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Seasonality of phytoplankton in subarctic Lake Saanajärvi in NW Finnish Lapland

Abstract We studied the phytoplankton seasonality in the subarctic Lake Saanajärvi, Finnish Lapland, in two successive years with slightly different weather conditions. The total number of taxa studied during the period was 148. Characteristic phytoplankton species were chrysophytes *Uroglena* sp., *Chrysococcus* spp., *Dinobryon* spp and diatoms *Cyclotella* spp. The results were analysed in relation to weather patterns and physico-chemical variables measured from the lake during the 2 years. The seasonal dynamics of phytoplankton were characterized by (1) maxima in total densities during autumn and minima in winter; (2) different species reaching maximum and minimum densities during different seasons; (3) close to equilibrium state during strong thermal stratification in 1997 with dominance of only a few taxa; and (4) two annual maxima in species diversity at the beginning of the thermal stratification and during the autumn overturn. According to canonical ordinations, calcium buffer capacity, nutrients and temperature all play a role in regulating algal biomass and species compositions. With regard to physical factors, the length of the mixing cycle, thermal stability of the water column and water temperature seem to have a major control over the plankton dynamics. The length of the ice-free season seems to be more decisive for biomass production than the thermal stability during this period, which, in turn, appears to affect the algal biodiversity.

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Introduction

Although the arctic tundra in Finland contains myriad lakes of all sizes, phytoplankton studies are rare. Earlier phytoplankton studies in Finnish Lapland have been mostly descriptive and based on occasional samples only (Levander 1901; Järnefelt 1934; Luther 1937; Eloranta 1986). Only recently more detailed limnological and biological studies were carried out in lakes in Finnish Lapland (Rautio et al. 2000; Sorvari et al. 2000; Korhola et al. 2002b). Situated outside the heavily inhabited and industrialized areas, the northern lakes provide a unique opportunity and a wide range of conditions to study the dynamics of water chemistry and succession of undisturbed phytoplankton communities. Moreover, as algal communities are known to be vulnerable to environmental changes (Reynolds 1984a), the alterations in phytoplankton communities in pristine lakes may serve as good tool to track environmental changes.

In general, seasonal changes in the plankton are strongly influenced by inter-annual changes in the weather conditions and associated changes in the lake thermal patterns (Goldman et al. 1996; Hinder et al. 1999; George 2000; Kunz and Diehl 2003). For Arctic lakes, major changes in their physical conditions occur during the ice melt in spring and rapid cooling in autumn. Especially during these periods, the phytoplankton communities may change substantially, with meteorological forcing having significant control over their development and seasonal successions.

Recent theory formulation in aquatic ecology has introduced the concept of "climax" into pelagic succession (see Naselli-Flores et al. 2003 and literature herein). According to this theory, phytoplankton assemblages or associations, similar to terrestrial vegetation, shall achieve steady state or equilibrium at some stage of their seasonal succession (Dokulil and Teubner 2003). Sommer et al. (1993) defined such an equilibrium phase as a period of more than 2 weeks of coexistence of one, two

or maximum of three species contributing not less than 80% to the standing biomass with no significant changes in the biomass. Rojo and Álvarez-Cobelas (2003) demonstrated that such steady-state phytoplankton assemblages are generated both in stable and perturbing environments.

Lake Saanajärvi (NW Finnish Lapland) has been the Finnish monitoring site for two European-wide research projects: Mountain Lake Research (MOLAR), and European Mountain Lake Ecosystems: Regionalisation, Diagnostics & Socio-economic evaluation (EMERGE), both funded by the EU. As a part of these programmes, the lake has been monitored for its physical, chemical, biological and sedimentological features since 1996. In this study, we describe the seasonality and inter-annual differences in phytoplankton community structure in relation to hydrochemical parameters based on regular monitoring carried out in the lake for two successive years. Our study site, Lake Saanajärvi, constitutes an interesting test laboratory for assessing the significance of stable environmental conditions to the formation of an equilibrium phase, since the values of the most common physical and chemical variables do not change much during the summer stratification period (Rautio et al. 2000; Sorvari et al. 2000).

Materials and methods

Study site

Lake Saanajärvi is a small (70 ha) clear-water lake in a remote mountain area in NW-Finnish Lapland (69°05′N, 20°87′E) near the border of Sweden and Norway (Fig. 1). Climatically, the lake environment lies between the North Atlantic oceanic climate and the Eurasian continental climate. The mean annual temperature is $-2.6°C$ (mean January $= -14.1°C$ and mean July $= 10.6°C$) and the growing season is ca. 110 days (Järvinen 1987). Lake Saanajärvi is located in the rainshadow of the Norwegian mountains and therefore rainfall is low in the area, mean annual precipitation being ca. 400 mm.

Lake Saanajärvi is located in a topographical pocket between two fells in the treeless tundra at 679.4 m above sea level. The catchment area is covered by subalpine vegetation and bare rock surfaces. The bedrock consists of sedimentary rocks, dolomitic limestones, Paleozoic Caledonian schist and gneiss (Atlas of Finland 1986). Due to the alkaline bedrock, Lake Saanajärvi has a good buffering capacity against acid substances. There is no direct human activity near the lake.

The lake is approximately 1.5 km long and has a maximum width of about 0.8 km. The shoreline is rocky and steep. Some aquatic mosses grow in the littoral region of the lake but macrophytes are absent. The maximum water depth is about 24 m and the lake is dimictic with a regular pattern of a short spring overturn, summer stratification and relatively long autumn overturn (Sorvari et al. 2000; Korhola et al. 2002a). The lake is ice-free for about 3 months from July to October. The summer stratification is usually well developed and the relatively steep thermocline lies at depths of 10–12 m before the autumn overturn. Maximum surface-water temperatures (13–15°C) are measured in the beginning of August and autumn overturn starts normally when the water is around 8°C in mid-September. The hypolimnetic water temperature is 3–4°C under ice, and varies from 5°C to 7°C during the summer stratification period. The autumnal mixing period in the lake is relatively long ($\approx$50 days). Ice cover reaches its maximum of ca. 1 m in May.

Lake Saanajärvi is an oligotrophic clear water mountain lake above the treeline with low nutrient levels, neutral pH (mean pH = 6.9), and low conductivity (mean conductivity = 27.5 μS cm^{-1}) (Sorvari et al. 2000). The dissolved oxygen is close to the saturation point for most of the year, with the exception of late spring (late May–early June) when the bottom waters are depleted in oxygen. Profiles of pH, conductivity, water temperature and chlorophyll-a were presented in Rautio et al. (2000) and Sorvari et al. (2000).

Meteorological measurements

Local weather conditions (air temperature and wind velocity) were measured from the beginning of August 1996 to the end of 1997 with automatic weather station (Vaisala Milos 500 Automatic Weather Station), installed 5 m SE of the lake shoreline. Variables measured included air temperature, humidity, wind speed and direction, and global radiation. The sensors were 3 m above ground level. Measurements were made every third hour using 30 min mean values. Monthly averages for air temperature and wind velocity were calculated from these measurements. In addition, weather data from the beginning of 1996 to the end of July 1996 were received from the nearby meteorological station of the Finnish Meteorological Institute, located at an open site about 600 m from the shoreline.

Sampling for physico-chemical variables

During the open-water season in 1996 (4 July–24 September), the lake was sampled twice a month for water chemistry. In the summer of 1997 the lake was sampled once a week from 10 June to August 13 and on a monthly basis from 13 August to 28 October. Samples for chemical analyses were taken in the deepest part of the lake (24 m) from ten different depths (0, 2, 4, 6, 8, 10, 12, 16, 20, 23 m) using a Limnos water collector (volume 2 L). In the winters of 1996–1997 and 1997–1998 water chemistry samples were taken approximately once every 2 months from the same location. Samples for silica (Si), ammonium nitrate (NH$_4$-N), nitrate nitrogen (NO$_3$-N),

Fig. 1 Map showing the location, catchment boundary and sampling site of Lake Saanajärvi in NW Finnish Lapland
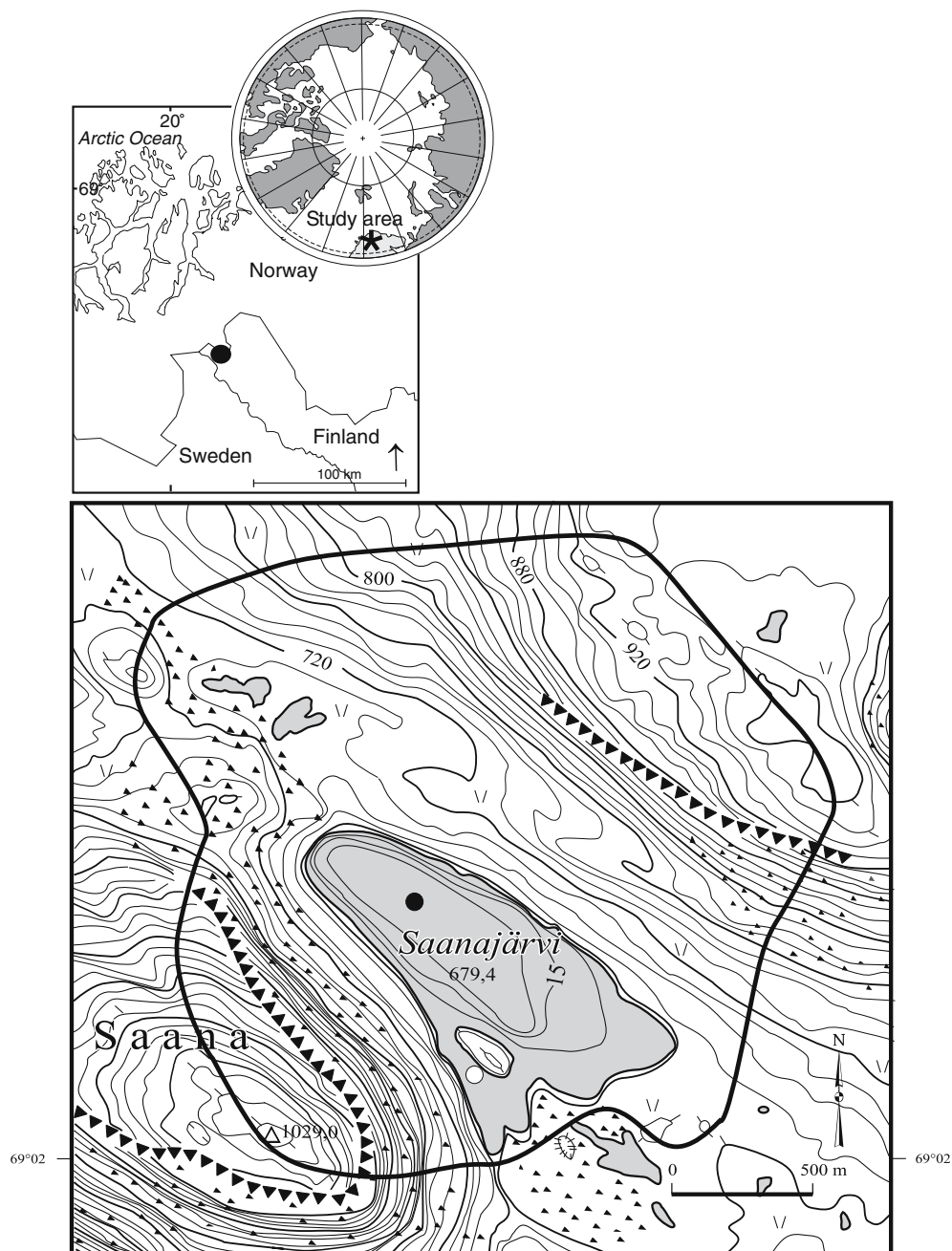
orthophosphate phosphorus (PO_4), total phosphorus (TP) and total nitrogen (TN) were analysed in the Laboratory of Physical Geography, University of Helsinki, while chlorophyll a (chl-a) was determined at the Lammi Biological Station. For chl-a analysis, 2–3 L of water was filtered through a GF/C Whatman filter and frozen for further analysis. In the laboratory, chl-a was extracted in 96% ethanol overnight at room temperature in the dark. After that the samples were filtered and measured for absorbance using wavelengths of 750, 663, 647, 630, 480, 430 and 410 nm. The chlorophyll-a concentrations were then calculated after Jefferey and Humphrey (1975). Oxygen, pH, temperature and conductivity were measured in situ using probes from HANNA instruments (for details see Sorvari et al. 2000). The main chemical parameters and lake characteristics are listed in Table 1.

The thermal stability of the water column was calculated from measured water temperature profiles using Brunt-Väisälä frequency and the following equation reported in Mortimer (1974):

$$N^2 = (g/\sigma_{avg})((\sigma_6 - \sigma_0)/z), \tag{1}$$

where $(\sigma_6-\sigma_0)/z$ (kg m^{-3}) is the mean density gradient of lake water between the surface (σ_0) and the depth of 6 m, σ_{avg}(kg m^{-3}) is the density given by $(\sigma_6-\sigma_0)/z$, and g is gravitational acceleration (m s^{-2}).

Table 1 Lake characteristics, minimum, maximum and median values of limnological variables during the two open water seasons 1996 and 1997 in Lake Saanajärvi. Limnological data is divided into upper and lower water column

Parameter	Value
Catchment area (ha)	460
Lake area (ha)	70
Maximum lake depth (m)	24
Shoreline length (m)	4,697
Length (m)	1,556
Width (m)	817
Thermal structure	Dimictic
Secchi (m)	8.5 (mean)

	Upper water column (0–8 m)		Lower water column (10–23 m)	
	Range	Median	Range	Median
Temperature (°C)	0.8–14.6	7.1	0.9–10.6	5.3
pH (unit)	5.4–7.9	7.0	6.1–7.6	6.9
Conductivity (μS cm^{-1})	8.5–31.7	27.1	18.1–40.8	25.8
Total P (μg l^{-1})	[a]–5.2	[a]	[a]–5.6	[a]
Total N (μg l^{-1})	29.8–141.0	107.9	58.9–157.0	111.7
NO$_3$-N (μg l^{-1})	[a]–107.3	[a]	[a]–128.4	[a]
NH$_4$-N (μg l^{-1})	[a]–37.9	8.1	[a]–26.5	7.0
Si (mg l^{-1})	0.2–0.6	0.5	0.4–1.7	0.6
Chl-a (μg l^{-1})	0–1.7	0.6	0–1.6	0.5

[a]Below detection limit: total $P < 5$ μg l^{-1}, NO$_3$-N < 40 μg l^{-1}, NH$_4$-N < 3 μg l^{-1}

Phytoplankton sampling, identification and enumeration

Phytoplankton samples were collected with a Limnos water collector at depths of 0, 2, 6, 10 and 23 m together with the water samples, but in the summer of 1997 when sampling interval was 1 week, phytoplankton was sampled only every second week. The samples were preserved with acid Lugol's iodine and stored under dark and cool conditions. Species composition and biomass were determined with an inverted microscope according to Utermöhl (1958). Water (100 ml) was sedimented for 48 h and depending on the algal density 75, 100 or 200 randomly selected fields were counted at 400× magnification. Additionally, the entire bottom of the chamber was counted at 125× magnification for large colonies, filaments and desmids. The counting units were cells, colonies or trichomes calculated as units of 100 μm length. The identification was done at the species level, whenever possible. The smallest algae (< 3 μm) were grouped together as picoplankton, and some small flagellates (5–8 μm) were identified only to the class level (especially in chrysophytes). Because of the constraints of light microscopy, the diatoms were mostly identified to the genus level. Phytoplankton biomass was calculated as wet weight (WW) from algal volumes, which were either based on measurements or taken from literature (Naulapää 1972). Phytoplankton biomass was estimated by assuming a biovolume-to-wet weight biomass factor of 1. Phytoplankton taxonomy and nomenclature are primarily based on Bourrelly (1966, 1968), Komárek and Fott (1983), Starmach (1985) and Tikkanen (1986). The functional groups, when possible, were determined based on literature (Reynolds 1988; Kruk et al. 2002; Reynolds et al. 2002), and for some species the functional group was decided based on the morphological and ecological characteristics of the species.

Community analyses

The richness, diversity (Shannon index H') (Krebs 1999) and evenness phytoplankton species (Pielou's J'; Pielou 1975) were calculated on the basis of the phytoplankton biomass of each species. The differences in phytoplankton diversity and evenness between the two monitoring years were analysed with paired t-tests (Hollander and Wolfe 1999).

Canonical correspondence analysis (CCA), a direct gradient analysis technique (Jongman et al. 1995; ter Braak and Smilauer 1998), was used to investigate the relationship between phytoplankton and physico-chemical parameters. The phytoplankton data were log-transformed prior to the analysis in order to stabilise the variance and to optimise the signal-to-noise ratio in the data set (Prentice 1980). Down weighting for rare species was performed. Forward selection and associated Monte Carlo permutation tests (199 unrestricted permutations) were used to identify a subset of environmental variables that contributed mostly to the distributions of phytoplankton in the data set.

The seasonality of phytoplankton assemblages was also studied using the functional groups approach (Reynolds 1988; Reynolds et al. 2002; Kruk et al. 2002), which classifies the phytoplankton species on the basis of

their adaptive strategies to various disturbance or stress factors.

The program R (http://cran.r-project.org/) was used for the calculation of Shannon and Evenness indices, SPSS version 10.0 for paired t-tests, and the CANOCO for Windows package (ter Braak and Smilauer 1998) for the CCA.

Results

Weather conditions 1996–1997

Only minor changes were observed in the weather conditions between the two sampling years. In 1996, the warmest month was August (monthly mean air temperature 9.1°C) and the maximum air temperature (19.4°C) was measured in the beginning of August. In 1997, the warmest month was July (monthly mean air temperature 9.8°C) and the maximum air temperature (19.6°C) was measured in mid-July. The monthly mean air temperatures were generally 1–1.5°C higher in 1997 than in 1996 from May to September, with the exception of August, which was warmer in 1996. The mean air temperature during the open water season was 3.6°C in 1996 and 3.8°C in 1997.

In both years the average wind velocity was lowest in July (4.7 ms^{-1} in 1996 and 4.8 ms^{-1} in 1997) and highest in October (8.6 ms^{-1} in 1996 and 8.7 ms^{-1} in 1997). However, in 1996 there were more periods of high wind velocity (> 15 ms^{-1}) than in 1997, especially in autumn (Fig. 2).

Physical and chemical properties of the lake

Lake Saanajärvi was covered by ice for about 9 months in both years and the ice cover reached its maximum thickness of 1 m in mid-May. In 1996, the ice on Lake Saanajärvi melted completely on 27 June, while in 1997, total ice-out took place ten days later. The spring overturn lasted for 34 days in 1996 but only 9 days in 1997. Thermocline formation occured at the end of July in 1996 and in mid-July in 1997. It appeared first at 4–6 m; later in the season it was at 10 m. The summer stratification period was 2 weeks longer in 1997 than in 1996, although the overall duration of the open water season was distinctively shorter in 1997 than in 1996. Maximum surface water temperatures of 14.6 and 13.3°C were reached in early August in 1996 and in late July in 1997, respectively. During the stratification period the water temperature in the hypolimnion was between 6°C and 7°C in 1996, but only 4.8°C in 1997. The water column thermal stability, expressed as the Brunt Väisälä frequency, was relatively low (< 0.0002 s^{-2}) throughout the monitoring period, except for mid-August in 1996 and the last 2 weeks of July in 1997 when the peak values were reached (Fig. 2).

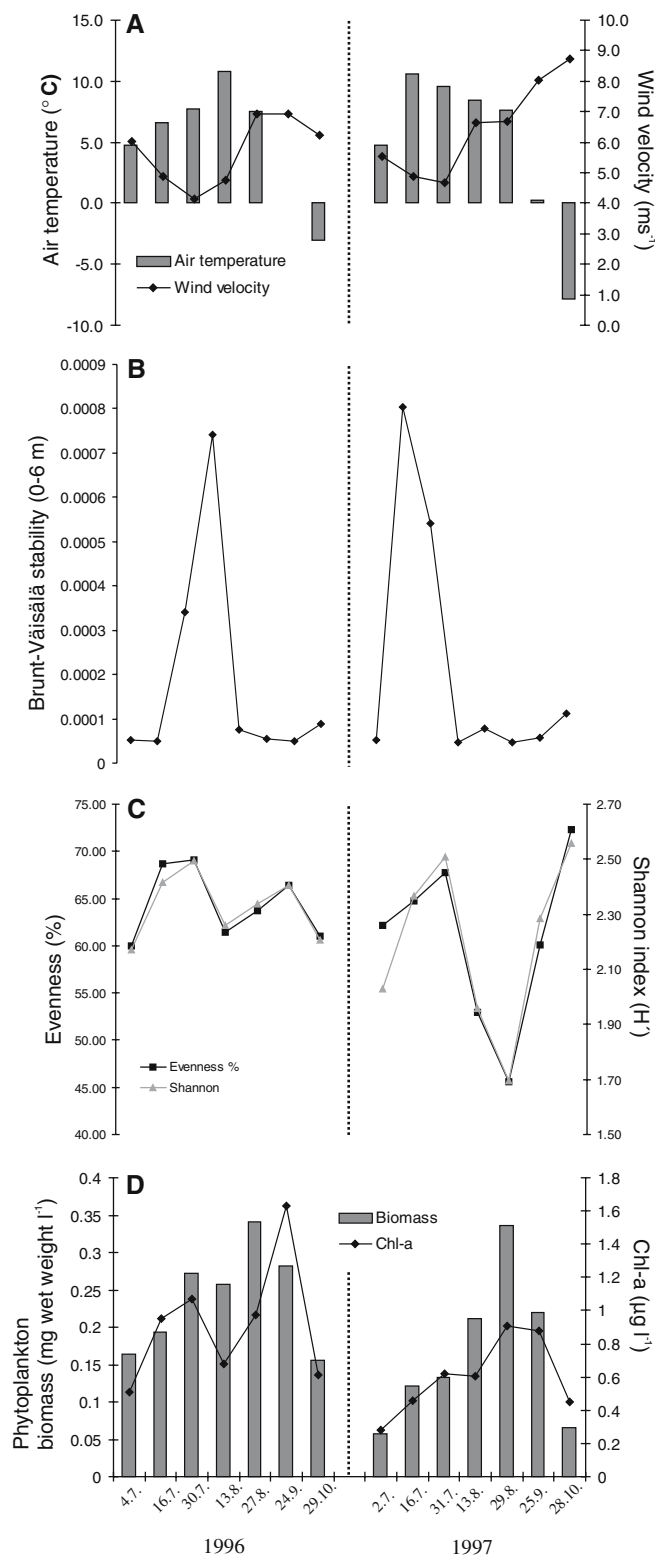The mean Secchi depth of the lake for the monitoring period 1996–1997 was 8.5 m (min 5.7 m, max 10.4 m).

Fig. 2 Selected meteorological, physical and biological characteristics during the open water season of the two study years. **a** Air temperature and wind velocity presented as running mean; **b** Brunt-Väisälä stability between the surface (0 m) and 6 m depth; **c** phytoplankton biodiversity (Shannon) and evenness (Pielou); **d** mean phytoplankton biomass and chlorophyll-*a* in the upper water column (0–6 m)

Water pH was almost constant throughout both sampling years (mean pH = 7.1, min 5.4, max 7.9), except for a very short period in the spring when waters of melting snow with lower pH drained into the lake. Alkalinity, conductivity and the concentrations of major ions were low and relatively stable throughout the study period (Table 1). Calcium concentration varied between 2.7 mg l^{-1} and 3.2 mg l^{-1}, with maximum values observed in late autumn of both years. Nutrient concentrations were low at all times, except for a short period of snow melting: PO_4-P was under detection limit of the analytical method (< 1 µg l^{-1}), TP concentrations varied from values under the detection limit to 5.6 µg P l^{-1} (median concentration below detection limit), nitrate (NO_3-N) varied from concentrations below detection limit to 128.4 µg l^{-1} (median concentration below detection limit), and ammonium (NH_4-N) from concentrations below detection limit to 26.5 µg l^{-1} (median 7.6 µg l^{-1}). Total nitrogen (TN) concentrations varied from 29.8 µg l^{-1} to 157 µg l^{-1}. In both years the maximum concentrations were measured in the spring after the ice out, minimum concentrations occurred in autumn. In 1997 the relatively high spring concentration of TN decreased rapidly and remained low (54 µg l^{-1}) for a period of 2 weeks at the end of July. Maximum values for TP and nitrate were observed in spring under ice and those for ammonium in the hypolimnion during the summer stratification period. In autumn, the concentrations of nutrients (NH_4-N, $NO_2 + NO_3$ and PO_4-P) were below the detection limit.

Seasonal and vertical distribution of chlorophyll

Chl-a concentrations in the water column were low (maximum 1.7 µg l^{-1}, median 0.6 µg l^{-1}) throughout the studied period, with one annual maximum phase during autumn in both years. In 1996 median Chl-a concentration during the open water season was higher than in 1997 (1996 median 0.8 µg l^{-1}; 1997 median 0.4 µg l^{-1}). During stratification Chl-a concentrations in the epilimnion (1 µg l^{-1}) were above values from the hypolimnion (0.3 µg l^{-1}) below the thermocline (Fig. 3). Within the thermocline (ca. 6–8 m depth), Chl-a showed a distinct maximum particularly during the stratification period in 1996. During the dark winter (November–May) chlorophyll-a concentrations declined to a value close to 0 µg l^{-1} in the entire water column.

Species composition and biomass

In total, 148 phytoplankton taxa (including some heterotrophic flagellates) belonging to 88 genera were identified during the two monitoring years (Table 2). The most important algal groups in terms of both abundance and total biomass were chrysophytes, diatoms and dinoflagellates.

Phytoplankton biomass based on the cell counts was low throughout the study period, ranging from 0.04 mg to 0.47 mg WW l^{-1} (mean 0.19 mg l^{-1}) (Fig. 3). In general, average biomasses were slightly higher in 1996 than in 1997. A single biomass maximum was measured in both years. In 1996 the annual maximum biomass of 0.47 mg WW l^{-1} was observed in mid-August at a depth of 10 m depth. In 1997, the maximum biomass was 0.42 mg WW l^{-1}, measured close to the surface in late August.

Frequently occurring cyanophyte species were Cyanodictyon reticulatum, C. planctonicum and Chroococcus minutus. Cyanophyte abundance and biomass was low throughout the study period (maximum biomasses of 0.004 mg WW l^{-1} in 1996 and 0.005 mg WW l^{-1} in 1997). Especially in 1997, the cyanophytes were most abundant in autumn, both in terms of biomass and the number of species present.

Cryptophytes occurred throughout the whole open water season, with highest abundances observed during the summer stratification period, except for Cryptomonas ovata, which was most abundant in the autumn. The mean biomass of cryptophytes was 0.02 mg WW l^{-1} for the open water season in both years.

Dinoflagellates were more common in 1996 than in 1997 (mean biomass in the open water season 0.03 mg WW l^{-1} in 1996 and 0.01 mg WW l^{-1}, respectively). Maximum biomass was observed in mid-August in 1996 (0.16 mg WW l^{-1}) and in mid-July in 1997 (0.06 mg WW l^{-1}). Most dinoflagellates belonged to the genus Gymnodinium, with Gymnodinium helveticum being a typical species especially in the summer and autumn of 1996.

Chrysophytes were the dominant algal group for most of the study period, especially in 1997 (mean biomass in the open water season 0.08 and 0.1 mg WW l^{-1}, respectively). The maximum biomass was observed in late-September in 1996 (0.16 mg WW l^{-1}) and in late-August in 1997 (0.33 mg WW l^{-1}). The most frequent chrysophyte taxa in both years were Uroglena sp, Chrysococcus spp., Dinobryon spp., Stichogloea olivaceae and Pseudopedinella sp.. Uroglena sp. contributed up to 45% of the total phytoplankton biomass in August 1996 and up to 65% in August 1997.

The mean biomass of the diatoms was 0.05 mg WW l^{-1} in the open water season of 1996 and 0.01 mg WW l^{-1} in 1997. Diatoms, especially the centric Cyclotella species (C. rossii and C. comensis) contributed 30–40% of the total phytoplankton biomass from late-August to late-October 1996. In 1996 the maximum biomass of diatoms was 0.2 mg WW l^{-1}, observed in late-August and consisted mostly of centric diatoms. In 1997, the maximum biomass was only 0.05 mg WW l^{-1} and the most common diatoms were Surirella species, most likely of benthic origin.

Chlorophytes were most abundant in the summer stratification period and at the start of the autumnal overturn in both years. The mean biomasses in the open water season were 0.04 mg WW l^{-1} in 1996 and 0.02 mg WW l^{-1} in 1997. In 1996, the most abundant chlorophyte species were Botryococcus braunii, Scenedesmus ecornis, Tetraëdron minimum and Elakatothrix gelatinosa. In
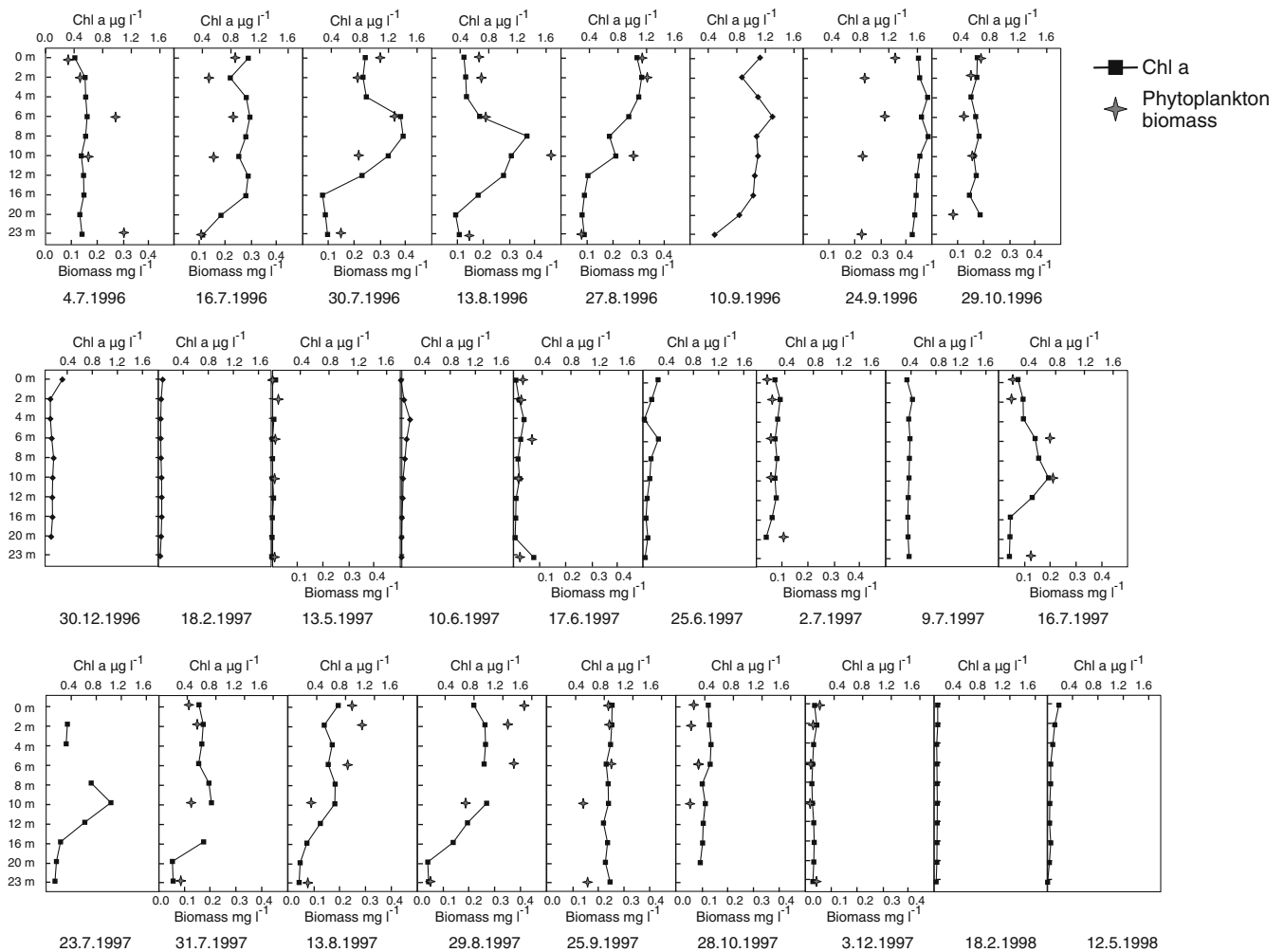
Fig. 3 Vertical profiles of chlorophyll-*a* and phytoplankton biomass during the monitoring period 4 July 1996–12 May 1998

1997, the most common chlorophytes were *Coenocystis subcylindrica, E. gelatinosa* and *Gloeotila fennica.*

The number of taxa per sample varied between 22 and 49 (mean 38). Phytoplankton diversity (Shannon) and evenness (Pielou's) showed similar patterns throughout the study period (Fig. 2) with two annual maxima in each year. The first one occurred at the beginning of the thermal stratification in late July and the second one during the autumn overturn. The mean values for phytoplankton biodiversity and evenness were higher in 1996 (diversity = 2.33, evenness = 0.64) than in 1997 (diversity = 2.09, evenness = 0.58), especially in summer. The differences in biodiversity and evenness between the 2 years were statistically significant, especially during the summer period (paired *t*-test, diversity: $P = 0.003$, evenness: $P = 0.002$, $n = 30$).

Vertical distribution of phytoplankton

The vertical distribution of phytoplankton in Lake Saanajärvi differed both seasonally and between taxa.

During the summer stratification period, the highest phytoplankton biomass was measured in the thermocline in 1996 and in the epilimnion in 1997 (Fig. 3). Biomass and chlorophyll a were significantly correlated ($r = 0.69$, $P = 0.01$, $n = 69$). In general, chrysophytes and chlorophytes preferred the epilimnia, whereas cryptomonads and dinoflagellates had their maximum biomasses usually at around 10 m.

Seasonal variation in phytoplankton assemblages

In early July 1996, the phytoplankton biomass was higher than in 1997 (total biomass in the upper water column (0–6 m), 0.16 and 0.06 mg WW l^{-1}, respectively). The biomass consisted mostly of chrysophytes, dinoflagellates, cryptophytes and chlorophytes until the end of August when diatoms became the dominant algal group. In 1997, the whole open water season was dominated by chrysophytes, with dinoflagellates being the subdominant group in July, followed by cryptophytes and chlorophytes later in the season (Fig. 4).

Based on the thermal structure of the lake, three seasonal periods can be identified in Lake Saanajärvi during the open water phase. The following thermal

Table 2 List of phytoplankton species and their occurrence (+ present, + + frequent, + + + dominant) in Lake Saanajärvi during the three seasonal periods (*SP* spring, *SU* summer, *A* autumn) in open water seasons 1996 and 1997

Taxon name	1996			1997		
	SP	SU	A	SP	SU	A
Cyanophyceae						
Anabaena sp.	+	−	−	−	+	+
Aphanocapsa sp.	−	+	+	−	+	+
Chroococcales sp.	−	−	−	−	−	+
Chroococcus minutus (Kützing) Nägeli	+	+	+	+	+	+
Chroococcus sp.	−	−	−	−	−	+
Coelosphaerium sp.	+	−	−	−	−	+
Cyanodictyon planctonicum Meyer	−	+	−	+	+	+
Cyanodictyon reticulatum (Lemmermann) Geitler	+	−	−	−	−	+
Eucapsis alpina Clements and Shantz	+	+	−	−	−	−
E. minuta Fritsch	−	−	−	−	+	+
Merismopedia glauca (Ehrenberg) Nägeli	−	−	−	−	−	+
M. warmingiana Lagerheim	−	+	−	−	−	−
Microcystis reinboldii (Richter) Forti	+	+	−	−	−	+
Microcystis sp.	−	−	−	−	−	+
Pseudoanabaena limnetica (Lemmermann) Komarek	+	−	−	−	−	−
Rhabdoderma lineare Schmidle and Lauterborn	+	−	−	−	−	−
Snowella sp.	−	+	−	−	+	+
Woronichinia naegeliana (Unger) Elenkin	−	−	+	−	−	+
Cryptophyceae						
Cryptomonas cf. *ovata* Ehrenberg	+	+	+	+	+	+ +
Cryptomonas spp.	+ +	+ + +	+ +	+ +	+ + +	+ +
Katablepharis ovalis Skuja	+	+	+	+	+	+
Rhodomonas lacustris Pascher and Ruttner	−	−	+	−	−	+
Dinophyceae						
Glenodinium sp.	+	+	+	+	+	+
Gymnodinium helveticum Penard	+	+ +	+ +	−	+	+
Gymnodinium spp.	+ + +	+ + +	+ +	+ +	+ +	+ +
Peridinium spp.	+	+	−	−	+	−
Chrysophyceae						
Bicosoeca spp.	−	−	−	+	+	−
Bitrichia chodatii (Reverdin) Hollande	−	+	+	+	+	+
Chromulina spp.	+	+	−	+	+	+
Chrysamoeba tetragene (Skuja) Matvienko	+	+ +	+	+	+	+
Chrysidiastrum catenatum Lauterborn	+	+ +	+	+	+	−
Chrysamoeba sp.	+	−	−	−	−	−
Chrysococcus cordiformis Naumann	+	−	−	−	−	−
C. rufescens Klebs	−	−	−	+	−	−
Chrysococcus spp.	+ + +	+ + +	+ +	+ +	+ +	+ +
Chrysolykos planctonicus Mack	+	−	−	+	−	−
C. skujai (Nauwerck) Bourrelly	+	−	−	+	+	−
Chrysophyceae flagellated	+ +	+ +	+ +	+ +	+ +	+ +
Dinobryon acuminatum Ruttner	−	+	+	+	+	−
D. bavaricum Imhof	+	+	+	+	+	+
D. borgei Lemmermann	−	−	−	+	+	+
D. crenulatum West and West	+ +	+ +	+	+	+ +	+
D. cylindricum Imhof	+ +	+	−	+	+	+
D. cylindricum var. *palustre* Lemmermann	−	−	−	+	−	+
D. divergens Imhof	+	+	−	+	+	+
D. sertularia Ehrenberg	−	−	−	−	+	−
D. sertularia var. *protuberans* (Lemmermann) Krieger	−	−	−	+	+	−
D. sociale Ehrenberg	+	+	+	+	+	−
D. sociale var. *americanum* (Brunnthaler) Bachmann	−	−	−	−	+	+
Dinobryon spp.	+	+	+	+	+	+
Kephyrion boreale Skuja	+	−	−	+	+	−
K. cupuliforme Conrad	+	+	+	+	+	−
K. ovale (Lackey) Huber−Pestalozzi	−	−	+	−	−	−
Kephyrion spp.	+	+	−	+	+	+
Mallomonas akrokomos Ruttner	+	−	+	−	−	−
M. caudata Ivanov	−	−	−	−	+	−
Mallomonas spp.	+	+	+ +	+	+	+
Pseudopedinella sp.	+	+	+	+ +	+ +	+ +
Spiniferomonas spp.	+	−	+	+	+	+
Stichogloea olivacea Chodat	+	+ +	+ +	+	+ +	+ +

Table 2 (Contd.)

Taxon name	1996			1997		
	SP	SU	A	SP	SU	A
Synura sp.	+	−	+	−	−	−
Uroglena sp.	+ +	+ + +	+ + +	+	+ + +	+ + +
Haptophyceae						
Chrysocromulina sp.	+	+	+	+	+	+
Prymnesium sp.	+	+	−	−	−	−
Bacillariophyceae						
Achnanthes minutissima Kützing	−	−	−	−	+	−
Asterionella formosa Hassal	−	+	+	−	+	+
Aulacoseira subarctica (Müller) Simonsen	+	+	+	+	+	+
Cyclotella spp. (mainly *C. rossii* & *C. comensis*)	+ +	+ + +	+ + +	+	+	+
Cymbella sp.	+	+	+	−	+	+
Fragilaria ulna (Nitzsch) Lange−Bertalot	−	+	−	−	−	−
Fragilaria spp.	+	+	+	+	+	+
Surirella delicatissima Lewis	−	+	−	−	−	−
Surirella spp.	+ +	+ +	+ +	+ +	+	+ +
Tabellaria fenestrata var. *asterionelloides* Grunow	−	+	+	−	−	−
T. flocculosa (Roth) Kützing	+	+	−	−	+	+
Xanthophyceae						
Goniochloris cf. *laeve* Pascher	−	−	−	+	+	−
Goniochloris mutica (Braun) Fott	+	−	−	−	−	−
Isthmochloron trispinatum (West and West) Skuja	−	+	−	−	−	−
Tetraëdriella jovetii (Bourrelly) Bourrelly	+	+	+	+	+	+
Tetraëdriella sp.	−	+	−	−	+	+
Euglenophyceae						
Euglena sp.	+	+	−	−	−	−
Trachelomonas hispida (Perty) Stein	+	+ +	−	−	−	−
Trachelomonas volvocina Ehrenberg	−	−	−	+	−	−
Trachelomonas spp.	+	−	−	+	+	−
Chlorophyceae						
Ankistrodesmus falcatus (Corda) Ralfs	−	+	+	−	−	−
A. fusiformis Corda	+	−	−	−	−	+
Ankistrodesmus sp.	+	+	+	+	+	+
Botryococcus braunii Kützing	+	+ +	+	+	+	+
Carteria spp.	+	+	+	−	+	−
Chlamydocapsa sp.	+	−	−	+	+	−
Chlamydomonas spp.	+	+	+	+	+	+
Coelastrum microporum Nägeli	+	−	−	−	−	−
Coenochloris sp.	−	−	−	−	+	−
Coenocystis subcylindrica Korshikov	−	+	+	−	+ +	+ +
Coenocystis sp.	−	−	−	−	+	−
Crucigenia fenestrata (Schmidle) Schmidle	+	−	−	−	−	−
Dictyosphaerium pulchellum Wood	−	−	+	−	−	−
Didymocystis bicellularis (Chodat) Komárek	+	+	+	+	+	+
Elakatothrix gelatinosa Wille	−	+	+	−	+ +	+
E. genevensis (Reverdin) Hindak	+	+	+	+	+	+
Eutetramorus fottii (Hindák) Komárek	−	−	−	−	+	−
Gloetila fennica Järnefelt	+	+	−	+	+	+
Gyromitus cordiformis Skuja	+	+	+	+	+	+
Kirchneriella sp.	+	−	−	−	−	−
Koliella sp.	+	+	+	+	+	+
Lagerheimia cf. *quadriseta* Lemmermann	+	−	−	−	−	−
Monomastix sp.	+	−	+	+	+	−
Monoraphidium arcuatum (Kors) Hindák	+	+	+	+	+	+
M. dybowskii (Woloszynska) Hindák & Komárková−Legenerová	+	+	+	+	+	+
Oocystis elliptica West	−	−	+	−	−	−
O. lacustris Chodat	+	+	+	+	+	+
O. rhomboidea Fott	+	+	+	−	+	+
Phacotus lenticularis (Ehrenberg) Stein	+	−	−	+	+	+
Phacotus sp.	−	−	−	−	+	−
Planktococcus sphaerocystiformis Korshikov	−	−	−	−	+	−
Planktosphaeria gelatinosa Smith	+	+	−	−	+	−
Prasinophyceae spp.	+	−	+	+	+	+
Scenedesmus cf. *denticulatus* Lagerheim	+	−	−	−	−	−
Scenedesmus ecornis (Ehrenberg) Chodat	+ +	+ +	+	+	−	+
Scourfieldia complanata West	+	+	−	+	+	−
S. cordiformis Takeda	−	−	−	+	+	+

Table 2 (Contd.)

Taxon name	1996			1997		
	SP	SU	A	SP	SU	A
Sphaerocystis schroeteri Chodat	–	+	–	–	–	–
Tetraedron minimum (Braun) Hansgirg	+ +	+ +	+ +	+	+	+
T. triangulare Korshikov	+	–	–	–	–	–
Tetrastrum sp.	+	+	+	+	+	+
Willea irregularis (Wille) Schmidle	–	–	–	–	–	+
unidentified chlorophyte colonies	–	+	+	+	+	+
Conjugatophyceae						
Arthrodesmus octocornis Ehrenberg	–	–	+	–	–	+ +
Closterium acutum Brébisson	–	–	–	+	–	–
Closterium sp.	–	–	–	–	+	–
Cosmarium bioculatum Brebisson	–	+	–	–	–	–
C. blyttii Wille	–	+	–	–	–	–
C. contractum Kirchner	+ +	+ +	+ +	–	–	+
C. depressum (Nägeli) Lundell	–	+	–	–	–	–
C. phaseolus Brebisson In Ralfs	–	+ +	–	+	–	–
C. pygmaeum Archer	–	–	–	+	–	–
Cosmarium sp.	+	+ +	+ +	+	+	+ +
Euastrum gemmatum Brebisson	–	+	–	–	–	–
Spondylosium planum (Wolle) West and West	+	+	+	–	+	–
Staurastrum anatinum f. *vestitum* (Ralfs) Brook	+	–	–	–	–	–
S. erasum Brebisson	–	+	–	–	–	–
S. paradoxum Meyen	–	+	–	–	–	–
S. teliferum Ralfs	+	–	+	+	–	+
Staurodesmus crassus (West and West) Florin	–	+	–	–	–	–
S. dejectus (Brebisson) Teil	–	–	–	–	–	+
Staurodesmus spp.	–	+	+	+	+	–
Others						
Heliozoa spp.	+	+	+	+	+	+
Paramastix conifera Skuja	+	+	+ +	+	+	+
Telonema sp.	+	+	+	+	+	+
Picoplankton	+	+	+	+	+	+
Unidentified monads	+	+	+	+	+	+
Unidentified small flagellates	+	+	+	+	+	+

periods are used below when describing the seasonality of phytoplankton:

Spring (period of spring overturn; late-June to mid-July): In 1996, the spring phytoplankton was dominated by chrysophytes (especially *Uroglena* sp., *Chrysococcus* spp. and small flagellates), dinoflagellates and cryptophytes. Highest biomass, 0.25 mg WW l^{-1} was measured in mid-July close to the surface, when the lake water was still circulating.

In spring 1997, chrysophytes dominated the algal assemblage, accounting for more than 80% of the total biomass in some samples. The most common taxa were *Pseudopedinella* sp., *Chrysococcus* spp., small flagellates and *Dinobryon cylindricum*. The highest biomass, 0.19 mg WW l^{-1}, was measured at a depth of 10 m in mid July.

Summer (period of thermal stratification; late July to mid-September): In the summer of 1996, the phytoplankton was first dominated by chrysophytes (mainly *Uroglena* sp., small flagellates, and *Chrysococcus* spp.) followed by centric diatoms. Dinoflagellates were subdominant especially below the thermocline. The highest summer biomass, 0.47 mg WW l^{-1}, occurred just below the thermocline at a depth of 10 m in mid-August, when the lake waters became stratified.

In 1997, the summer phytoplankton was dominated by chrysophytes, especially *Uroglena* sp., which made up over 60% of the total biomass in some samples. Dinoflagellates and cryptophytes were the subdominant algal groups in most samples. Highest summer biomass, 0.42 mg WW l^{-1}, occurred close to the surface in late August, when lake stratification started to break up.

Autumn (period of autumnal overturn; mid-September to October): In September 1996 centric diatoms contributed about 30% of the total biomass followed by *Uroglena* sp. (about 15%). Centric diatoms were still
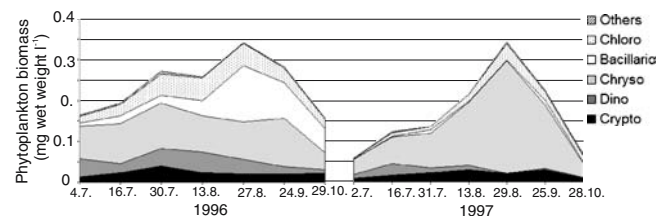

Fig. 4 Phytoplankton biomass of different algal groups in the upper water column (mean biomass of depths 0, 2 and 6 m) during the studied open water seasons in 1996 and 1997. *Crypto* Cryptophyceae, *Dino* Dinophyceae, *Chryso* Chrysophyceae, *Bacillario* Bacillariophyceae, *Chloro* Chlorophyceae

dominant in late October, but the subdominant *Uroglena* sp. was replaced by *Chrysococcus* spp. Other important algae were cryptophytes and *Cosmarium* sp. The highest biomass, 0.35 mg wet weight l^{-1}, was measured at the end of September close to the surface.

In September 1997, the phytoplankton consisted mostly of chrysophytes (60–80% of the total biomass), most important species being *Uroglena* sp., *Stichogloea olivacea*, and *Chrysococcus* spp. In October 1997 chrysophytes dominated the phytoplankton together with colonial chlorophytes such as *C. subcylindrica*. Highest biomass, 0.25 mg WW l^{-1}, was measured at the end of September between 0 m and 6 m.

Functional groups

In both years the spring phytoplankton was dominated by small C-strategist algae (eukaryotic picoplankton, *Chrysococcus* spp. and *Chrysocromulina* sp.). In the summer of 1996, the algal biomass was a mixture of C, S and later R strategists, whereas in summer 1997 only C and S strategists were common. In autumn 1996 over 30% of the total biomass consisted of R strategists, while S strategists, mainly *Uroglena* sp., were subdominant. In autumn 1997 the S strategists were dominant while the R strategists made up only 2–3% of the total biomass.

Community analysis

Canonical correspondence analysis analyses were used to produce bi-plots for sample scores, phytoplankton taxa and environmental variables (Fig. 5), separately for the two sampling years as well as eigenvalues, percentage of explained variance and correlation coefficients with environmental variables for the first four axes (Table 3). 49.9 and 47.8% of the variance in the fitted species data with respect to the environmental variables were explained by the first two axes for the 1996 and 1997 data-sets, respectively. Of the tested environmental variables, forward selection with Monte Carlo permutations showed temperature and calcium (Ca) to be significant in explaining the ordination in 1996, and temperature and TN in explaining the ordination in 1997.

The seasonal variability in phytoplankton communities can be followed by moving clockwise from spring samples to autumn samples in Fig. 5a and c. Spring samples occupy the right side of the plot in both years, associated with lower calcium and pH and higher nutrient concentrations in 1996, and higher nutrient (in particular TN) concentrations in 1997. With few exceptions, the late spring and summer samples are located below axis 1 at the side of the temperature vector. All autumn observations are situated above axis 1 opposite to the temperature vector. Besides temperature, autumn samples were characterized by high calcium values, especially in 1996.

The species bi-plots (Fig. 5b, d) for years 1996 and 1997 reveal both similarities and differences in the arrangement of the taxa in the ordination space. For 1996, *r*-strategists, diatoms (e.g. *Tabellaria flocculosa* and *Aulacoseira subarctica*), some chrysophytes (e.g. *D. cylindricum*) and desmids are associated with higher nutrient concentrations and lower Ca and pH. In both years, motile or non-motile, colonial algae (predominantly chrysophytes along with chlorophytes), such as several species of *Dinobryon*, *Chrysidiastrum catenatum*, *Oocystis lacustris* and *Elakatothrix gelatinosa* were associated with higher water temperatures. In 1996, large-celled flagellates, centric diatoms and non-motile colonial associations, representing predominantly dinoflagellates, chlorophytes and cyanophytes (e.g. *G. helveticum*, *Cryptomonas* cf. *ovata*, *Monoraphidium arcuatum*, and *Aphanothece* sp.), were situated at the upper part of the plot, characteristic for lower water temperatures. In 1997, the autumn samples (upper part of the diagram) were similarly dominated by non-motile colonial associations, albeit by different taxa, together with flagellated species (e.g. *Willea irregularis*, *Botryococcus braunii*, *Chroococcus* spp. and *Rhodomonas lacustris*). In conclusion, similar phytoplankton associations dominated during the stratification periods in 1996 and 1997, whereas clear differences were observed during the mixing periods of spring and autumn. The main spatial and seasonal gradients were associated with Ca and pH (buffer capacity), nutrients and temperature.

Discussion

Lake Saanajärvi is a typical oligotrophic, subarctic lake with regard to its physical and chemical properties (low temperatures, low nutrient concentrations and close to neutral pH) (Pienitz et al. 1997; Rühland and Smol 1998; Duff et al. 1999; Korhola et al. 2002b). The Chl-*a* concentration and phytoplankton biomass classify Lake Saanajärvi as ultra-oligotrophic or oligotrophic lake (Heinonen 1980; Vollenweider and Kerekes 1980; Wetzel 2001) with values below those in natural forest lakes in central and southern Finland (e.g. Heinonen 1980; Eloranta 1995) but comparative to other Arctic lakes (e.g. Hobbie 1980). Arctic lakes are typically low energy systems that are subjected to extreme seasonal variations in day length (Duff et al. 1999). Further, additional abiotic characteristics may limit the growth of algal biomass, including ice and snow coverage, short growing season, low temperature, and reduced absorbed radiation (see. Flanagan et al. (2003) for further details).

Chrysophytes are often noted as the most abundant algal group in oligotrophic, dimictic high latitude lakes (Moore 1978; Nygaard 1978; Eloranta 1986; Duthie and Hart 1987) including this study. Chrysophytes, more generally, dominate in lakes with low summer water temperatures, productivity, nutrient availability, alkalinity and conductivity, and with neutral pH (Sandgren
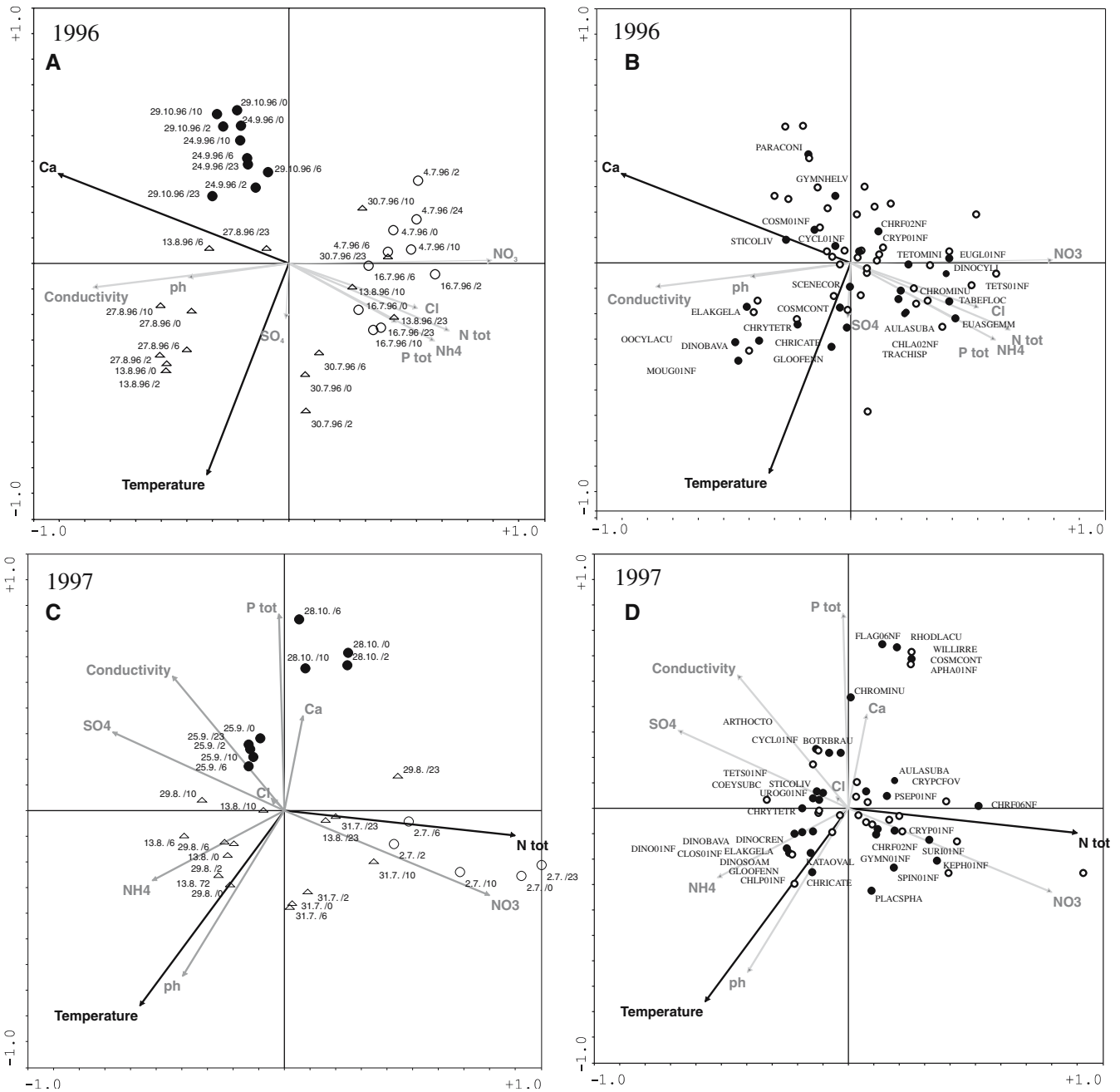
Fig. 5 Canonical correspondence analysis (CCA) ordination diagram showing the relationship between the samples (**a, c**) and the phytoplankton species (**b, d**). Samples are coded 4.7.96 /0 = 4 July 1996 0 m sampling depth. The displayed species are selected on the basis that more than 30% of their variance is accounted for by the diagram. Full taxon names are given in Table 2

1988). According to Eloranta's (1986) classification of phytoplankton assemblages based on 34 lakes in NE Finnish Lapland, the phytoplankton composition of Lake Saanajärvi resembled the assemblages in 'Chrysophyceae' or 'Mixed' types in Finnish subarctic lakes, which are characterized by having relatively low nutrient concentrations and dilute waters. The dominant chrysophyte genera in Lake Saanajärvi, *Uroglena* and

Dinobryon are typical for oligotrophic clear water lakes in Finland (Lepistö and Rosenström 1998).

The seasonal distribution pattern of phytoplankton in subarctic lakes varies from unimodal (Nauwerck 1968; Winberg et al. 1973) to bimodal (Holmgren 1983). A typical spring peak of phytoplankton, related to increased light intensity, long periods of daylight and excess of nutrients after winter remineralization, was not seen in Lake Saanajärvi. The small population of algae living under the ice in Lake Saanajärvi might not be able to cope with the rapid change in underwater light climate during the ice break-up. Further, since the nutrient-rich melt waters draining into the lake during the snowmelt period are less dense than the

Table 3 Results of the canonical correspondence analysis (CCA)

Axis	1996				1997			
	1	2	3	4	1	2	3	4
Eigenvalues	0.162	0.142	0.083	0.063	0.220	0.159	0.100	0.085
Total inertia	1.421				1.820			
Variance explained (%) of species data	11.4	10.1	5.8	4.4	12.1	8.7	5.5	4.7
Variance explained (%) of species-environment relationship	26.6	23.3	13.5	10.3	27.7	20.1	12.6	10.7
Correlation coefficient								
Temperature	−0.308	−0.778	−0.061	0.092	−0.514	−0.724	−0.113	0.073
Calcium	−0.869	0.331	0.026	−0.146	0.068	0.354	−0.683	0.165
Total-N	0.602	−0.248	0.221	−0.211	0.820	−0.092	0.126	0.050

Inter-set correlations of the three most important environmental variables (temperature, calcium, total nitrogen) with axes are also shown

lake water, they will exit through a surface outflow within a few days without mixing to any greater depths. Therefore, organisms can hardly profit from this extra nutrient source. In addition, the length of vernal mixing was very short (from a few days to a few weeks); therefore there was only a limited time for the species that favour turbulent conditions to increase. Phytoplankton biomass in Lake Saanajärvi increased gradually towards autumn and reached its maximum during the final part of the summer stratification period or at the beginning of the autumnal overturn. A similar kind of plankton dynamics was seen in many high mountain lakes in the European alpine region (Pechlaner 1971; Hinder et al. 1999). Goldman et al. (1989) and Hinder et al. (1999) found biomass production to be highest in sub-alpine lakes after a relatively long water column stratification phase followed by a sufficiently long mixing period. It is assumed that the effective mixing after stratification allows only low amounts of nutrients from the hypolimnion to be re-circulated and utilized by algae.

Nutrient concentrations, especially for phosphate, were low throughout the sampling period (e.g. PO_4 below the detection limit), and their role as explanatory factors remained relatively low in the CCA analysis (except for TN in 1997). Among different groups of algae, chrysophytes have the best abilities for growth and storage under low phosphorus concentrations (Sandgren 1988). In addition, many chrysophyte species are mixotrophic (Sandgren 1988), which is advantageous especially in oligotrophic conditions. This was supported by the CCA, as most of the chrysophytes belonging to the summer group of algae (i.e. situated in the lower left part of the diagram) are mixotrophic (Holen and Boraas 1995). While diatoms are good competitors for P, they require sufficient Si concentrations (Sommer 1983). In Lake Saanajärvi the mean Si concentration was slightly lower in 1997 than in 1996 (0.47 mg l^{-1} and 0.59 mg l^{-1}, respectively), which may partly explain the differences in autumnal diatom species composition and abundance between the years.

In the CCA analysis, calcium concentration of water was a significant explanatory factor for phytoplankton distribution in 1996. The ecological role of Ca in regulating species composition and abundance is still unclear (Sandgren 1988; Wetzel 2001). Ca has a central role in the dynamics of pH, carbon dioxide and bicarbonate, influencing the supply of photosynthetically-available carbon and affecting the capacity of water to buffer fluctuations in pH (Reynolds 1984b). These processes are important in controlling photosynthesis and possibly also the species composition (Sandgren 1988; Wetzel 2001). It is likely, that Ca itself may not be the main factor affecting the species compositions, but may represent a surrogate variable reflecting other linearly related water quality parameters, such as major ions, pH, alkalinity and conductivity, which also play an important role in regulating algal composition and activity. Hence, the low calcium concentration in the spring water samples can be interpreted as an indication of declined bi-carbonate buffering capacity associated with the acid melt water.

In a relatively small and shallow lake such as Lake Saanajärvi, the seasonal sequence of phytoplankton species is strongly influenced by stochastic (i.e. meteorological and hydrological) events (Salmaso and Decet 1997). Table 4 presents a summary of the main differences in meteorological conditions, lake physical characteristics and biological response between the two study years. Water temperature is an important factor controlling the growth rates and spatial distribution of many algal taxa (Reynolds 1984a; Flanagan et al. 2003). In this study, the importance of water temperature for phytoplankton assemblages was clearly stated in the CCA as the main environmental gradient was formed by the seasonal temperature changes. Chrysophytes and diatoms are most competitive at low water temperatures and dominate especially in lakes with cool summer water temperatures (Hutchinson 1967; Sandgren 1988). Siver and Chock (1986) have demonstrated that *Uroglena* often prefers temperatures less than 12°C, which might be one reason for the disappearance of *Uroglena* sp. in Lake Saanajärvi during the warm August of 1996 which had surface water temperatures in mid-August of 14.6°C in 1996, but only 10.6°C in 1997. The most abundant diatoms species in autumn 1996 *Cyclotella rossii* and *C. comensis* are often characterized as subalpine or alpine (arctic) taxa according

to their latitudinal/altitudinal affinities, reflecting low water temperature and oligotrophic conditions (Weckström et al. 1997; Krammer and Lange-Bertalot 1988; Hausmann and Lotter 2001).

In addition to water temperature sensu stricto, the timing and length of different thermal periods of a lake plays an important role in phytoplankton species succession and periodicity (Reynolds 1980). Teubner et al. (2003) demonstrated that the development of a stable phytoplankton composition, when three dominant species contributed more than 80% of total phytoplankton biomass, was associated with the increase of thermal water stability in a deep pre-alpine lake in Germany. The distinct differences in the timing and length of different thermal periods between the two sampling years in our study (Table 4) may explain, at least partially, the differences in species compositions and dominance. In 1996, the open water season was longer, but the stratified period shorter than in the following year. The large colonial Uroglena sp. favors thermally stratified periods as during summer 1997, whereas most diatoms are favored by turbulence to stay in the euphotic layer as in 1996 (Reynolds 1988). Heavy winds exceeding 15 ms^{-1} were less frequent in year 1997 than in 1996 suggesting less wind mixing and more stable thermocline in 1997. The stronger thermal water stability is also expressed in the Brunt Väisälä frequency diagram (Fig. 2) with higher stability values in the end of July in 1997. Hence, compared with 1996, the thermal stratification in 1997 started earlier, was stronger (steeper thermocline), and lasted 2–3 weeks longer (Table 4) with stable environmental conditions in physical and chemical variables for at least 4–5 weeks. Although our measurements represent coarse-resolution sampling, they suggest that

phytoplankton assemblages in late summer 1997 reached a state close to equilibrium, as only a few species of Chrysophyceae (mainly Uroglena sp.) contributed more than 80% of the standing biomass. Moreover, their coexistence persisted for a long enough period (more than 1–2 weeks) during which no significant changes in total biomass took place (cf. Sommer et al. 1993). The similar dominance pattern with only a few species occupying more than 80% of the total phytoplankton biomass observed in Swedish alpine lakes was attributed to the harsh climate as a major stress factor (Willén 2003).

The length of the mixing cycle, thermal stability of the water column and water temperature seemed also to control additional phytoplankton parameters (Table 4), such as the total biomass and diversity. The average chlorophyll-a concentrations and the maximal biomasses were somewhat higher in 1996 than in 1997, which relates to higher temperatures and longer duration of the ice-free season. Stable weather conditions and well-developed thermal stratification led also to a summer decline of the diversity in spite of an unchanged species number. These observations suggest that, quite contrary to the results by Hinder et al. (1999), the length of the ice-free season is more decisive for biomass production than the thermal stability during this period, which in turn seems to affect the algal diversity.

Similar year-to-year differences were seen in the proportions of the total phytoplankton biomass expressed by functional groups. C-strategists are small, rapidly growing species that can effectively and quickly utilize the available light and nutrients (Reynolds 1984a). They typically dominate the spring communities, including Lake Saanajärvi in both years. The larger and

Table 4 Main differences in meteorological characteristics, lake physical features and biological response during the open water season in the two study years

Meteorological characteristics	1996	1997
Mean air temperature (°C)	3.6	3.8
Maximum air temperature	Early August	Mid-July
No. of measurements (30 min average) with high wind velocity (> 15 m s^{-1})	66	40
Lake physical features	1996	1997
Date of ice-out	27 June	7 July
Duration of spring overturn (days)	34	9
Onset of stratification	End-July	Mid-July
Duration of stratification (days)	41	55
Duration of open-water season (days)	126	111
Thermal stability	Weaker	Stronger
Biological response	1996	1997
Chlorophyll a (μg l^{-1})	0.9	0.4
Average phytoplankton biomass * (mg wet weight l^{-1})	0.22	0.15
Maximal phytoplankton biomass (mg wet weight l^{-1})	0.47	0.42
Date and location of max. biomass	Mid-August, 10 m	Late-August, 0 m
Autumn assemblage close to equilibrium	No	Yes
Dominant algal groups in decreasing order	Chrysophytes, diatoms, chlorophytes, dinoflagellates	Chrysophytes, cryptophytes, chlorophytes, dinoflagellates
Shannon diversity (H')	2.33	2.09
Pielou's evenness	0.64	0.58

*Average calculated based on all vertical sampling depths: 0, 2, 6, 10 and 23 m

slower growing S-strategists exhibit low sinking and grazing rates. With good capacity for nutrient storage they tolerate very low external nutrient concentrations. The R-strategists are relatively large and rapidly growing. They need turbulent mixing in order to stay in the euphotic layer. In 1996 when the summer stratification period was short, the disturbance tolerant R-strategists started to increase in late summer and dominated the autumn period. In 1997, the proportion of the R strategists remained very low for the whole study period, whereas the S strategists constituted up to 90% of the biomass.

Climate change is expected to have direct and indirect consequences on the biota and the structure and functioning of Arctic freshwater ecosystems. Changes in key physical and chemical parameters described above will affect phytoplankton community attributes such as species richness and diversity, species composition and primary production levels. However, although the measured physico-chemical parameters explained almost 50% of the phytoplankton species' distribution in the CCA, many unmeasured biological factors, such as grazing and parasitism, may also have an effect on the phytoplankton species composition and dynamics. Hence, species interactions should be considered more properly in future studies in order to make more comprehensive predictions about the future phytoplankton directions.

Conclusions

Many physical and chemical factors affect the phytoplankton seasonality and species composition in a lake. These factors include the lake's trophic status, annual mixing events and thermal structure. While the productivity determines the abundance of different algal groups in a lake, based on our data it seems that the length of the mixing cycle and the water temperature regulated the seasonal occurrences of different species in the subarctic Lake Saanajärvi. Our observations suggest that the length of the ice-free season is more decisive for biomass production than the weather conditions and lake thermal stability during this period, which in turn affects the algal diversity. However, more detailed studies are needed for a better understanding of the importance of different factors and to find out, for example, how global warming would change the productivity and species composition in these sensitive environments.

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