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Diatom, chrysophyte and protozoan distributions along a latitudinal transect in Fennoscandia

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Diatoms, chrysophyte scales and cysts, and the siliceous plates of thecoamoebae were studied from the surface sediments of 20 freshwater habitats in Fennoscandia. The study sites are distributed along a latitudinal transect extending from southern Finland to northern Norway, spanning boreal forest through arctic tundra vegetational zones. Diatom assemblages were usually dominated by acidophilic, periphytic members of the genera *Achnanthes*, *Fragilaria* and *Navicula*. Marked shifts in diatom assemblage composition were recorded along the latitudinal transect, whereas scaled chrysophytes were rare in all study sites. Meanwhile, siliceous protozoa were common, but did not exhibit any noticeable trends in assemblage composition with changing latitude. A comparison of the Fennoscandian diatom assemblages with those recorded from freshwater sites near Yellowknife (central Northwest Territories, Canada) revealed similar trends in diatom assemblage composition with changing ecoclimatic zones in both regions. Moreover, canonical correspondence analysis showed that diatom assemblages in cold, dilute tundra sites were effectively separated from sites with forested catchments from both the Fennoscandian and Canadian transects. The general similarity between the two regions suggests that autecological data and the resulting environmental transfer functions based on diatom assemblages may eventually be joined from North American and European regions.

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Introduction

High latitude regions are receiving increased attention as important reference sites for the study of environmental change. Equally, the strength and versatility of using diatoms and other aquatic bioindicators as monitors of environmental change continues to be recognized (e.g. Dixit et al. 1992). Unfortunately, relatively little ecological and distributional data are as yet available on diatom, chrysophyte and siliceous protozoan assemblages from northern latitudes.

Surveys of the diatom and chrysophyte flora of lakes in boreal regions of Finland (e.g. Cleve-Euler 1934, Meriläinen 1967, Foged 1968, Mölder and Tynni 1967–1973, Tynni 1975, 1976, 1978, 1980, Ilmavirta et al. 1984, Eloranta 1986, 1989, 1995, Christie et al. 1988, Ilmavirta and Huttunen 1989, Huttunen and Turkia 1990, 1994) have shown that these algae respond to changes in environmental variables, such as water pH and dissolved organic carbon content. However, additional data on distributions with respect to latitudinal gradients are still needed.

In an attempt to understand species distributions, we have been studying algal (e.g. diatoms, chrysophyte cysts and scales) and invertebrate (e.g. siliceous plates of the thecoamoebae, chironomids) remains in the surficial sediments of large numbers of lakes, and relating the species distributions to environmental variables of interest in order to determine the ecological optima and tolerances of aquatic indicators. Recent examples of such

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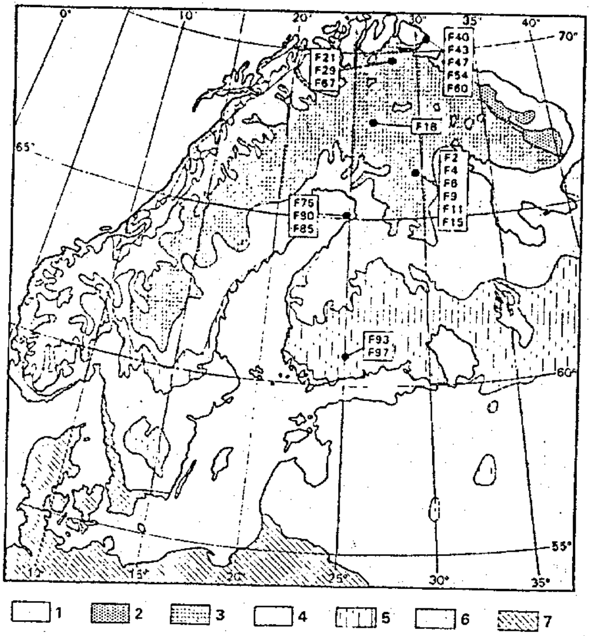

Fig. 1. Map showing the location of study sites in Fennoscandia, as well as vegetation zones in northwestern Europe (according to Ahti et al. 1968). 1) Oroarctic zone; 2) Orohemiarctic zone; 3) Northern boreal zone; 4) Middle boreal zone; 5) Southern boreal zone; 6) Hemiboreal zone; 7) Temperate zone.

work include a series of limnological and paleolimnological studies in Canadian arctic and subarctic regions (e.g. Walker et al. 1991, Douglas and Smol 1993, Pienitz and Smol 1993, Pienitz et al. 1995). For example, using multivariate statistical techniques, the relationship between diatom taxa preserved in surface lake sediments and measured limnological and environmental variables in 22 freshwater lakes near Yellowknife (Northwest Territories, Canada) was explored. The results showed marked floristic changes that could be related to drainage basin characteristics (such as the presence of trees) as well as other related limnological and climatic variables (Pienitz and Smol 1993). These data can eventually be used in paleoclimatic reconstructions (Pienitz et al. 1995).

The Canadian Arctic, however, represents just one portion of the northern circumpolar ecosystem. Lakes at similar latitudes but in other regions, such as Lapland, may share similar light/dark cycles and similar nutrient levels, but because of differences in oceanic currents and other factors, experience a significantly warmer climate. We therefore analysed the siliceous remains of diatoms (class Bacillariophyceae) and chrysophytes (classes Chrysophyceae and Synurophyceae) preserved in the surface sediments of freshwater habitats distributed along a latitudinal transect in Fennoscandia (Fig. 1). Comparisons of freshwater biota from different regions of the northern hemisphere are necessary to shed light on the major factors determining their distributional patterns in high latitude environments.

The objectives of this paper are to: i) document the distributions of siliceous aquatic bioindicators along a latitudinal transect in Fennoscandia, and ii) to compare our data with previous work from similar latitudes in North America. In short, we wish to determine how similar species shifts are across tree-line between northern Canada and Fennoscandia.

The main focus of this paper is diatoms because the results of our survey consisted mostly of the diatom distributional data. However, we also noted the presence of chrysophyte scales and cysts. In addition, we enumerated siliceous protozoan plates from testate amoebae. These thecoamoebae (Sarcodina; Rhizopoda) are often the most common animal group living in bog vegetation.

Table 1. Limnological data from the Fennoscandian study sites.

Site	Elevation (m a.s.l.)	pH	Conductivity (µS cm⁻¹)	Temperature (°C)
Sirkkalampi (F2)	285	7.8	NA	14.0
Upper Sirkkalampi (F4)	285	8.0	NA	14.0
Putaanlampi (F6)	246	7.5	162	14.0
Kourulampi (F9)	156	7.2	30	16.0
Hiidenlampi (F11)	219	6.0	24	14.0
Ruoppilampi (F15)	224	7.2	NA	14.0
Ilmakkiaapa (F18)	NA	6.3	27	10.0
Skallivarri (F21)	NA	5.7	NA	9.0
Pingo Lake (F29)	NA	5.0	NA	8.0
Vesterelva River (F40)	NA	6.8	NA	7.0
Lake #1 (F43)	NA	6.5	NA	9.0
Pond #2 (F47)	NA	6.8	NA	8.0
Pond #3 (F54)	NA	6.2	NA	7.2
Pond #4 (F60)	NA	6.7	NA	9.0
Kevojärvi (F67)	NA	6.9	NA	11.0
Hannuksenrantalampi (F75)	1.8	6.4	NA	17.0
Hannuksenlampi (F80)	4.0	5.3	NA	16.0
Kangasjärvi (F85)	9.2	4.7	NA	14.0
Rautajärvi (F93)	NA	6.3	NA	NA
Unnamed Lake (F97)	NA	NA	NA	NA

NA = not available

Table 2. Climate data from the Fennoscandian study region.

Station	mean annual temperature [°C]	mean annual precipitation [mm]	growing season [days]	average ice freeze-up [date]	average ice break-up [date]
Lammi (61°03'N; 25°03'E)	3.5 to 4.0	550 to 600	165 to 170	25 – 30.11	5 – 10.5
Hailuoto (65°01'N; 24°43'E)	2.5 to 3.0	400 to 450	145 to 150	10 – 15.11	10 – 15.5
Kuusamo (66°22'N; 29°19'E)	0.0 to 0.5	500 to 550	125 to 130	30.10 – 5.11	25 – 30.5
Utsjoki (69°45'N; 27°02'E)	–1.0 to –0.5	400 to 450	115 to 120	25 – 30.10	5 – 10.6
Vardø (70°21'N; 31°00'E)	–2.0 to –1.1	500 to 700	about 110	NA	NA

NA = not available

Study sites

Fennoscandia

Surface sediments were collected in August 1988 from a total of 20 aquatic habitats such as lakes and ponds, ditches, string bogs, thermokarst ponds and rivers. The sampling sites are distributed along a latitudinal transect between roughly 60° and 70°N, including several vegetation zones in Finland and northern Norway (Fig. 1). The basic limnological measurements that were taken in the field (surface water temperature, pH, and specific conductance) are summarized in Table 1.

The study area encompassing the 20 sites contains significant climatic gradients which are summarized in Table 2. In order to group our study sites according to vegetation zones, we adopted the widely used scheme of Ahti et al. (1968). The two southernmost sites (F93, F97) lie within coniferous forests that are interspersed with areas of mixed deciduous forests. Within the zone of continuous coniferous forests, Scots pine (*Pinus sylvestris*) usually predominates. In Finnish-Lapland, the subarctic forest-tundra ecotone is situated near Utsjoki, where birch (*Betula pubescens* ssp. *tortuosa*) is the predominant tree species.

Regional comparison Fennoscandia – Yellowknife

The two data sets (Fennoscandia and Yellowknife; Fig. 2) used for comparing the diatom floras are very similar in that both consist of study sites distributed along latitudinal transects that include large climatic and vegetational gradients. Some significant differences exist, however, between the arctic tundra in northern Europe and in the central Northwest Territories (N.W.T.). In Fennoscandia, tree-line is defined largely by an altitudinal limit, thereby explaining the existence of extensive barren fjells on high elevation plateaus near the North Cape and other areas bordering the Arctic Ocean. However, patches of deciduous woodland with birch (*Betula pubescens* ssp. *tortuosa*) and other species, such as *Alnus incana*, *Populus tremula*, *Sorbus aucuparia* and a few *Salix* species, are found where the soil is suitable for trees on Varanger Peninsula (more "scattered" tree-line). The whole region lies north of the limit of the coniferous forest zone. It is only on the Kola Peninsula that tree-line changes to a real northern limit at sea level (Müller 1986).

In the Yellowknife area (62°27' – 65°30'N, 110°00' – 114°21'W), the comparatively sharp ecotonal boundary at tree-line more or less coincides with the mean position in summer of the Arctic Front, the boundary between colder northern and warmer southern airstreams (Bryson

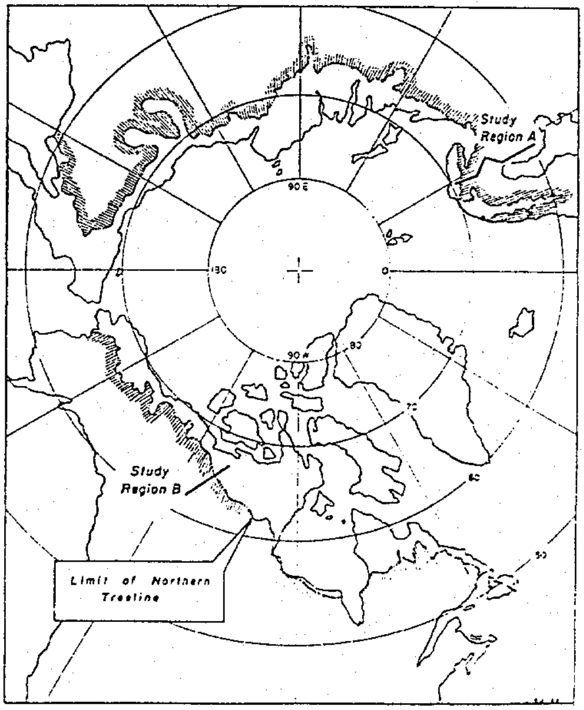

Fig. 2. Location of the two study regions (Fennoscandia = study region A; Yellowknife = study region B) and limit of northern tree-line in the northern hemisphere.

1966). Thus, in the central part of the N.W.T., tree-line represents a climatically-induced, "true" northern limit. Boreal forest, forest-tundra, and tundra comprise the vegetation of the Yellowknife area, which lies on the boundary between the high subarctic and low arctic ecoclimatic regions (Environment Canada 1989). Lone individuals or small clusters of stunted prostrate black spruce (*Picea mariana*) and, less commonly, white spruce (*Picea glauca*) are the two dominant species at tree-line (Larsen 1989).

The structural geology of Fennoscandia and the Yellowknife area is similar. In both areas, the bedrock consists mainly of acid granitic gneisses of Precambrian age, belonging to the Baltic shield and Canadian shield physiographic regions, respectively. Likewise, the topography of both areas is typified by a rolling terrain with only gentle relief.

Materials and methods

Sample preparation

The preparation of microscope slides followed standard techniques outlined in Pienitz and Smol (1993). The siliceous algal and protozoan remains were mounted in Hyrax®, a permanent mounting medium with a high refractive index (R.I. = 1.71). For each sample, a minimum of 300 diatom valves was counted and identified in random fields using oil immersion objectives of up to 1000x magnification. The taxonomy and identification of the diatoms followed standard floras (e.g. Mölder and Tynni 1967–1973, Tynni 1975, 1976, 1978, 1980, Foged 1981, Germain 1981, Krammer and Lange-Bertalot 1986, 1988, 1991a, b, Hein 1990) and the PIRLA Diatom Iconograph (Camburn et al. 1984–1986). At the same time, the frequency of chrysophyte stomatocysts, relative to diatoms, was determined while doing the diatom counts (Smol 1985). Chrysophyte scales were also identified, but they were quite rare. Individual protozoan plates were identified and enumerated according to Ogden and Hedley (1980) and Douglas and Smol (1987).

Data analysis

The direct application of multivariate statistical techniques on the Fennoscandian data set was impossible because of the limited number of study sites and available limnological data. However, a regional comparison based on biological composition was achieved by including the diatom data from the 20 Fennoscandian

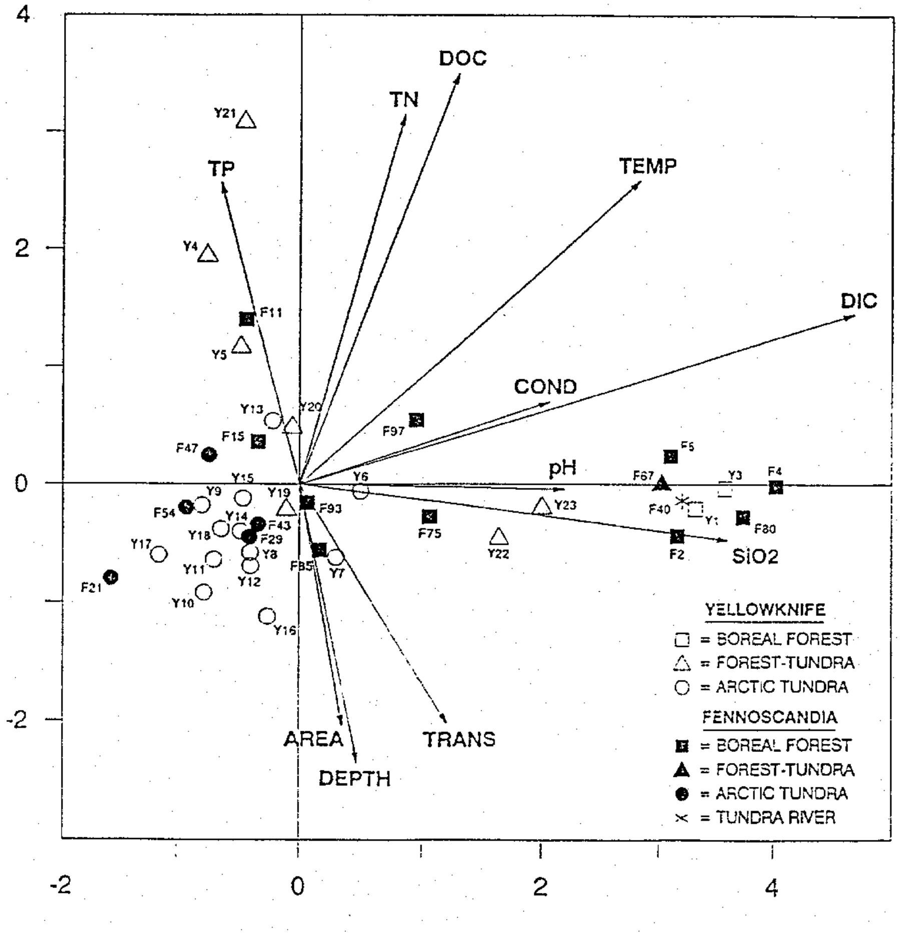

Fig. 3. Combined CCA Fennoscandia – Yellowknife.

sites as passive samples in a canonical correspondence analysis (CCA) of the Yellowknife data (Pienitz and Smol 1993). CCA is a direct gradient analysis technique developed by Ter Braak (1986, 1987) that can be used to investigate patterns of floristic or faunistic variation in relation to the measured environmental variables. All sites were classified according to three major catchment vegetation zones, including boreal forest (including some lakes in peatlands), subarctic woodland (including both forest-tundra and lichen-woodland), and arctic tundra (including sites in Fjell- and Maritime Lapland). Three sites (F9, F18 and F60) were excluded from the analysis, because of the absence of diatoms in their surface sediments. Thus, in the combined CCA biplot of the 39 sites, the 17 samples from Fennoscandia are represented by solid symbols, whereas those from the Yellowknife area (20) are represented by open symbols (Fig. 3). The ordination was performed using the computer program CANOCO, ver. 3.10 (Ter Braak 1990a, b).

The position of a sample or study site in the CCA biplot (Fig. 3) relative to all other sites and environmental gradients is based on the weighted averages of the 76 diatom taxa included in the analysis. Environmental variables (represented by arrows) included TP (total phosphorus), TN (total nitrogen), DIC (dissolved inorganic carbon), DOC (dissolved organic carbon), SiO_2 (total silica), COND (specific conductance), pH, TEMP (surface water temperature), TRANS (water transparency), AREA (lake surface area), and DEPTH (maximum lake depth). These were the environmental variables to be included in an exploratory CCA of the Yellowknife data set, the results and underlying methods of which are discussed in Pienitz and Smol (1993).

Using SYSTAT (Wilkinson 1988) a cluster analysis (single linkage, Euclidean distance) of the protozoan data was performed in order to determine if any distributional pattern existed.

Results

A total of 209 diatom taxa from 31 genera were identified in samples from the remaining 17 Fennoscandian sites, comprising predominantly boreal-subarctic species. The number of taxa per sample ranged between 10 and 72, the mean value being 42. Some diatom assemblages were dominated by only a few species (e.g. site F97).

Chrysophyte stomatocysts varied considerably in diversity and abundance relative to the diatoms (ranging from absent to more abundant than diatom valves). In general, scaled chrysophytes were rare, although in a few lakes several *Mallomonas* and *Synura* scales were identified.

Siliceous protozoan plates were generally abundant, but varied considerably amongst sites. A total of 17 generic groups of protozoan plates, representing 11 genera were counted. Identification of individual plates is based on morphology. The net result is that in many cases, siliceous plates can be only reliable assigned to a genus (generic) grouping. The most common genera present in our Fennoscandian study sites are *Trinema* and *Euglypha*. A cluster analysis (not shown) of the siliceous protozoan plates clustered the sites into two main groups. However, the lake clusters separated at a very low dissimilarity distance reflecting the similarity of the testate amoebae (protozoan) assemblages.

Limnological measurements revealed that almost all the study sites in Fennoscandia and the Yellowknife area were oligotrophic freshwater systems. Most of the study sites in Fennoscandia were small, dilute forest and peat bog lakes with acid to slightly alkaline water (pH range from 4.7 to 8.0; mean = 6.5), ranging from clear to distinctly humic, with only minor human disturbance in the catchment areas. The water in many lakes was tea-coloured, with relatively low conductivities (< 220 µS cm^{-1}). The only dystrophic, nutrient-poor, and strongly acid habitat was site F85 (Kangasjärvi).

Lakes in the Yellowknife area were generally shallow (Z_{max} = 2.5–20 m), with slightly acidic to alkaline pH (6.2–8.9) and low specific conductance (at detection limit to 100 µS cm^{-1}). Eutrophic localities were not sampled in either of the study areas.

Diatom, chrysophyte and protozoan distributions

Southern boreal forest zone
F93 (Rautajärvi)

The most striking feature of the diatom assemblage preserved in the sediments of this lake was the dominance of the benthic diatom *Achnanthes subatomoides* (Hustedt) Lange-Bertalot et Archibald (72.6%) and the absence of *Fragilaria* spp. taxa. *Achnanthes subatomoides* is a species that usually thrives in boreo-alpine environments, preferring oligotrophic, electrolyte-poor, circumneutral to slightly acidic waters (Krammer and Lange-Bertalot 1991b). It is accompanied by acidophilic and acidobiontic taxa of the genera *Eunotia* (e.g. *E. vanheurckii* Patrick, *E. meisteri* Hustedt), *Achnanthes* (e.g. *A. austriaca* Hustedt, *A. levanderi* Hustedt, *A. marginulata* Grunow) and *Tabellaria* (e.g. *T. flocculosa* (Roth) Kützing, *T. quadriseptata* Knudson). Chrysophyte cysts were rare. A few scales of *Mallomonas crassisquama* (Asmund) Fott, *Synura petersenii* Korshikov, *S. sphagnicola* (Korshikov) Korshikov and *S. echinulata* Korshikov were also recorded. A moderate number of plates, mostly from *Trinema*, were recorded.

F97 (Unnamed lake)

This is a clear, acid lake. A low number of species (10) was recorded, in part due to poor preservation. The diatom assemblage was dominated by acidophilic/acidobiontic taxa, such as *Eunotia* spp., *E. meisteri*, *E. exigua* var. *compacta* Hustedt, *Navicula bryophila* Petersen, *N.*

subtilissima Cleve and *Neidium bisulcatum* (Lagerstedt) Cleve. Chrysophyte cysts, however, were abundant, although this may be an artifact because cysts are more thickly silicified than the diatoms. No scales were recorded. Interestingly, a large number of *Lesquereusia* protozoan plates were present. This protozoan was not recorded in the Adirondack (New York, USA) mountain lakes, but was recorded in Labrador (eastern Canada) (Douglas and Smol 1987).

Middle boreal forest zone
F75 (pond near Hannuksenrantalampi)

This is the first of three sites sampled on Hailuoto Island, which is located in the northern part of the Baltic Sea (Fig. 1). The abundance of macrophytes in the littoral zone of this pond is indicated by a relatively diverse diatom assemblage with increased percentages of epiphytic forms (i.e. *Amphora* spp., *Cymbella* spp., *Gomphonema* spp.). Planktonic diatoms were absent. A few chrysophyte cysts were recorded, but no scales. A relatively diverse protozoan assemblage, consisting mostly of small plates (i.e. *Cyphoderia/Trinema* and *Corythion/Trinema*) and some larger plates (i.e. *Trinema* and *Trinema/Sphenoderia/Euglypha*) was identified.

F80 (Hannuksenlampi)

Sphagnum mosses surround the margin of this small, shallow pond, whose acid waters were relatively warm. Small benthic acidophils, such as *Fragilaria virescens* var. *exigua* Grunow, *Eunotia* spp., *Frustulia* spp. and *Navicula mediocris* Krasske were more abundant than in the previous site. Assemblage composition was quite similar to that of oligotrophic, slightly acidic lakes in the Yellowknife area. Chrysophyte cysts were also more abundant (5.6%) and some *Synura sphagnicola*, *S. echinulata* and *S. petersenii* scales were identified. These taxa are typical of these environments. This shallow pond also supports several protozoan plate taxa, including several larger forms such as *Trinema/Sphenoderia/Euglypha* and *Tracheleuglypha/Sphenoderia*.

F85 (Kangasjärvi)

This lake is the most acidic of all study sites, and is characterized by emergent and submergent *Sphagnum* mosses. *Frustulia rhomboides* (Ehrenberg) De Toni and its varieties dominate (26.5%) an assemblage consisting of only a few acidophilic and acidobiontic taxa, such as *Eunotia* spp. (17.9%), *Tabellaria quadriseptata*, *T. flocculosa* and *Fragilaria virescens* var. *exigua*. The weighted pH average calculated for *Tabellaria quadriseptata* was 5.3 according to Huttunen and Turkia (1990), a taxon that is common in electrolyte-poor, oligo- to dystrophic waters (Krammer and Lange-Bertalot 1991a). Chrysophyte cysts were relatively abundant (11.5%), but no scaled chrysophytes were recorded. Protozoans from only two groups (*Cyphoderia/Trinema* and *rinema*) were identified.

Northern boreal forest zone
F2 (Sirkkalampi)

The diatom assemblage preserved in the sediments of this small pond was dominated by small benthics, in particular by species of the genus *Fragilaria* spp. (53.8%) (mainly *Fragilaria pinnata* Ehrenberg, *F. brevistriata* Grunow, *F. pinnata* var. *intercedens* (Grunow) Hustedt, *F. pinnata* var. *lancettula* (Schumann) Hustedt in Schmidt et al. and *F. pseudoconstruens* var. *bigibba* Marciniak). Besides this group, small taxa such as *Achnanthes lanceolata* (Brébisson) Grunow (7.3%), *A. minutissima* Kützing (4.7%), *Amphora pediculus* (Kützing) Grunow (5.0%) and *Navicula minima* Grunow (4.7%) were also important. The latter four cosmopolitan taxa are known from a wide variety of habitats and therefore seem to have broad ecological tolerance ranges. Human disturbance in the form of organic pollution in the watershed (border house near border with Russia) might be indicated by the abundance of these forms, since they are known to be tolerant of alpha- to beta-mesosaprobic waters (Krammer and Lange-Bertalot 1986, 1991b). Centric diatoms (*Cyclotella* spp. (1%)) and chrysophyte cysts (1%) were rare, and no scales were recorded. In general, the assemblage is typical of circumneutral to slightly alkaline waters, reflecting the measured pH of 7.8.

F4 (Upper Sirkkalampi)

This pond is very similar to the above site, but smaller and slightly shallower. Diatom assemblage composition is also very similar, characterized by the predominant *Fragilaria* spp. group (60.1%), of which *F. pinnata* and *F. brevistriata* are the most abundant taxa. *Achnanthes minutissima* (4.4%) is another important taxon. The presence of diatoms such as *Denticula kuetzingii* Grunow (3.2%) and *Mastogloia smithii* var. *lacustris* Grunow is indicative of the slightly elevated conductivity. Only a few centrics (*Cyclotella* spp. (3.2%)) and chrysophyte cysts (1.6%) were present, and only one scale of *Mallomonas crassisquama* was recorded.

F6 (Putaanlampi)

This pond supported a diatom assemblage which was, in general, very similar to that of the above two sites. However, the increased abundance of acidophilic forms, such as *Fragilaria virescens* var. *exigua* (6.5%) and *Cymbella microcephala* Grunow (4.6%) reflects the slightly lower pH, as well as the presence of a *Sphagnum* bog in the pond's catchment. Almost no centrics, chrysophyte cysts (0.9%), or scales were recorded. *Denticula kuetzingii* was present at 5.6%. Interestingly, protozoan plates were relatively rare at this site. The absence of protozoan plates in the surficial sediments is surprising because this pond is surrounded by a bog environment which would appear to be prime habitat for testaceans. It is possible that the testaceans are not being transported from the peripheral bog environment to the sediment.

F9 (Kourulampi)

Evidence of a forest fire c. 50 years ago is present in the lake's catchment. No diatom count was possible because the sediment is almost devoid of diatoms. The few identifiable individuals seem to be covered by a film of mucilage. Neither chrysophytes nor protozoans were recorded.

F11 (Hiidenlampi)

The diatom assemblage preserved in the surface sediments of this lake was fundamentally different from those of the previous ponds/lakes, as it is characterized by the predominance of acidophilous benthic and tychoplanktonic diatoms. Most abundant are the benthic taxa *Eunotia flexuosa* (Brébisson) Kützing (20.6%), *Anomoeoneis brachysira* (Brébisson) Grunow (10.6%), *A. vitrea* (Grunow) Ross (5.0%), *Frustulia rhomboides* (8.3%), *Navicula subtilissima* (5.3%), *N. mediocris* (4.7%), *Cymbella gracilis* (Ehrenberg) Kützing (3.3%), as well as the (tycho-) planktonic taxa *Aulacoseira distans* (Ehrenberg) Simonsen (5.6%) and *Tabellaria flocculosa* (3.3%). All of the above taxa typically occur in the littoral zone of oligotrophic, acid lakes of low electrolyte content or associated with *Sphagnum* mosses in peatlands. The above assemblage clearly reflects the relatively low pH and conductivity values of this acid brown-water lake which is surrounded by a *Sphagnum* bog. The slightly increased number of planktonic diatoms (9.8%), and chrysophyte cysts (22.6%) may be due to the lower pH and to the greater depth of this lake. The small benthic *Fragilaria* spp. are only of minor importance (5.9%) of which *F. construens* (Ehrenberg) Grunow is the most abundant species. Chrysophyte scales were rare, but a considerable number of *Euglypha* apertural plates were identified.

F15 (Ruoppilampi)

The surface sediment of this shallow pond contained a very diverse diatom assemblage, the most prominent feature being its species richness and the absence of dominant diatoms. Most of these taxa are small pennate, periphytic diatoms that belong to the genera *Achnanthes*, *Navicula* and *Cymbella*. *Achnanthes pusilla* (Grunow) De Toni (12.6%), *A. minutissima* (9.6%), *Nitzschia* spp. (11.6%), *Tabellaria flocculosa* (5.0%) and *Cyclotella atomus* Hustedt (4.3%) are the most abundant diatoms. *Achnanthes pusilla* is known to thrive in oligotrophic, circumneutral waters of low to medium electrolyte content (Krammer and Lange-Bertalot 1991b), and is widely distributed in the northern hemisphere in boreal-alpine regions. Thus, its abundance in this pond is not surprising. It is interesting to note that *Aulacoseira* spp., which were the most abundant centric taxa in the previous site, are replaced in this pond mostly by centrics belonging to the genera *Cyclotella* (e.g. *C. atomus*, *C. iris* Brun & Héribaud, *C. bodanica* var. *lemanica* (O. Müller) Bachmann) and *Stephanodiscus* (e.g. *S. alpinus* Hustedt). The relative abundance for the planktonic component of the diatom assemblage and the chrysophyte cysts totals 14.3 and 3.3%, respectively. We did not record any scales, but a relatively diverse, albeit low abundance, assemblage of protozoan plates was present at this site.

F18 (Ilmakkiaapa)

Quantitative analysis of the sediment sample recovered from this typical northern string bog (*Betula*, *Sphagnum*) was impossible due to the extreme paucity of diatoms. Only a few *Fragilaria pinnata*, *F. construens* var. *venter* (Ehrenberg) Grunow, *Tabellaria flocculosa*, *T. quadriseptata*, *Stauroneis anceps* cf. var. *siberica* Grunow in Cleve & Grunow, *Navicula laevissima* Kützing and *Cymbella gracilis* valves could be identified. Similar poor preservation of diatoms is known to typically occur in acid bogs with low concentrations in silica. No chrysophytes or protozoans were recorded. As in the case for F16, it is interesting that no siliceous protozoan plates were observed in this bog environment.

F21 (Skallivarri)

The predominance of acid-tolerant taxa is the characteristic feature of the diatom assemblage preserved in this acidic, shallow and small (diameter < 1.5 m) polygon tundra pool, which was formed as a result of thermokarst processes in permafrost soils that surround this site. *Aulacoseira distans* var. *nivalis* (W. Smith) Haworth (18.0%), *A. lirata* (Ehrenberg) Ross (4.7%), *Eunotia* spp. (21.3%), *Navicula subtilissima* (6.7%), *N. soehrensis* Krasske (4.7%), *Pinnularia biceps* Gregory (11.6%), *P. microstauron* (Ehrenberg) Cleve (6.0%) and *P. appendiculata* (Agardh) Cleve (4.7%) are the most abundant taxa. Other important taxa are *Fragilaria constricta* Ehrenberg, *F. virescens* var. *exigua*, *Achnanthes marginulata*, *Anomoeoneis brachysira* and *Caloneis bacillum* (Grunow) Cleve. All of the above diatoms have been referred to as circumneutral, acidophilic or acidobiontic species of boreo-alpine affinity, which commonly occur in dystrophic, electrolyte-poor habitats like peatlands and bogs. The large number of aerophils (i.e. species closely associated with moist *Sphagnum* mosses/moss polsters, such as *Eunotia* spp., *Navicula subtilissima*, *N. soehrensis*, *Caloneis bacillum* and *Pinnularia appendiculata*) is also not surprising. Chrysophyte cysts were far more abundant than diatoms in the sediment, revealing a surprisingly large and diverse (species-rich) chrysophyte population in this shallow pool. Similarly, scaled chrysophytes were abundant, and overwhelmingly dominated by the acidophilous *S. echinulata*. Protozoan plates were also at maximum relative values (with regard to diatoms) with high diversity.

F29 (Pingo Lake)

The surface sediment from this small acidic pond contains a relatively species-rich diatom assemblage of acidophilous taxa. Most of the identified taxa are of boreo-alpine affinity and belong to the genera *Aulacoseira* (e.g. *A. subarctica* (O. Müller) Haworth, *A. lirata*, *A. distans* var. *nivalis*), *Eunotia* (e.g. *E. lapponica* Grunow, *E. exigua* var. *compacta*), *Achnanthes* (e.g. *A. flexella* var. *alpestris* Brun, *A. marginulata*), *Anomoeoneis* (e.g. *A. brachysira*), *Pinnularia* (e.g. *P. rupestris* Hantzsch) and *Cymbella* (e.g. *C. hebridica* (Grunow) Cleve). *Fragilaria virescens* var. *exigua* is the dominant taxon (30.0%), a diatom whose distribution is not well known due to taxonomic uncertainties. According to Krammer and Lange-Bertalot (1991a), it is especially common in oligotrophic, electrolyte-poor, circumneutral aquatic habitats of northern Europe. It has been commonly found in surface sediments from slightly acidic lakes near tree-line in the Yellowknife area (Pienitz and Smol 1993), as well as Alaskan lakes, ponds and streams (Hein 1990). Other common taxa include *Aulacoseira distans* (6.8%), *A. subarctica* (5.8%), *Tabellaria flocculosa* (5.1%), *Anomoeoneis brachysira* (4.5%) and *Achnanthes marginulata* (3.9%).

The low summer surface water temperatures recorded for both this pond and the previous site (F21) underscore the harsh environmental conditions that prevail in the fjell tundra of northern Finnish-Lapland, which may explain that almost all the taxa encountered in these two sites are of boreo-alpine affinity. It is interesting to note that, although the components of (tycho-) planktonic diatoms were almost identical in both sites (22.9% in Pingo Lake and 22.7% in F21), the number of chrysophyte cysts was considerably lower in the sediments of Pingo Lake (3.2% as opposed to >100% in F21). Similarly, no scales were recorded in this lake, whereas they were most abundant at F21. A similar pattern was observed with the protozoan plates.

F67 (Kevojärvi)

Small benthic taxa of the genera *Fragilaria* (e.g. *F. brevistriata*, *F. pinnata* and *F. pseudoconstruens* Marciniak), *Achnanthes* (e.g. *A. minutissima*, *A. microcephala* (Kützing) Cleve, *A. levanderi* and *A. lanceolata*), as well as *Navicula* (e.g. *N. jaernefeltii* Hustedt, *N. minima* and *N. seminulum* Grunow) were the dominant components of a relatively diverse diatom assemblage preserved in the surface sediment of this forest-tundra lake. Only very few planktonic diatoms and almost no chrysophyte cysts or scales were found, but we recorded moderate numbers of protozoan plates.

Oroarctic zone

F40 (Vesterelva River)

The sediments of this slowly running, cold river represent the first of four sampling sites in the Vardö area on Varanger Peninsula, near the Arctic Ocean. The diatom flora is dominated by small benthic *Achnanthes* (34.1%) and *Fragilaria* (32.3%) taxa, which often have been found to be abundant in lotic systems of Finnish and Swedish Lapland (e.g. Cleve-Euler 1934, Müller-Haeckel and Håkansson 1978). *Fragilaria pinnata* (22.2%) was found to be the dominant taxon.

The presence of many euryhaline species (sensu Simonsen 1962), such as *Achnanthes delicatula* (Kützing) Grunow, *Fragilaria virescens* var. *oblongella* f. *clavata* Grunow (synonymous with *Fragilaria schulzi* and *Opephora schulzi*), *Opephora olsenii* Möller, *Navicula gregaria* Donkin and *N. menisculus* Schumann, reflects the site's proximity to marine waters from Persfjorden Bay. All of the above taxa have been found along the coast of nearby Varangerfjorden (Tynni 1991). Such species are able to withstand large salinity fluctuations and are commonly found in electrolyte-rich inland or coastal waters (e.g. Simonsen 1962, Germain 1981). Among these were many epipsammic taxa, such as *Achnanthes delicatula* and *Opephora olsenii*, reflecting the sandy texture of the sediments recovered from the bed of Vesterelva River. Being a lotic habitat, it is not surprising we recorded almost no chrysophyte or protozoan indicators.

F43 (lake #1)

The bottom of this slightly acid and cold lake is almost completely rock-covered. *Fragilaria virescens* var. *exigua* (27.8%) is the dominant taxon in a diatom assemblage composed of small benthic species, especially acidophilic *Fragilaria*, *Achnanthes* and *Navicula* taxa. The reduced number of typically epiphytic diatoms reflects the absence of macrophytes. The most abundant taxa other than *Fragilaria virescens* var. *exigua* are *Fragilaria pinnata* var. *lancettula* (14.7%), *F. pinnata* (6.5%), *Achnanthes minutissima* (6.2%), *A. levanderi* (4.6%), *A. oestrupii* (Cleve-Euler) Hustedt (3.6%) and *Navicula jaernefeltii* (4.9%). A (tycho-) planktonic component is practically non-existent, since only a few individuals of centric species and chrysophyte cysts (0.3%) were found. No chrysophyte scales were identified, and only relatively few plates were recorded. In general, the assemblage reflects oligotrophic conditions of a circumneutral to slightly acidic lake.

F47 (pond #2)

The limnological conditions recorded for this shallow pond are comparable to those of the previous site, but it differs mainly by its much smaller size and the presence of submerged mosses on a mostly sediment-covered bottom. Diatom assemblage composition showed an increased number of species belonging to the genera *Anomoeoneis*, *Pinnularia* and *Cymbella*. *Achnanthes pusilla* (12.2%), *A. minutissima* (5.0%), *Anomoeoneis brachysira* var. *zellensis* (Grunow) Krammer (3.6%), *A. vitrea* (3.3%), *Cymbella microcephala* (3.1%) and *Nitzschia* sp. 1 (5.3%) are the most abundant taxa in an assemblage that is again dominated by *Fragilaria virescens* var. *exigua* (37.5%). Chrysophyte cysts (1.0%), scales and protozoan plates were all rare, and centric diatoms were absent.

F54 (pond #3)

This pond is even more acid and colder than the previous site. The presence of *Sphagnum* mosses and sedges (*Carex*) at the lake's margin, as well as its brown water colour, are indicative of high concentrations of organic acids. We recorded only a species-poor diatom assemblage composed mostly of benthic acidophils, which is characterized by an even more pronounced dominance of *Fragilaria virescens* var. *exigua* (69.7%). All other taxa are only of minor importance, with percentages not exceeding 4.0%. Of these, *Tabellaria flocculosa* (3.9%), *Achnanthes minutissima* (3.6%), *A. pusilla* (2.0%), *A. marginulata* (1.6%) and *Anomoeoneis vitrea* (2.0%) are the most abundant. Cyst percentages total 2.3%, scales were absent, and only a few protozoan plates were recorded.

F60 (pond #4)

This small pond located in the Kiberg area in the south-easternmost part of the Varanger Peninsula was surrounded by a mire and had strongly coloured water. It was limnologically comparable to the previous sites, but diatom counts were not possible as the diatoms were poorly preserved and seemed to be covered by a film of mucilage. Most of the few diatoms that could be identified were *Fragilaria virescens* var. *exigua*. Chrysophytes and protozoans were absent.

Discussion

Regional comparison of diatom floras

In general, the diatom floras from Fennoscandia and Yellowknife showed many similarities. For example, of the 209 diatom taxa identified in the Fennoscandian sites, 158 (≈76%) were also commonly found in the Yellowknife area. Diatom assemblages consisted mainly of small benthic (periphytic) *Fragilaria*, *Achnanthes* and *Navicula* taxa. These taxa are widely distributed throughout the entire northern hemisphere. Centric diatoms as well as alkaliphilic-alkalibiontic diatom taxa were extremely rare in the surficial sediments of both study areas. Only the following 15 (tycho-) planktonic taxa were found: *Stephanodiscus alpinus*, *Aulacoseira ambigua* (Grunow) Simonsen, *A. distans*, *A. distans* var. *nivalis*, *A. subarctica*, *A. lirata*, *A. nygaardii* Camburn, *Cyclotella atomus*, *C. bodanica* var. *lemanica*, *C. iris*, *C. stelligera* Cleve & Grunow, *Asterionella formosa* Hassall, *Diatoma tenuis* Agardh, *Synedra acus* Kützing and *Tabellaria flocculosa*. The relative abundance and number of these taxa appears to be related also to lake water acidity, since planktonic diatoms were usually rare or totally absent in the more acidic sites, whereas they tended to increase in abundance with higher pH (regardless of basin morphometry). According to several studies (e.g. Flower and Battarbee 1983, Charles 1985, Huttunen and Turkia 1990), planktonic diatoms are rare or totally absent at low pH values. The paucity of centric diatoms was particularly obvious in the Fennoscandian sites. Although lakewater pH and other limnological factors may have been partially responsible for the observed trends, an overriding factor responsible for the paucity of planktonic diatoms was likely the shallowness of the study sites.

Both floras were characterized by a predominance of circumneutral to acidiphilic diatoms, most of which were of boreo-alpine affinity and circumpolar distribution. The overall floristic similarity between the two study areas seems to be primarily related to the relatively homogeneous physico-chemical conditions of oligotrophic freshwater habitats on Precambrian bedrock. Diatom assemblages contained in lakes/ponds located north of the limit of coniferous forest in the Oroarctic zone of Fennoscandia, such as sites F21 and F29 from Fjell Lapland, as well as sites F43, F47 and F54 from Maritime Lapland were most similar to those observed in arctic tundra sites of the Yellowknife area (e.g. sites Y8 – Y18) (Fig. 3). In contrast, closest resemblance in diatom communities of lakes in forested watersheds was observed between sites F2, F4 and F6 from the Northern boreal forest zone and site F80 from the Middle boreal forest zone in Fennoscandia and sites of the Boreal forest zone near Yellowknife (e.g. sites Y1 and Y3).

The only minor floristic differences appeared to result mainly from the presence of some slightly more eutrophic freshwater bodies in Fennoscandia, as evidenced by the greater number of taxa such as *Stephanodiscus alpinus*, *Synedra parasitica* (W. Smith) Hustedt, *Navicula pseudotuscula* Hustedt, *N. tuscula* (Ehrenberg) Grunow, *Cymbella cymbiformis* Agardh, *C. ehrenbergii* Kützing, *Epithemia adnata* (Kützing) Brébisson and *E. sorex* Kützing. In addition, the occurrence of euryhaline taxa, such as *Fragilaria virescens* var. *oblongella* f. *clavata*, *Opephora olsenii*, *Achnanthes delicatula*, *Mastogloia smithii* var. *lacustris*, *Caloneis amphisbaena* var. *subsalina* (Donkin) Cleve, *Navicula gregaria*, *N. meniscu-lus* and *N.* cf. *soodensis* Krasske, reflects marine influences in coastal areas of Fennoscandia (i.e. the Varanger Peninsula). It is interesting to note that the diatom *Cymbella gaeumannii* Meister, which was an important and often dominant taxon in Yellowknife lakes, was not found in any of the study sites in Fennoscandia.

Combined CCA Fennoscandia - Yellowknife

The relative positioning in the CCA biplot of sample scores for the 39 sites from Fennoscandia and Yellowknife shows fairly good correlation between sites of corresponding vegetational zones (Fig. 3), thereby reflecting similar patterns in diatom distributions in both study areas. Cold, dilute tundra habitats (e.g. sites F21, F29, F43, F54, as well as Yellowknife sites Y8 to Y12 and Y14 to Y18), clustered in the lower left quadrant of the biplot, are effectively separated from sites with forested catchments which are more widely scattered on the right-hand side of the biplot. The latter are usually characterized by higher concentrations in ions, as well as higher pH and temperature. Interestingly, the two boreal forest sites (F11 and F15) surrounded by *Sphagnum* bogs are positioned in the upper left quadrant along with forest-tundra sites located in peatlands of the Yellowknife area (e.g. Y4, Y5, Y20, Y21), thereby possibly reflecting low water transparency and high [DOC]. The position of sample F40 is somewhat difficult to interpret because it was derived from a lotic environment (Vesterelva River).

Regional comparison of siliceous protozoan plates

The distribution of thecoamoebae in the western Arctic is as yet undescribed. The results presented here are similar to other Finnish data that we have gathered (unpubl.). This ongoing research and earlier work (Douglas and Smol 1987) have examined protozoan plates in the surficial sediments of 168 lakes in Finland and of 38 lakes in the Adirondacks (New York, USA). In the latter study, the relationship between testacean plate abundance and the amount of peatland within the catchment was examined. In both cases, percent peatland within the catchment seemed to be a significant environmental variable, whereas water chemistry did not appear to strongly affect the abundance of protozoan plates. Protozoan plates were more abundant in the Adirondack samples (i.e. the plate:frustule ratio was higher) and differed at a taxonomic level as well (Douglas and Smol 1987). Although *Trinema* plates were the most abundant in both lake sets, there were fewer *Euglypha* plates in the Finland samples. However, *Lesquereusia*, which was never recorded in the Adirondacks, was common in the eastern Finland lakes. The difference in abundance may be related to factors affecting the rate of transport of the plates. The catchments of the Adirondack lakes are relatively small but the slope steepness creates a greater elevational gradient and hence a faster transport mechanism. Other factors such as precipitation, tributaries, extent of habitat (i.e. presence of *Sphagnum* and other mosses) and factors affecting the concentration of the reference diatoms, need also to be considered.

No distinct latitudinal gradient of the testaceans emerged from our observations. Such a result can be explained and attributed to their microhabitat, which is mainly moss- and *Sphagnum*-based, and is present throughout the latitudinal transect.

Conclusions

The results obtained from the combined CCA seem to confirm a general relationship between the distribution of diatom and ecoclimatic/vegetational zones. Water chemistry and habitat affinities reflected by the diatom assemblages confirm that diatom distributions are strongly associated with lake water acidity and depth/habitat availability. In addition, substrate texture seems to be an important factor in determining diatom assemblage composition. In general, floristic changes across tree-line in Fennoscandia are rather obscure when compared to those observed in the Yellowknife area and other regions in the western Canadian Arctic (i.e. the Mackenzie Delta area; Pienitz et al. 1995). The more pronounced floristic changes across tree-line in North America are most likely the result of particularly steep ("zonal") climatic and vegetational gradients in this part of the northern hemisphere. In addition, climatically induced floristic changes may be obscured by the much greater diversity of sampling sites/habitats included in the Fennoscandian sampling transect. Interestingly, although there were marked differences in chrysophytes and protozoan assemblages between sites, there were no discernable patterns with respect to latitude.

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