper lakes (depth > 6 m) containing higher abundances of planktonic centric species (Fig. 2a). AWM estimates for depth calculated for centric taxa were all > 6.85 m (range for all 52 taxa = 2.28–9.48 m; Table 3).

Analysis of similarity tests indicated that diatom assemblages were significantly different between tundra and forest sites and between forest-tundra and forest sites (Table 4). Diatom assemblages in forested lakes were associated with higher temperatures and higher conductivity values (Fig. 2b), and contained greater abundances of planktonic *Fragilaria* species (Fig. 2a). Tundra lakes were dominated by small benthic *Fragilaria* species, and also several small *Achnanthes* and *Navicula* species (Fig. 2a). Typically, these taxa had AWMs in the lower range of temperature values (<12.5°C; range for all 52 taxa = 9.80–15.12°C; Table 3). Overall, mean relative abundances of all benthic *Fragilaria* species were significantly different ( $p < 0.01$ ) between tundra lakes (mean = 67%) and forested lakes (mean = 27%). Diatom assemblages in forest-tundra sites were not significantly



**Fig. 2.** Canonical Correspondence Analysis (CCA) of diatom species assemblages in the 23 lake calibration set near Norilsk, Russia. **(a)** CCA showing relationship between 52 most abundant diatom taxa and measured environmental variables. Numbers correspond to diatom taxon names in Tables 2 and 3. Solid arrows represent forward-selected environmental variables that explained a significant and additional proportion of the variation in species assemblages. **(b)** CCA showing main environmental gradients explaining the variation in diatom species assemblages. Dotted arrows represent passive variables which explained a significant proportion of the variation in a CCA constrained to a single variable, but were not forward-selected. **(c)** CCA showing the relationship between the centroids of assemblages in each vegetational zone (solid symbols) and the “disturbed” lakes (open symbols).

different from tundra lakes (Table 4), and contained many of the same benthic *Fragilaria* taxa (Fig. 2a).

A subset of the forested lakes located close to Norilsk, which we have designated as “disturbed” forest lakes, were associated with slightly higher Cu concentrations, and contained higher abundances of *Nitzschia* species compared to the undisturbed forest lakes (Fig. 2a,c). Few trends in species composition or water chemistry were noted for the “disturbed” tundra sites close to Norilsk.

## DISCUSSION

### How unique are diatom assemblages from the 23 Siberian sites?

Comparison of diatom assemblages in our study sites with other floristic studies for Siberia indicates that many taxa have been reported from other areas in Russia. For example, 33 of our taxa (= 64%) are described in Sabelina *et al.* (1951), 17 (= 33%) in Loseva (1982), and 16 (= 31%) from the Lake Baikal region (Foged 1993). Our lakes showed little overlap with Lake Baikal assemblages. This is not surprising, given the extreme morphometric and limnological differences between the sampled lakes and Lake Baikal, and the well-documented prevalence of endemic diatom species there.

Overall, diatom assemblages in our study lakes were very similar to other circumpolar treeline floras. For example, 33 of our 52 most abundant species (= 64%) were also abundant (1% in at least one sample lake) in a set of lakes located in the treeline region in the Yukon, northern Canada (Pienitz *et al.* 1995b). Not surprisingly, lakes sampled in the Yukon were generally alkaline and dilute, corresponding to limnic conditions in our sample set. Diatom assemblages in the sample lakes near Norilsk were also similar in composition to those found in lakes within the treeline region in Labrador and the Northwest Territories, northern Canada, Alaska, and Fennoscandia. Many of our diatom taxa were also commonly found in boreal forest lakes (Huttunen & Turkia 1990, Moser 1996). Apart from the 4 unidentified taxa, only 3 of the remaining 48 taxa were not present in any of the other circumpolar treeline or boreal forest calibration sets: *Navicula detenta*, *N. libonensis*, and *Thalassiosira pseudonana*. The strong similarities between diatom species assemblages in the Norilsk lakes and those from other treeline regions suggest that our Siberian flora may be representative of a circumpolar arctic treeline flora, rather than forming a distinct regional assemblage.

### Ecology of diatoms in the surface calibration set

Diatom assemblages in the Norilsk lakes were generally characteristic of alkaline or circum-neutral conditions, reflecting the alkaline nature of the study sites (mean pH = 8.0; Table 1). Assemblages were largely dominated by benthic forms belonging to *Achnanthes*, *Fragilaria*, and *Navicula* (Table 3). These genera have also been reported as prevalent in other arctic treeline regions with similar alkaline limnological conditions (e.g. Pienitz *et al.* 1995b, Röhland 1996).

Depth was the strongest variable influencing diatom assemblage composition within our sample set of lakes. Deeper lakes (> 6 m) were characterized by a higher abundance of planktonic centric diatoms, such as *Cyclotella* spp., *Stephanodiscus minutulus*, and *Thalassiosira pseudonana* (Fig. 2a). These taxa had amongst the highest AWM optima for depth (Table 3). Increasing lake depth is often correlated with decreases in the proportion of benthic and epiphytic habitats, as the area of lake bottom within the photic zone decreases (Wolin & Duthie 1999). The shallow nature of the majority of our lakes (mean depth = 4.8 m) explains the overall predominance of benthic taxa in the study sites. Interestingly, several benthic taxa were common in deep lakes (e.g. *Pinnularia balfouriana*,

*Nitzschia dissipata*; Fig. 2a). Both of these taxa were most abundant in TS-1, the only deep (= 11.5 m) tundra lake in our data set, and it is possible that other unmeasured variables (such as the amount of moss habitats for the aerophilic species *P. balfouriana*) may explain the abundance of these taxa in this lake.

Diatom species assemblages also reflect the strong differences in water chemistry amongst the three vegetational zones. An analysis of similarity (ANOSIM) indicated that assemblages in the tundra and forest-tundra lakes were significantly different from those in forested lakes. Several taxa were important in accounting for differences between diatom assemblages in tundra vs. forest regions. For example, forested lakes were characterized by higher abundances of *Cyclotella stelligera*, *Stauroneis anceps*, and *Navicula seminulum*. Our results agree well with a study within the treeline region in the Yukon, northern Canada, which found these species to be associated with higher temperature optima (Pienitz *et al.* 1995b). Planktonic *Fragilaria* taxa, such as *F. delicatissima*, *F. tenera*, and *F. nanana*, were also more abundant in the forest lakes of our sample set (Fig. 2a). The higher abundance of planktonic taxa in forested lakes has been noted in other treeline regions (Pienitz 1993, Rühland 1996, Allaire 1997), and may partly reflect the relatively longer ice-free period compared with lakes in tundra environments. This longer ice-free period would permit diatom assemblages to reach a later successional stage in comparison with tundra lakes (Smol 1988), and lead to an earlier onset of thermal stratification in deeper lakes, resulting in the continued presence of these planktonic taxa in the photic zone (Fee *et al.* 1992). Planktonic pennate taxa have also been associated with higher water temperature optima (Pienitz *et al.* 1995b). Our findings are similar, as the planktonic *Fragilaria* taxa generally showed higher temperature optima in comparison with other species (Table 3).

Tundra lakes were typically dominated by small benthic *Fragilaria* taxa, such as *F. pinnata*, *F. construens* var. *venter*, *F. brevistriata* var. *inflata*, and *F. pseudoconstruens*. The predominance of such taxa in shallow arctic lakes has been well documented in many arctic studies (e.g. Smol 1988, Pienitz 1993, Rühland 1996), and it has been suggested that these taxa are more competitive in lakes with long periods of ice cover (Smol 1988, Rühland 1996). In addition, these benthic *Fragilaria* species may have an advantage in extremely oligotrophic or nutrient-limited lakes, as they are able to take up nutrients directly from the sediment-water interface (Sheath *et al.* 1982). Benthic *Fragilaria* species can also be considered as opportunistic taxa which are able to outcompete other slower-growing species during the short growing seasons and oligotrophic conditions of tundra environments (Pienitz 1993).

Forest-tundra lakes, being a transitional ecotone between tundra and forest lakes, contained an intermediate abundance of many of the more abundant taxa in the tundra and forest zones. Diatom assemblages in forest-tundra lakes were not significantly different from assemblages found in tundra lakes, and many of the same benthic *Fragilaria* species were present (e.g. *F. pseudoconstruens*, *F. pinnata*, *F. brevistriata* var. *inflata*), albeit at lower overall abundances.

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**PLATE 1.** Diatom taxa recovered from surficial sediments of Norilsk lakes, Siberia. LM. Scale bar = 10  $\mu$ m.  
**Figs 1, 2.** *Achnanthes laterostrata*, raphid and araphid valves, respectively. **Figs 3, 4.** *A. minutissima*. **Figs 5, 6.** *A. pusilla*, raphid and araphid valves, respectively. **Figs 7, 8.** *A. suchlandtii*, raphid and araphid valves, respectively. **Figs 9–11.** *Amphora inariensis*. **Figs 12, 13.** *Asterionella formosa*. **Figs 14, 15.** *Caloneis bacillum*. **Figs 16, 17.** *Cyclotella comensis*. **Figs 18, 19.** *C. stelligera*. **Fig. 20.** *Cyclotella* sp. 1. **Figs 21, 22.** *C. tripartita*. **Figs 23, 24.** *Cymbella minuta*. **Figs 25–27.** *Fragilaria brevistriata*. **Figs 28, 29.** *F. brevistriata* var. *inflata*. **Figs 30, 31.** *F. capucina* var. *vaucheriae*. **Figs 32, 33.** *F. construens*. **Fig. 34.** *F. construens* var. *venter*. **Figs 35–37.** *F. pinnata*. **Figs 38, 39.** *F. pinnata* var. *intercedens*. **Fig. 40.** *F. lapponica*. **Fig. 41.** *F. parasitica*. **Fig. 42.** *F. pseudoconstruens*. **Fig. 43.** *F. capucina* var. *gracilis*. **Fig. 44.** *F. tenera*. **Fig. 45.** *F. delicatissima*. **Fig. 46.** *F. nanana*.

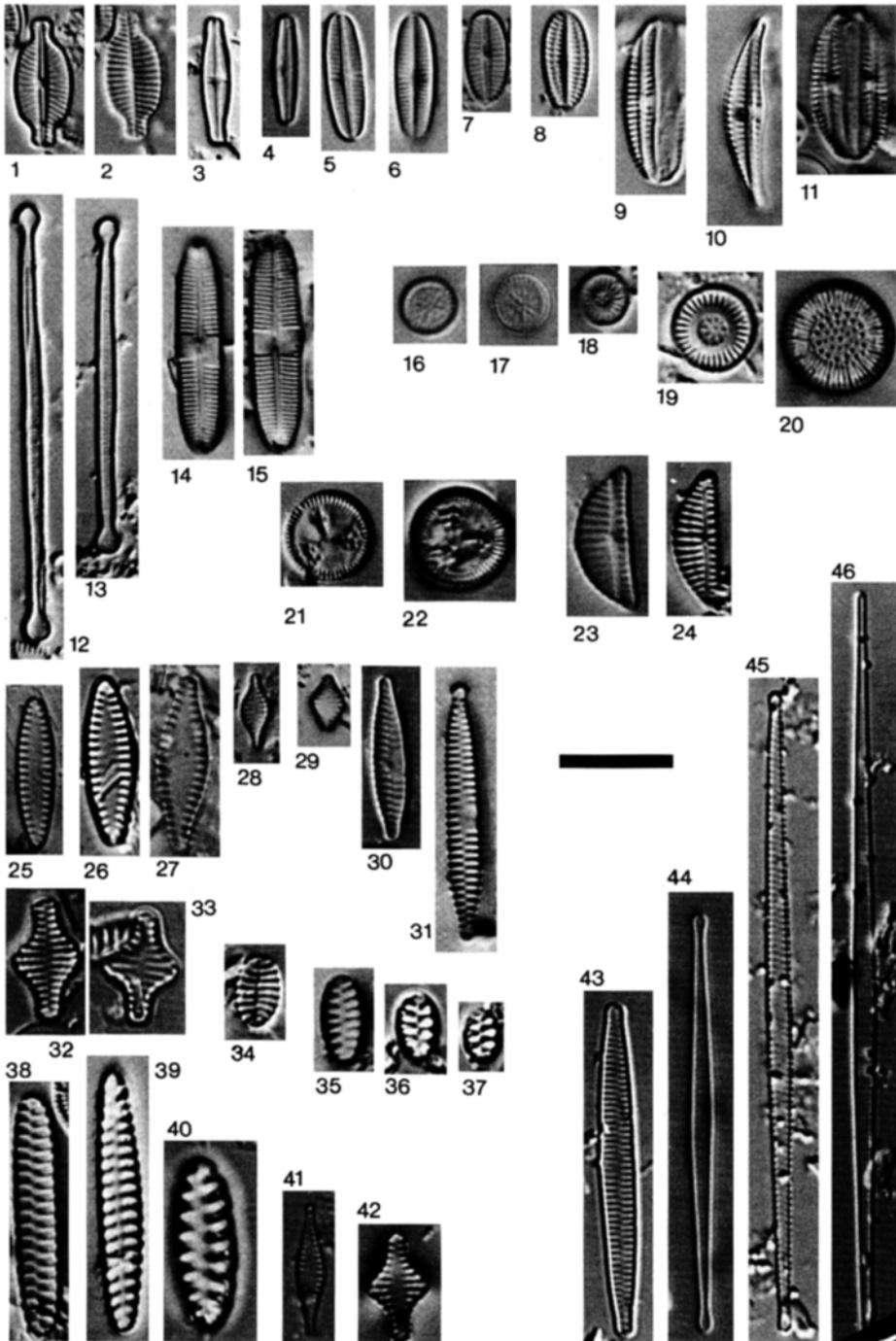


Table 3. Abundance weighted means (AWM) for the 52 most abundant diatom taxa in the Norilsk set of lakes.

No.	Taxon	Abundance categories*	Cu † ( $\mu\text{g L}^{-1}$ )	Depth † (m)	Temp (°C)	Cond † ( $\mu\text{S cm}^{-1}$ )	Hill's N2
1	<i>Achnanthes laterostrata</i>	2A, 1C	2.81	3.53	11.92	33.65	2.6
2	<i>Achnanthes minutissima</i>	4A, 3B, 10C, 3D, 1E	4.48	4.90	12.54	50.93	16.6
3	<i>Achnanthes pusilla</i>	6A, 3B, 7C, 1E	4.66	4.85	12.86	47.42	14.3
4	<i>Achnanthes suchlandtii</i>	5A, 2B, 1C	2.72	6.50	11.58	32.51	7.4
5	<i>Amphora inariensis</i>	3A, 1C	3.18	7.64	10.54	34.75	3.4
6	<i>Amphora</i> sp. 1	3A, 1C	3.40	7.10	11.92	33.34	3.5
7	<i>Asterionella formosa</i>	7A, 1B, 3C, 1D	4.03	6.08	11.92	37.58	7.4
8	<i>Caloneis bacillum</i>	2A, 2B, 1C	5.40	3.78	13.03	69.50	3.7
9	<i>Cyclotella comensis</i>	1A, 1C	4.29	9.48	10.88	34.99	1.7
10	<i>Cyclotella stelligera</i>	5A, 1B, 2C, 1D, 4E	2.77	6.85	12.07	32.89	6.8
11	<i>Cyclotella tripartita</i>	2A, 1D	3.81	8.61	10.75	36.64	2.3
12	<i>Cyclotella</i> sp. 1	1A, 1C	4.13	7.52	13.78	38.02	1.5
13	<i>Cymbella minuta</i>	5A, 1C	2.24	4.76	11.43	36.81	4.0
14	<i>Fragilaria brevistriata</i>	2A, 5B, 2C, 2D	2.74	5.26	11.66	31.55	9.4
15	<i>Fragilaria brevistriata</i> var. <i>inflata</i>	1A, 3B, 5C, 2D, 2E	2.70	5.48	11.32	36.39	11.7
16	<i>Fragilaria capucina</i> var. <i>gracilis</i>	7A, 4B, 1C	4.33	5.41	12.57	44.36	9.3
17	<i>Fragilaria capucina</i> var. <i>vaucheriae</i>	4A, 1C	5.28	4.53	14.31	51.17	3.4
18	<i>Fragilaria construens</i>	1A, 1C	2.72	6.01	10.83	42.36	1.7
19	<i>Fragilaria construens</i> var. <i>venter</i>	2A, 2B, 3C, 4D, 9E	4.04	4.29	12.54	49.09	14.6
20	<i>Fragilaria delicatissima</i>	5A, 3B, 1C	5.26	5.26	12.97	53.09	7.4
21	<i>Fragilaria lapponica</i>	5A, 2C	2.67	4.83	12.00	32.51	6.0
22	<i>Fragilaria nanana</i>	7A, 2B, 1C, 1D	5.30	5.32	13.51	52.97	7.9
23	<i>Fragilaria parasitica</i>	7A, 1B, 1C	2.76	6.89	10.43	39.54	7.0
24	<i>Fragilaria pinnata</i>	1B, 1C, 3D, 17E	3.30	5.00	11.49	41.40	17.9
25	<i>Fragilaria pinnata</i> var. <i>intercedens</i>	5A, 3B, 1C	2.97	5.30	11.84	34.83	6.7
26	<i>Fragilaria pseudoconstruens</i>	1A, 2B, 6C, 4D, 2E	2.90	6.03	11.01	37.58	11.9
27	<i>Fragilaria tenera</i>	3A, 1C, 1D	3.94	4.98	12.95	37.15	3.3
28	<i>Navicula</i> cf. <i>absoluta</i>	3A, 2B, 2C	5.21	3.63	12.65	63.24	4.5
29	<i>Navicula agrestis</i>	13A, 3B, 1C	3.56	5.02	12.19	40.09	13.3
30	<i>Navicula capitata</i>	1C, 1D	19.32	2.28	15.12	175.39	1.9
31	<i>Navicula cryptocephala</i>	4A, 2B, 1C	7.00	3.72	12.98	73.96	5.3
32	<i>Navicula detenta</i>	3A, 2C	4.21	5.40	11.08	29.31	3.3
33	<i>Navicula laevis</i>	8A, 1B, 2C	5.79	4.55	13.79	58.34	8.6
34	<i>Navicula libonensis</i>	1E	15.00	2.40	15.00	209.89	1.0
35	<i>Navicula minuscula</i>	1A, 5B, 1C	3.18	6.47	13.49	45.60	4.9
36	<i>Navicula seminulum</i>	6A, 5B, 4C, 1D, 2E	5.43	3.86	13.32	58.75	11.4
37	<i>Navicula vitiosa</i>	4A, 1B, 1C	3.19	4.21	12.40	46.56	6.8
38	<i>Navicula</i> sp. 1	5A, 4B, 2C	2.98	4.34	11.79	42.95	10.2
39	<i>Nitzschia acicularis</i>	7A, 1D	5.48	4.17	13.51	46.13	4.6
40	<i>Nitzschia dissipata</i>	3A, 2B, 1C	2.70	8.36	10.16	42.76	5.4
41	<i>Nitzschia gracilis</i>	4A, 1B, 1C	4.12	3.81	13.38	46.67	5.4
42	<i>Nitzschia palea</i>	7A, 4B, 1D	6.18	3.98	13.66	66.37	9.6
43	<i>Nitzschia paleacea</i>	2A, 2C	7.48	3.93	13.96	65.77	3.1
44	<i>Nitzschia perminuta</i>	7A, 7B, 1C	3.98	5.18	11.87	40.93	13.1
45	<i>Nitzschia pura</i>	2A, 2C	8.28	3.76	14.25	94.84	3.3
46	<i>Pinnularia balfouriana</i>	2A, 1C	2.52	8.99	10.67	65.77	2.4
47	<i>Pinnularia interrupta</i>	5A, 1B, 1D	5.08	4.62	13.53	59.98	4.1
48	<i>Stauroneis anceps</i>	3A, 1B, 2C, 1D, 1E	5.47	4.68	13.89	49.55	6.0
49	<i>Stephanodiscus minutulus</i>	1A, 1E	2.00	8.99	10.80	27.99	1.0
50	<i>Tabellaria flocculosa</i> IIIp	3A, 1B, 1C	3.90	7.13	11.71	39.17	4.5
51	<i>Tabellaria flocculosa</i> IV	5A, 1B, 1C, 2D	3.24	4.71	12.40	29.79	5.4
52	<i>Thalassiosira pseudonana</i>	1A, 1E	2.00	7.74	9.80	35.97	1.5

\* Relative abundance categories for lakes in which a taxon was present are as follows: A = <1%; B = 1 to <2%; C = 2 to <5%; D = 5 to <10%; E =  $\geq$ 10%. For example, a taxon with an abundance category of 2A, 1C indicates this taxon had a relative abundance <1% in 2 lakes and between 2 and 5% in 1 lake, and was absent in the counts from 20 lakes.

† AWM estimates based on transformed data [ $\log(x)$ ]; back-transformed estimates are presented here.

Table 4. Results of analysis of similarity (ANOSIM) tests showing differences between lakes from the three vegetational zones of the treeline region based on diatom species assemblages.

Comparison	R statistic	p-value
Tundra vs. forest-tundra	0.164	0.048
Tundra vs. forest	0.261	0.006*
Forest-tundra vs. forest	0.313	0.001*

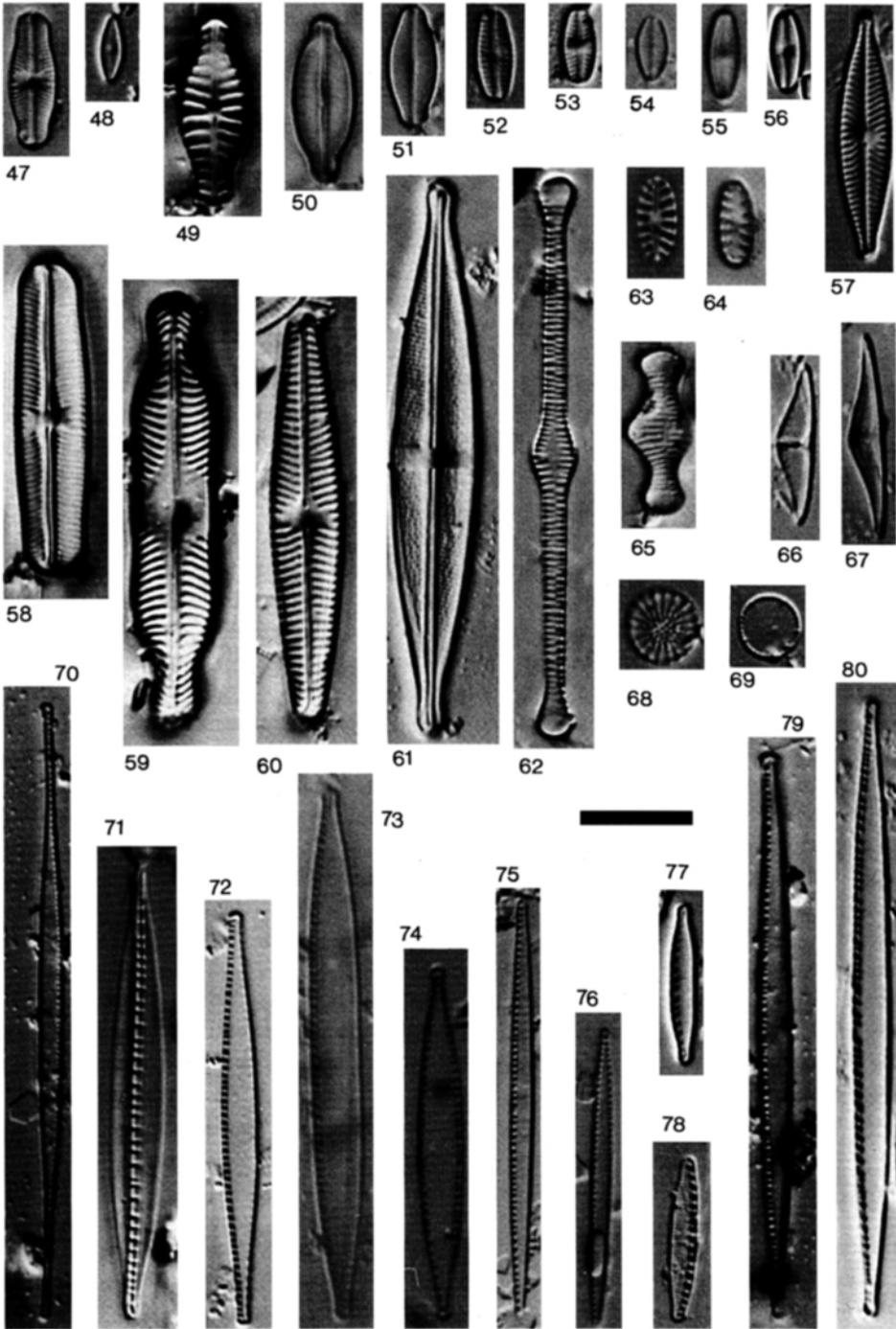
\* denotes statistical significance ( $p < 0.016$ )

The sample set of lakes also included a subset of “disturbed” forest and tundra lakes located close to the mining industry of Norilsk. Water chemistry and geochemical analyses indicated that these “disturbed” lakes were associated with higher concentrations of heavy metals and major ions (Blais *et al.* 1999, Duff *et al.* 1999), and this is reflected by the importance of Cu in explaining the variation in diatom assemblages within the lake set. Taxa that were most abundant in “disturbed” forested lakes include *Navicula capitata*, *N. libonensis*, *Nitzschia paleacea* and *N. pura*. These taxa are representative of waters with elevated electrolyte concentrations (Krammer & Lange-Bertalot 1986–1991). Furthermore, these species are able to tolerate pollution in the  $\alpha$ –mesosaprobic range (Lange-Bertalot 1979, Krammer & Lange-Bertalot 1986–1991, van Dam *et al.* 1994). The higher abundance of these diatoms in lakes located close to Norilsk probably reflects the influence of heavy metal input and atmospheric pollution from mining and smelting operations (Blais *et al.* 1999).

In comparison with taxa indicative of acidic and high heavy metal concentrations in the Sudbury (Ontario) region, such as *Frustulia rhomboides* var. *saxonica* (Rabenhorst) De Toni, the Siberian taxa are more representative of alkaline, pre-disturbance conditions (Dixit *et al.* 1992). This is not surprising, as lakes in the Norilsk area are presently alkaline due to the local geology, in comparison with the acid-sensitive lakes located on Precambrian Shield rocks in the Sudbury area. Heavy metal precipitation is linked with aqueous pH, and, under alkaline conditions, most heavy metals form insoluble metallic complexes in water (de Filippis & Pallaghy 1994). While metal and ion concentrations in the “disturbed” lakes close to Norilsk were slightly elevated, they were much lower than levels reported for impacted lakes near Sudbury, Canada; instead, most of the heavy metal contaminants were contained within the lake sediments (Blais *et al.* 1999). The lack of a distinct diatom assemblage characteristic of heavily impacted conditions in the Norilsk lakes most likely reflects the suppression of high aqueous heavy metal and sulphate concentrations due to the influence of regional alkaline bedrock.

## CONCLUSIONS

Our survey of diatom assemblages in the surficial sediments of lakes near Norilsk, Siberia, has revealed strong similarities with diatom floras reported from other circumpolar treeline regions. This most likely indicates that, despite regional differences in local climate regimes and different degrees of anthropogenic disturbance, overall environmental gradients influencing diatom assemblage composition within the treeline region appear to be comparable in these circumpolar environments, resulting in similar treeline diatom assemblages. Comparisons of important water chemistry gradients



amongst the different circumpolar treeline calibration sets suggest that this is indeed the case (Rühland & Smol 1998). In addition, the similarities between inferred ecological preferences for dominant diatom taxa in our study region and those from other treeline regions suggest commonalities in the response of individual taxa to regional environmental gradients. Such results indicate the potential for paleoclimatic reconstructions based on changes in diatom assemblages preserved in sediment cores, similar to studies conducted in Northern Canada (Pienitz & Smol 1993, Pienitz *et al.* 1995b). Furthermore, combining circumpolar treeline calibration sets to produce more reliable estimates of past climatic variables may be possible, providing the overall gradients influencing diatom species assemblages are similar in each region.

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**PLATE 2.** Diatom taxa recovered from surficial sediments of Norilsk lakes, Siberia. LM. Scale bar = 10  $\mu\text{m}$ . **Fig. 47.** *Navicula cf. absoluta*. **Fig. 48.** *N. agrestis*. **Fig. 49.** *N. capitata*. **Fig. 50.** *N. detenta*. **Fig. 51.** *N. minuscula*. **Figs 52, 53.** *N. seminulum*. **Fig. 54.** *Navicula* sp. 1. **Figs 55, 56.** *N. vitiosa*. **Fig. 57.** *N. cryptocephala*. **Fig. 58.** *N. laevisissima*. **Fig. 59.** *Pinnularia interrupta*. **Fig. 60.** *Navicula libonensis*. **Fig. 61.** *Stauroneis anceps*. **Fig. 62.** *Tabellaria flocculosa* strain IIIp. **Figs 63, 64.** *Pinnularia balfouriana*. **Fig. 65.** *Tabellaria flocculosa* strain IV. **Figs 66, 67.** *Amphora* sp. 1. **Fig. 68.** *Stephanodiscus minutulus*. **Fig. 69.** *Thalassiosira pseudonana*. **Fig. 70.** *Nitzschia acicularis*. **Fig. 71.** *N. dissipata*. **Fig. 72.** *N. gracilis*. **Figs 73, 74.** *N. palea*. **Figs 75, 76.** *N. paleacea*. **Figs 77, 78.** *N. perminuta*. **Figs 79, 80.** *N. pura*.

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