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Changes in Physical and Chemical Limnology and Plankton during the Spring Melt Period in a Subarctic Lake

key words: subarctic lakes, springtime, melting, acid pulse, Lake Saanajärvi

Abstract

The springtime limnology of subarctic Lake Saanajärvi, NW Finnish Lapland, was studied in 1999 with particular interest on the estimation of the effects of acid pulse. No clear pH depression was seen during the study year with exceptionally thin snow cover, in contrast to the year 1997, when a clear episodic decline in surface water pH was measured. In contrast to many Arctic lakes, no phytoplankton spring bloom was observed, probably because of the combination of low nutrient concentrations, dilution effect, flushing and rapid change in light climate. Low temperatures and limited food resources, resulting in long life cycles of zooplankton and with a clear winter maximum, may be the main factor controlling the atypical succession of zooplankton in Lake Saanajärvi.

1. Introduction

Subarctic lakes are covered with ice and snow for 6–9 months in winter, followed by rapid warming after melting, a short period of high heat content and a long cooling period until freezing. This natural rhythm is determined by solar radiation, which has a large annual variation. During polar winter the sun is below the horizon for almost two months, while during summer the sun does not set for two months. Throughout the year, the environment in these lakes shows periods of certain stability followed by short episodes of drastic changes (e.g. changes in thermal structure, increase in UV-radiation after the ice melt, dilution due to meltwaters) (SCHINDLER *et al.*, 1974; HOBBIE, 1980; SORVARI *et al.*, 2000; FORSSTRÖM *et al.*, 2005). Many of these changes are caused by climatic factors. Interannual variability within weather and climate around the Northern Hemisphere is mostly determined by the North Atlantic Oscillation (NAO) and the Arctic Oscillation (AO) (HURRELL and VAN LOON, 1997; THOMPSON *et al.*, 2000).

Spring is usually the most differentiated period of the year for subarctic lakes in terms of changes in their water chemistry (SORVARI *et al.*, 2000; CATALAN *et al.*, 2002). In early spring the snow that has accumulated throughout the winter melts and flows into streams and lakes. When snow begins to melt there is a concentrated surge of acidifying ions, which can cause a drastic drop in pH in the receiving water body. As a consequence, lakes may become as much as 100 times more acidic in just a few days or weeks. This spring pH

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depression (also known as the 'spring acid pulse' or 'acid shock') has been observed in many Arctic lakes and rivers and can adversely affect aquatic biota (KINNUNEN, 1990; BISHOP and PETTERSSON, 1996; THORSTEN, 1998; MOISEENKO *et al.*, 2001; SORVARI *et al.*, 2000). Spring pH depression associated with snow melt is a natural process in aquatic systems, but may be amplified by acid deposition during the winter months. The accumulation of anthropogenic acids (SO_4^{2-} and NO_3^{-}) in catchments abruptly intensifies the episodic acidification in flood periods.

In addition to changes in pH, other chemical, physical and biological processes also undergo marked changes as winter gives way to spring. For example, it has been shown that dilute meltwaters together with changes in the lake's thermal structure affect nutrient concentrations and oxygen levels in lakes (SCHINDLER *et al.*, 1974; O'BRIEN *et al.*, 1997). The light climate in the water column also quickly changes from darkness to the highest radiation levels during the year, as ice break tends to be close to summer solstice. Ecologically the changes in limnological parameters come at a critical time. Spring is the time when the reproductive cycles of most aquatic species are entering full swing (BAKER and CHRIS-TENSEN, 1991). As a consequence, plankton communities are affected and potentially stressed by high dilution, high flushing rate, spring overturn and fluctuations between exposure to harmful radiation and light-limited conditions (CATALAN, 1992; RAUTIO and KORHOLA, 2002).

Earlier studies conducted in Finnish Lapland have indicated spring in lakes as the period with drastic and rapid changes in several limnological parameters including thermal structures, nutrient concentrations and both phyto- and zooplankton species abundance. The complete annual cycle of physical and chemical events in a subarctic lake was described for the first time by SORVARI *et al.* (2000). Later, RAUTIO *et al.* (2000) studied the seasonal variability in diatoms and zooplankton, while FORSSTRÖM *et al.* (2005) described the seasonal dynamics of phytoplankton in relation to environmental factors. All these studies were conducted in a subarctic lake Saanajärvi that was monitored between 1996 and 1998 in association with the EU-funded project MOLAR. However, the above mentioned studies were all based on rather coarse seasonal sampling resolution.

Although spring is the period with most dramatic changes in lake limnology and climatic factors in arctic and subarctic areas, this season has rarely been studied in any details with regard to limnological patterns. There are only a limited number of studies concerning the overall seasonal changes in the limnology of arctic or subarctic lakes (e.g. KEREKES, 1974; SCHINDLER et al., 1974; O'BRIEN et al., 1997), and we are not aware of a single lake study with a focus on spring that would cover environmental, physical, chemical and biological changes during this season. In order to obtain more information about the spring processes in a subarctic lake, a new study with higher sampling resolution was launched in Lake Saanajärvi in 1999 with particular attention to the changes in physical and chemical limnology and plankton during the spring melt period. These unique data were analysed so as to explicitly test two main hypotheses: (i) The occurrence and intensity of acid shock is controlled by climatic factors; (ii) The acidic meltwater does not mix with the lake water, and the effect of acid pulse is therefore restricted to the surface water. In addition, our aim was to provide new information on the water chemistry and plankton dynamics during the polar spring. In this paper we compare the findings from 1999 with other monitoring years in Lake Saanajärvi and also discuss how representative the results are compared with other high-latitude lakes. Such seasonal limnological data are also important for a better understanding of ecological calibration (e.g. KORHOLA et al., 2005) paleolimnological studies in subarctic regions (e.g. RÜHLAND et al., 2003; SOLOVIEVA et al., 2005), as well as similar studies in cold, alpine lakes (e.g. KARST-RIDDOCH et al., 2005).

2. Materials and Methods

2.1. Study Site

Lake Saanajärvi (69°05' N, 20°87' E) is a small (70 ha) 'fell' lake situated in NW-Finnish Lapland in the treeless tundra at 679 m above see level (Fig. 1). Climatically, the area lies between the North Atlantic oceanic climate and the Eurasian continental climate. The mean annual temperature is -2.3 °C (mean January = -13.6 °C and mean July = +10.9 °C) and the growing season is *ca*. 101 days; minimum temperatures may fall below -40 °C (DREBS et al., 2002). The site is located in the rain-shadow of the Norwegian mountains and therefore rainfall is one of the lowest in Finland with approximately 459 mm per year, while the evapotranspiration is approximately 100 mm (DREBS et al., 2002). In Kilpisjärvi area, where Lake Saanajärvi is located, about 80% of total precipitation runs to waterbodies. Approximately 60% of the annual total precipitation occurs as snow, which covers the ground for an average of 210-220 days per year. Based on the snow conditions, the catchment area of Lake Saanajärvi belongs to the tundra zone (STURM et al., 1995; RASMUS, 2005), which is characterised by wind packed dense layers of snow. In Finland the greatest variation in snow depth has been observed in Kilpisjärvi, where the maximum snow depth can vary between 60 and 250 cm (SOLANTIE, 2000). In the open fell area, where wind and local topography shape the snow distribution, snow beds with several meters of snow depth as well as nearly snowless areas can be found. In general, the deepest snow cover is found just above the tree line at an elevation of 600 masl (EUROLA et al., 1980). The average maximum annual depth of snow, about 1 m, is usually attained in March or April (FINNISH METEOROLOGICAL INSTITUTE, 1980–1995; 1996–2006). Snow melts first from the windswept areas in May, next from the birch forest area and last from the late snow-bed areas as late as mid-July. The lake is somewhat difficult to access especially during the melting conditions as the site is located along a narrow footpath about 5 km away from the Biological Field Station of Kilpisjärvi.

Lake Saanajärvi is 1.5 km long and has a maximum width of 0.8 km. The shoreline is rocky and steep. The basin is generally well shielded by high mountains against the southwest and to the northeast side. Other parts of the drainage basin are lower, and gently rolling. The catchment area is 461 ha, covered by subalpine vegetation, bare rocks and boulder fields. The bedrock consists of sedimentary rocks including dolomitic limestones, as well as metamorphic rocks (Paleozoic Caledonian schist and gneiss) (ATLAS OF FINLAND, 1986). Due to the alkaline bedrock, Lake Saanajärvi has a good buffering capacity against acid substances. Lake Saanajärvi has clear water with mean Secchi disk transparency 8.5 m and total organic carbon (TOC) concentrations close or lower than the detection limit (1 mg l⁻¹) (SORVARI *et al.*, 2000). There is no direct human activity near the lake, and the region is considered one of the cleanest in Europe in terms of atmospheric pollution (RÜHLING *et al.*, 1992). Acid deposition has not been measured in the exact study area, but reported sulphate concentrations in the snow of Northern Finland and Northern Sweden are well below 0.5 mg l⁻¹, whereas in the industrialized regions of Northern Russia the snow sulphate concentrations may rise up to 22 mg l⁻¹ (DE CARITAT *et al.*, 2005; HOLE *et al.*, 2006). Nevertheless, winds may episodically bring contaminants to the area particularly from the Kola Peninsula industrial area located in northwest Russia.

The maximum water depth of Lake Saanajärvi is about 24 m and the lake is dimictic. The lake is ice-free for about 4 months from July to October. The summer stratification is usually well developed and the relatively steep thermocline lies at depths of 10-12 m during the stagnation period (SORVARI *et al.*, 2000). Maximum surface-water temperatures (13–15 °C) are measured in the beginning of August and autumn overturn typically starts in mid-September when the water is approximately 8 °C. The autumnal mixing period in the lake is relatively long (~50 days). Ice cover reaches its maximum of *ca*. 1m in May. More information on the general physical and chemical characteristics of the lake can be found in RAUTIO *et al.* (2000), SORVARI (2001) and SORVARI *et al.* (2000).

2.2. Meteorological Data

Meteorological data for 1999 were provided by the Finnish Meteorological Institute from two meteorological stations located in the vicinity of Lake Saanajärvi. Temperature and wind data were obtained from the automatic weather station (AWS) located on the top of the fell Saana, ca. 1.5 km south-west of the lake at an altitude of 1060 m a.s.l. (i.e. 381 m above the lake surface). Precipitation regimes were derived from the manned meteorological station of Kilpisjärvi about 4 km from the lake. This station lies in the village of Kilpisjärvi at an elevation of 473 m a.s.l. Total precipitation was obtained from a rain gauge located 1.5 m above the ground surface.

Because correlations between air temperature and elevation are high for the study area (see OLAN-DER *et al.*, 1999) the lapse rate method was used to interpolate temperatures spatially. The lapse rate method uses the temperature value of the nearest weather station and the difference in elevation to estimate temperature at the unmeasured site. This method makes the assumption that the lapse rate is constant for the study region. A consistent regional lapse rate of 0.57 °C/100 m (*cf.* LAAKSONEN, 1976) was used here to interpolate the temperatures from the fell Saana AWS to Lake Saanajärvi. Interpolation is especially important in mountainous regions where variables may change over short spatial scales. Large spatial coherence has been achieved in lapse rates in European mountain regions, and the method is believed to be reliable (AGUSTI-PANAREDA and THOMPSON, 2002).

Weather conditions during spring 1999 were compared with spring conditions in 1996 and 1997 when both meteorological and limnological data (with coarser sampling resolution) were available. Meteorological data (air temperature, precipitation, wind speed and wind direction) for 1996 and 1997 were obtained using Vaisala Milos 500 AWS located about 5 m from the south-eastern lake shore (Fig. 1). These measurements were made every 30 min at 3.5 m height. The precipitation gauge only functioned at positive air temperatures; therefore very little information on precipitation is available. Water temperature was recorded every 30 min by a Vaisala Milos 500 water temperature sensor installed 1 m below the lake surface. Arctic Oscillation (AO) index was obtained from http://www.cpc.noaa.gov/prod-ucts/precip/CWlink/daily_ao_index/ao_index.html.



Figure 1. Map of Lake Saanajärvi. MS = main sampling point, NWS = northwest shoreline sampling point, IL = inlet sampling point, AWS = automatic weather station.

2.3. Sampling

Sampling for water chemistry was conducted approximately once a week for the whole spring period of approximately two months. Samples for chemical analyses were taken from the deepest point of the lake (main sampling point, MS) from 10 different depths (0, 2, 4, 6, 8, 10, 12, 16, 20, 22m), from the northwest shoreline (NWS) from 3 depths (0, 2, 5) and from the inlet (IL) at a depth of 30 cm (Fig. 1). The inlet was frozen until May 22; otherwise sampling started on April 22 and lasted until June 22, 1999. All water samples were collected using a Limnos water collector (volume 2 L). Samples for ammonium nitrogen (NH_4 –N), nitrate nitrogen (NO_3 –N), orthophosphate phosphorus (PO_4 –P), total phosphorus (TP), total nitrogen (TN) and sulphate (SO₄) were analysed at the Lapland Regional Environment Centre using standard methods of the National Board of Waters in Finland (SFS 3032; SFS 3030; SFS 3025; VALDERRAMA, 1981; EATON, 1995; SFS 5738). Oxygen, pH, temperature and specific conductance were measured in situ using probes from HANNA Instruments. For the analysis of oxygen isotopes (sampled in 1996–1998 during the monitoring), water samples were equilibrated with CO_2 at 25 °C overnight. The oxygen isotope ratio of equilibrated dried CO₂ was measured on a mass spectrometer (Finnigan MAT Delta E, Bremen, Germany). The δ^{18} O values are expressed as per mil relative to the Vienna Standard Mean Ocean Water (V-SMOW) standard. The laboratory reference water samples are normalized on the VSMOW-SLAP scale. The standard deviations of the δ^{18} O values for repeated measurements of laboratory reference water samples were 0.15% or lower.

Snow samples were taken on April 27 and May 11 from above the lake ice close to the main sampling hole. Samples were melted and analysed for pH, conductivity, TP, TN, NO₃–N and NH₄–N.

Samples for phytoplankton were taken with a Limnos Water sampler (2L) every second week (24 April to 22 June). Sampling was done together with water chemistry, but only from 5 depths (0, 2, 6, 10, 22 m). Phytoplankton samples were fixed with acid Lugol's solution and stored under dark and cool conditions. The species composition and biomass were determined by counting 100 randomly selected fields at 400× magnification with an inverted microscope after sedimenting for 48 h in a 100 ml Utermöhl-chamber (UTERMÖHL, 1958). Additionally, the whole bottom of the chamber was counted at 125× magnification for large colonies, filaments and desmids. Phytoplankton biomass was calculated as wet weight from algal volumes measured or as given in the literature (NAULAPÄÄ, 1972).

Samples for zooplankton were taken with a Limnos water sampler (2 L) from 5 depths (0, 2, 6, 10, 24 m). 10 L of water were taken from each depth, and concentrated through a 50 μ m net. Samples were preserved with formaldehyde (4% final concentration) and later counted using an inverted microscope for identification to species level.

2.4. Numerical Analysis

For the statistical analysis, missing values of pH (5 samples) were filled by linear fitting, and the missing values of NH_4 –N (5 samples) were calculated on the basis of TN (correlation 0.74). We used linear-based direct ecological gradient analysis technique of RDA (TER BRAAK, 1996) to identify, in a more quantitative manner, which physical and chemical factors influenced most significantly the phytoplankton biomasses in our study site during spring. For the statistical analysis we used environmental data that were collected from the same depths that the phytoplankton samples were taken (0, 2, 6, 6)10, 22m). The compositional phytoplankton data were $\log (x + 1)$ transformed due the skewed distribution of the species but no transformation was performed for the environmental data. In all partial RDA analyses, phytoplankton data were considered as response or dependent variable, whereas the relevant physical (temperature, ice) and chemical (pH, conductivity, NH_4 –N) variables were treated as predictor or explanatory variables. The effect of time-dependent ecological and environmental processes was removed by introducing sampling time (Julian Day) as a covariable in all experiments. At each step the analysis was done by constraining the first ordination axis to the environmental variable of interest and by using other relevant variables as covariables in order to assess the unique and independent contribution of the different explanatory factors. The significance of the first RDA ordination axis under different model conditions was tested using a constrained Monte Carlo permutation test with 199 permutations.

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3. Results

3.1. Weather Conditions and Physical Limnology

The meteorological data collected by the two weather stations gave an overview of the variability in weather conditions prevailing at Lake Saanajärvi. April and June were approximately 2 °C warmer in 1999 than the long-term means, while May was about 2 °C colder than the average. Reflecting its high-latitude location, daily mean air temperatures at Lake Saanajärvi were below 0 °C during about 8 months of the year in 1999, from October to May. During the observation period (April 27–June 22), the daily mean air temperatures fluctuated between -10.1 °C and +16.3 °C (Fig. 2).

Precipitation in the study area in 1999 was 514 mm which is slightly above the long-term yearly average (DREBS *et al.*, 2002). This increase was due to higher summer precipitation, while winter precipitation remained clearly below average. Precipitation was particularly low in February, 15.4 mm, which is only half of the long-term monthly average. As a consequence the snow depth in 1999 was one of the lowest (max. 60 cm) recorded during the >40 years of weather monitoring in Kilpisjärvi (FINNISH METEOROLOGICAL INSTITUTE, 1991; DREBS *et al.*, 2002). The snow melted very quickly (in just one to two weeks) from the catchment area in early June. During the eight-week sampling period, 32 days were without rain, and the mean daily precipitation was 0.7 mm. Maximum daily amount of rain, 8 mm, was received on May 23.

Winds during the sampling period were quite strong, with daily mean wind speeds exceeding 5 m s⁻¹ for two-thirds of the monitored time. Prevailing wind directions during the observation period (Fig. 3), assessed in terms of vector-averaged daily means, were south (18%), west (16%) and northwest (15%). Winds from the north (11%) and east (11%) were of less significance. During the winter of 1999, prevailing wind directions were south (26%), west (16%) and northwest (15%). Winds from the east occurred quite seldom (6%).



Figure 2. Daily mean air temperature and depths of ice and snow cover on the lake ice during the study period.



Figure 3. Rose diagram showing the prevailing wind directions and wind speeds for the study period.

During the sampling period, ice reached a maximum thickness of 95 cm in late April (Fig. 2). However, only 35 cm of ice was clear congelation or black ice, while 60 cm was white, snow, or slush ice overlying the older black ice. The proportion of white ice, which is formed when snow cover depresses the ice and lake water flows through cracks on the ice and freezes, was unexpectedly high given the small amount of precipitation in the winter of 1999. When launching the monitoring work in late April, there was only 20 cm of snow on top of the ice (Fig. 2). In mid-May the snow depth on the lake was reduced to 1-5 cm reflecting both strong winds and melting. By the end of May, the total ice thickness in the middle of the lake was still 95 cm (Fig. 2). Thawing commenced along the lake shores, so that on June 8, a moat of about 5-10 m wide had formed around the lake. However, a small open area of about 2 m wide existed already at the end of May in the eastern edge of the lake, where the major inlet to the lake drains (Fig. 1). There, the molten area was about 30 m wide on June 8. At that time open water co-existed with a thick sheet of free-floating ice (60 cm) overlain with some snow in the centre of the lake. From that point onward, melting progressed rapidly. On June 15, the moat had widened so that an ice-free zone of ca. 50 m wide had formed around the lake. At that time the thickness of the ice in the middle of the lake was reduced to 20 cm (Fig. 2). On June 18, only small remnants of ice were left, and by the following day the ice had disappeared completely. Figure 4, taken in spring 2001, illustrates a similar melting process of Lake Saanajärvi. The melting of the entire ice sheet lasted for approximately 3 weeks. The fast thawing of L. Saanajärvi in June 1999 was due to a combination of rapidly increasing air temperatures and the strong winds (average wind speed during the five last days of ice cover was 10.7 m s⁻¹). It appears that when night temperatures reached above 0°C on June 6, was particularly critical for ice melt as thawing progressed rapidly thereafter.

The water temperature isotherms (Fig. 5a) suggest continuous slight warming of Lake Saanajärvi over the spring. Water mass in Lake Saanajärvi was cold throughout the early spring of 1999 with temperatures below +1.7 °C in the upper 4 metres of the water column and below +2.8 °C also in the lowermost water layers (Fig. 5a). Inverse thermal stratifica-



Figure 4. Photo series showing the melting progress of ice cover in Lake Saanajärvi, a: beginning of May, b: mid-June, c: end of June. Pictures taken by T. PERKKIÖ.

tion remained in the lake until June 15, when the entire water mass was isothermal at about 2.5 °C. The epilimnion tended to be colder than the overlying air in June but warmer than air later in summer. A Secchi depth reading of 10 m was recorded immediately after the ice break-up. However, based on visual observations the water looked more coloured and turbid in the IL sampling point where the major inlet enters the lake. Inlet water was colder than the surface lake water in late May/early June (inlet: $0.1-0.7^{\circ}$ C; surface lake water: $0.4-1^{\circ}$ C) but warmer thereafter (inlet: $3.1-8.5^{\circ}$ C; surface lake water: $1.4-3.5^{\circ}$ C) (Fig. 5a). Water temperature in NWS tended to be slightly warmer compared to the main sampling point, except in early June when meltwaters came from the catchment.



3.2. Water Chemistry during Spring

The winter oxygen profile (Fig. 5b) in Lake Saanajärvi resembled the situation commonly observed in eutrophic lakes with good oxygen concentrations in the epilimnion but lower oxygen concentrations in the hypolimnion (<5 mg l⁻¹) (WETZEL, 2001). Oxygen concentrations for the study period varied from 3 to 12.5 mg l⁻¹. The highest oxygen values were mea-



Figure 5d-f

sured in the surface water in the beginning of the study. Surface water oxygen decreased gradually towards the end of June along with increasing water temperatures. Lowest surface water concentrations (9.2 mg l⁻¹) were measured in June 15, when the water column had started to circulate. Hypolimnetic oxygen values were low $(3.0-4.4 \text{ mg l}^{-1})$ until June 15.



Figure 5. Seasonality of various limnological parameters during the sampling period. Sampling days and depths are indicated with black crosses, duration of the ice cover by a white bar and inlet conditions by squares (with same scale as main pictures) above each picture.

The stable oxygen isotope values in the water profiles of 1997 and 1998 show δ^{18} O values between -13.5 and -13.8% for all depths, except in surface waters during spring (Fig. 6). A minimum value (-15.9%) for δ^{18} O was measured at 2 meters depth in June 10.

Specific conductivity (Fig. 5c) varied during the sampling period from 16.3 μ S cm⁻¹ to 46.6 μ S cm⁻¹ (median 30.5 μ S cm⁻¹). In surface water the conductivity was higher during April and May (32.1–46.6 μ S cm⁻¹), but decreased during the period of most intense melting in June (16.3–18.2 μ S cm⁻¹). In the hypolimnion, conductivity was relatively high until the melting of the ice progressed (mid-June, end of June) and the water column started to mix. By the end of June the conductivity was 29.0 μ S cm⁻¹) compared to surface lake water throughout the sampling, reflecting the lower ion concentrations of the melting snow. Further, conductivity in the surface layers of NWS was lower than in the corresponding samples from the main sampling site, except in June. Snow on top of the lake ice had very low conductivity (7.1–9.9 μ S cm⁻¹).

The lake water pH was circumneutral for most of the study period (median pH 6.6). The highest pH (7.0) was measured in April 27 just below the ice, whereas the lowest pH (6.1) was measured close to the bottom on several occasions (Fig. 5d). In general, pH was higher in the epilimnion than in the hypolimnion until isothermal conditions were reached on



Figure 6. Stable oxygen isotope values in the water profile during the monitoring period (1997–1998).

June 22. Surface water pH decreased from 7.3 to 6.6 towards the end of the study period. Inlet water (pH 6.1-6.2) was slightly more acidic than the surface lake water (pH 6.6-6.9), especially at the end of May and the beginning of June when runoff was highest (Fig. 5d). Compared to the lake water, the pH of snow was low (5.5–5.7), but comparable to the pH of rainwater, indicating that the area was relatively free from atmospheric acid deposition.

Total nitrogen (TN) concentrations varied between 90 and 200 μ g l⁻¹ during the study period. Highest surface water concentrations (190 μ g l⁻¹) were measured at the end of May, and the lowest concentrations (120 μ g l⁻¹) were measured in June 8 (Fig. 5e). The concentrations in mid-water layers (between 6 and 12 meters) were fairly constant, 90–110 μ g l⁻¹, until mid-June, when the water column started to circulate and the concentration of TN was around 120 μ g l⁻¹ throughout the water column. TN concentration in the hypolimnion was relative-

Figure 7. A box-plot presentation of epilimnetic (0–8 m) lake water temperature and chemistry during the spring and the remainder of the open water season (July–October). Summer and autumn values are from our own monitoring data from 1996 and 1997. The box length is the interquartile range. Empty circles denote outliers (cases with values between 1.5 and 3 box lengths from the upper and lower edge of the box). Stars denote extremes (cases with values more than 3 box lengths from the upper or lower edge of the box).



ly high and constant (170–200 μ g l⁻¹) until mid-June. The TN concentration of the inlet was highest (260 μ g l⁻¹) at the beginning of the melting period (end of May) and remained high relative to the lake surface until mid-June. TN concentrations in snow (149–150 μ g l⁻¹) were comparable with surface lake water values.

Nitrate (NO₃ + NO₂–N) concentrations varied between 8 and 100 μ g l⁻¹ during the study period. Concentrations were highest near the bottom of the lake and were lowest (10–15 μ g l⁻¹) in the mid-water layers (between 6 and 12 meters) (Fig. 5f). The highest surface water nitrate concentration (57 μ g l⁻¹) was measured on May 25. When the whole water column became isothermal, the nitrate concentration was around 22 μ g l⁻¹. Concentration of nitrate in the inlet and NWS decreased towards the end of the sampling period and was always much lower than in the lake. The concentration of nitrate in snow was between 36–60 μ g l⁻¹.

Ammonium (NH₄–N) concentrations varied between 5 and 21 μ g l⁻¹ (median 15 μ g l⁻¹). The vertical distribution of NH₄ was fairly uniform (between 15 and 20 μ g l⁻¹) until the beginning of June, when the concentrations in the epilimnion started to decrease until mixed conditions were reached in mid-June. The concentration of ammonium decreased to 7 μ g l⁻¹ throughout the whole water column on June 22 (Fig. 5g). Ammonium concentrations in the inlet were under the detection limit of the method (<5 μ g l⁻¹) throughout the sampling period. In NWS the concentration of NH₄ was fairly similar to concentrations measured in the main sampling point of the lake. The concentration of ammonium in snow was much higher than in the lake and in the inlet (28–43 μ g l⁻¹).

Total phosphorus (TP) concentrations were low throughout the study period (mostly below detection limit of 6 μ g l⁻¹) and no seasonal trend was observed. Phosphate (PO₄–P) concentrations were below the detection limit for the entire study period. TP concentrations in the inlet were two to three times higher than in the surface lake water. The highest inlet TP concentration, 10 μ g l⁻¹, was measured at the beginning of the melting period (end of May). The concentrations of TP in snow were under the detection limit.

Sulphate concentrations varied between 2.1 and 5.3 mg l^{-1} (Fig. 5h). The highest concentrations were measured close to the bottom, whereas the lowest concentrations were observed from the surface layer. Melting of snow and ice resulted in low sulphate concentrations in the surface water.

Relatively large differences were seen between the springtime water chemistry and summer and autumn (Fig. 7). In general, pH was slightly lower in the spring, whereas conductivity had both its highest and lowest concentrations during the spring. Springtime nutrient concentrations were higher, with the exception of nitrate. The average concentration of sulphate was lower during spring than the rest of the open water season.

3.3. Spring Plankton Dynamics

Altogether 144 phytoplanktonic taxa were identified during the study. Species richness varied between 11 (May 11) and 39 taxa (June 22). Both cell numbers and biomass were very low throughout the study (maximum values 35,800 cells 100 ml⁻¹ and 0.09 mg l⁻¹, respectively) compared to mean values calculated from the open water seasons of 1996 and 1997 (Fig. 8). Chrysophytes and unidentified small flagellates dominated the algal community throughout the sampling period, but occasionally cryptophytes, dinoflagellates and cyanophytes comprised relatively large parts of the biomass.

Phytoplankton cell densities were very low $(12,700 \text{ cells } 100 \text{ ml}^{-1})$ at the end of April, but increased in the surface water layer almost 3-fold within 2 weeks time. The highest cell densities were always observed close to the surface (0 or 2 meters depth), with the exception of the last sampling in June, when the lake ice had melted completely and the highest cell densities were observed close to the lake bottom at 22 meters depth (Fig. 8a). Surface cell den-



Figure 8. Vertical profiles of (a) phytoplankton cell densities (cells/100 ml) during the sampling period and mean cell densities of the open water season (mean OW, calculated from data from 1996 and 1997), and (b) vertical profiles of phytoplankton biomass (mg/L) during the sampling period and mean biomass of the open water season (mean OW, calculated from data of 1996 and 1997).

sities were highest on May 11, but the cell numbers in deeper waters remained very low until the ice had melted completely.

Initial phytoplankton biomass was very low (0.01 mg l⁻¹) and increased under the ice (Fig. 8b). There was a marked increase in total biomass between June 8 and June 22, which is not seen in cell densities (Figs. 8 and 9). This is due to changes in algal composition coincident with the ice break-up: very small flagellates (e.g. *Chromulina* sp.) were replaced by larger chrysophycean species, such as *Pseudopedinella* sp., *Mallomonas* sp., colony-forming *Dinobryon cylindricum*, and benthic diatoms *Surirella* sp. and *Amphora* sp. Coincident with the change in algal composition, the concentration of NH₄ decreased, indicating increased algal uptake of nutrients. Similar to cell densities phytoplankton biomass (0.09 mg l⁻¹) was measured in June 22 at the surface.

The springtime zooplankton community consisted mostly of copepods *Eudiaptomus* graciloides and Cyclops abyssorum, the cladoceran Daphnia umbra and rotifers Kellicottia longispina and Keratella cochlearis. E. graciloides had its maximum abundance, 35,500



Figure 9. Seasonal succession of main zooplankton species (mean number of individuals/m³ of all sampling depths) and phytoplankton groups (mean biomass (mg l⁻¹) of all sampling depths) during the study period. DapUmb = *Daphnia umbra*, EudGra = *Eudiaptomus graciloides*, CycAbu = *Cyclops abyssorum*.

individuals m⁻³, at the beginning of the study period, and the abundance decreased towards the summer. The abundance of *C. abyssorum* was much lower, and it seemed to increase towards the summer. The maximum abundance, 7,100 individuals m⁻³, was observed at the beginning of June. Both rotifer species occurred in relatively high numbers at the beginning of the study period (*K. cochlearis* 14,400 individuals m⁻³, *K. longispina* 5,200 individuals m⁻³), decreased until end of May, and increased again in June. *D. umbra* was found in relatively low and constant numbers throughout the study period (max abundance 700 individuals m⁻³).

3.4. Variance Decomposition Experiment

Variance decomposition experiments, using a series of partial RDA analyses, explained 30.8% of the variance in the phytoplankton data (P = 0.045), leaving 69.2% unexplained by the available variables. When the various environmental factors were analysed individually, only the nominal factor 'ice' (ice cover present – ice cover absent) proved to be statistically significant in independently explaining the variation in the phytoplankton biomass data (Table 1). Lake water pH, on the other hand, only explained 0.4% and was clearly non-significant.

3.5. Year-to-Year Variation

During the spring of 1997 the air temperature varied between -11.1 °C and +15.5 °C. April 1997 was 3 °C colder than the long-term means (long-term mean: -4.8 °C), while May was very close to the average (1.5 °C). Spring 1997 was exceptionally rainy: total precipitation in April was 152 mm, which is almost nine times higher than the 30-year average (17 mm) (FINNISH METEOROLOGICAL INSTITUTE, 1997). The prevailing wind directions during winter 1997 were south and northwest.

Explanatory variable	Covariable	Variance explained	<i>P</i> -value
All	time	30.8	0.045
temperature	ice, pH, conductivity, NH_4 –N, time	4.5	0.245
ice	temperature, pH, conductivity, NH ₄ –N, time	9.9	0.010
pН	temperature, ice, conductivity, NH ₄ -N, time	0.4	0.990
conductivity	temperature, ice, pH, NH ₄ -N, time	3.9	0.405
NH ₄ –N	temperature, ice, pH, conductivity, time	1.8	0.735

Table 1. Variance partitioning results of the phytoplankton biomass data for five explanatory variables using partial RDA analysis and significance testing using a Monte Carlo permutation test.

In winter 1996/97 the snow cover in Kilpisjärvi area was exceptionally deep, 180 cm (Table 2). In mid-May 1997 the snow depth was still 133 cm, which is almost three times higher than average (50 cm), and more than six times higher than in 1999 (21 cm) (FINNISH METEOROLOGICAL INSTITUTE, 1997; 1999).

In 1999 ice-out happened relatively early compared to the observations in other years: in 1996 ice had melted completely 8 days later and in 1997 even 18 days later than in 1999 (Table 2). The thermal structure of the lake (from inverse stratification to spring overturn) had similar time lags to melting. In 1997 the surface water pH dropped from 6.7 to 5.4 in mid-June, when snow-melt was intense and conductivity was very low (8.5 μ S cm⁻¹). Such a dramatic decline in pH and conductivity during the melting period was not observed in 1999 or 2001 (PERKKIÖ, 2003), which were both years with below average snow thicknesses.

In spring 1997, TN concentrations varied between 30 and 163 μ g l⁻¹. The highest surface water concentrations (163 μ g l⁻¹) were measured on June 10, and the lowest (30 μ g l⁻¹) on June 17. In mid-June TN concentrations were very low throughout the whole water column (0–16m: 30–70 μ g l⁻¹). In general, TN concentrations were clearly lower than in 1999. Nitrate concentrations in spring 1997 were fairly similar to 1999, with the exception of much higher surface water concentrations in 1997 (1997: up to 178 μ g l⁻¹; 1999: up to 57 μ g l⁻¹).

	1997	1999
Prevailing wind directions (January–June)	south, northwest	south, west
Total precipitation in April (mm)	152	34
Depth of snow cover in mid-May (cm)	133	21
Time of ice break	July 7	June 19
pH (unit)	5.4-6.7	6.3-7.3
Conductivity (μ S cm ⁻¹)	8.5-45.1	16.3-46.6
TN ($\mu g l^{-1}$)	30-115	90-190
$NO_3 + NO_2 - N (\mu g l^{-1})$	*-101	*-57
NH_4 -N (µg 1 ⁻¹)	7–30	6-20
TP ($\mu g l^{-1}$)	*-11	*-6
Dominant phytoplankton group	small flagellates, cryptophytes, dinoflagellates	chrysophytes, small flagellates

Table 2. Range of measured climatological and limnological values (upper water column: 0-8 m) during spring 1997 and 1999.

* = Below detection limit: TP < 5 μ g l⁻¹, NO₃ + NO₂-N < 40 μ g l⁻¹

Ammonium concentrations in 1997 were slightly higher than in 1999, especially in mid-June. Phosphorus concentrations were similar during both springs (Table 2). Sulphate concentrations in the surface layer were lower in 1997 compared to 1999 (mean concentrations were 2.1 and 2.6 mg l⁻¹, respectively). The lowest sulphate concentration in spring 1997, 0.8 mg l⁻¹, was measured one week before ice-out.

In spring 1997 phytoplankton cell numbers and biomass were fairly similar to spring 1999. The community was dominated by small flagellates, and especially by cryptohytes and dinoflagellates, which were not common in 1999.

Spring community of zooplankton consisted of similar species in 1999 and 1997. The maximum biomass of *E. graciloides* was remarkably higher in 1999 compared to 1996 and 1997 (35,500 individuals m⁻³ in 1999 and only 900 individuals m⁻³ in 1996 and 1997). However, this difference was due to different sampling methods between the years. In 1999 a 50 μ m plankton net was used to collect zooplankton whereas during other years, zooplankton were sampled with a 200 μ m net. As a result, only in 1999 all life-history stages of copepods were captured, especially the numerous nauplia.

4. Discussion

4.1. Acid Pulse and Its Occurrence

Short-term acidification (i.e. acid shock) of surface waters during spring floods has been documented virtually all over the world, including Arctic regions (TRANTER *et al.*, 1987; KINNUNEN, 1990; MOISEENKO, 1999; LAUDON *et al.*, 2000, 2004a, b; MOISEENKO *et al.*, 2001). In the Arctic, the phenomenon is especially powerful as snow, and in many cases also contaminants from the atmosphere, accumulates for a long period during the polar winter. The Kilpisjärvi region receives precipitation mostly in the form of snow, which results in a deep snowpack. When the snowpack melts during a relatively short period in the spring, large amounts of moderately acidic and dilute meltwater is released quickly into the terrestrial and aquatic ecosystems. The terrestrial ecosystem provides little buffering capacity because the soil is still fully frozen when the snow is melting and there is no infiltration (Luo *et al.*, 2003). Thus, snowmelt moves rapidly into lakes and streams with little modification. Generally, bedrock in the Kilpisjärvi area consists mostly of alkaline sedimentary rocks which give good buffering capacity during the open water season.

Acid shock can be caused by several factors including base cation dilution, release of mineral acids (sulphates and nitrates stored in the snowpack), or leaching of natural organic acids from soils in forested or wetland catchments (LAUDON and BISHOP, 1999). Among these, base cation dilution is usually the most common cause of episodic acidification (MOLOT *et al.*, 1989; WIGINGTON *et al.*, 1996; SULLIVAN, 2000). Based on the springtime water chemistry (Fig. 5) (especially apparent in conductivity) base cation dilution seems to be the mechanism that is operating in Lake Saanajärvi. However, dilution does not itself generate acidity but leaves the water more sensitive to acids (both natural and anthropogenic) which are present.

Sulphate and nitrate release is typically a result of acidic deposition from anthropogenic sources; their introduction intensifies substantially the episodic acidification of headwater lakes and streams during flood periods (JOHANNESSEN and HENRIKSEN, 1978). Nitrate is the principal mineral acid anion implicated in the pH depressions observed in northern Europe and north-eastern United States (GALLOWAY *et al.*, 1980; JEFFRIES, 1990; SULLIVAN, 2000), although others studies have shown that sulphate is the dominant ion responsible for the temporary pH decline (MOLOT *et al.*, 1989). During the study period sulphate and nitrate concentrations in the surface water, inlet and snow of L. Saanajärvi were very low (Fig. 5), sug-

gesting that anthropogenic sources are not the major cause of episodic pH depression in the area.

On the basis of studies across the northern Boreal region, the spring pH pulse decline can be considered a natural property or 'norm' of the aquatic ecosystems (SCHAEFER *et al.*, 1990; LAUDON *et al.*, 2000). However, as shown by this study, its effectiveness may vary considerably from year to year depending particularly on winter precipitation and prevailing wind directions along with spring air temperatures. In 1999, no clear evidence of acid shock was observed in Lake Saanajärvi, whereas in 1997 our data indicate moderate acidification during high flow events (Table 2).

One of the main drivers for the winter/spring precipitation seems to be the Arctic Oscillation (AO). The AO is the dominant pattern of non-seasonal sea-level pressure (SLP) variations north of 20°N used commonly as a measure depicting large-scale climatic variation/change (THOMPSON and WALLACE, 1998). Most of the relevant snow and winter weather variables in Finnish Lapland seem to be correlated significantly with the AO. High AO values results in increased precipitation in northern Fennoscandia with rainy summers and autumns, deep snow in winter, and moderate temperature. Low AO values indicate less precipitation, colder winters, and deeper frost in the ground.

Wind direction and wind speed should be taken into account when assessing the role of the anthropogenic component of the pH decline in the spring flood of the study region. Northern Fennoscandia lacks big point pollution sources, yet the Kola Peninsula in northwest Russia is exceptional as an area where massive emissions of sulphur dioxide and toxic metals are produced by the metallurgical processes. Correspondingly, the estimated annual deposition of SO₂ in Finnish Lapland is highest $(0.5-1.0 \text{ g S m}^{-2})$ in the east close to the Russian and Norwegian borders (cf. Fig. 1). The values decline gradually towards western Lapland, where they are below 0.3 g S m⁻² (TUOVINEN *et al.*, 1993). Atmospheric SO₂ concentrations in the Kilpisjärvi area are highest in winter, but show marked temporal fluctuations depending on the prevailing winds. Based on stable oxygen isotopes, the Kilpisjärvi region receives both coastal and continental air masses (SONNINEN, unpublished data). During the preceding winters and springs of 1997 and 1999, the dominating wind directions were south and west/northwest, thus not carrying pollutants from Kola Peninsula. In terms of atmospheric pollution, the study area represents one of the cleanest environments in Europe (RÜHLING et al., 1992) and sulphate and nitrate concentrations in the snow pack from anthropogenic sources are moderate compared to densely populated areas (DE CARITAT et al., 2005: HOLE et al., 2006).

The most obvious reason for the lack of pH depression in 1999 is the exceptionally low precipitation and the consequent thin snow cover in the winter of 1998/99 (Table 2). If there is only a small amount of snow in the catchment area, the melting is short-lived and the volume of meltwaters entering the lake might not be large enough to cause considerable drop in lake water pH. Conversely, in a winter with thick snow cover, such as 1996/97, the melting process was longer in duration and its intensity was higher. The difference in melting processes and the severity of the dilution effect during springs 1997 and 1999 can be seen especially in conductivity, which dropped considerably more in 1997 compared to 1999 (Table 2). Higher nitrate concentrations in surface water in 1997 indicated that larger amounts of nitrate accumulated in snow during the year of heavier snow cover. Hence, dilution by low ionic strength snowmelt water, together with nitrate, caused rapid decline in the acid neutralising capacity (ANC) and resulted in a pH depression in the receiving water body in 1997. These results support our first hypothesis of the role of climatic factors in the formation of the acid pulse.

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4.2. Springtime Water Chemistry

In contrast to lakes in high mountainous areas, such as in the Alps, the effect of local topographic shading on the freezing and thawing processes at Lake Saanajärvi is presumably negligible, so that the timing of freeze-up and break-up will be determined largely by synoptic-scale climate integrated over several weeks (*cf.* PALECKI and BARRY, 1986). The timing of break-up is thus likely to reflect the air temperatures prevailing during May/June.

Usually lakes in northern Finland are warmer during winter than lakes in southern Finland, because winter comes quickly in the north and the water mass has not as much time to cool off as lakes in the south before the formation of ice cover. A long ice-cover period together with a relatively high oxygen consumption (e.g. caused by microbial activity and *Eudiaptomus graciloides* winter maximum), lead to low oxygen levels during springtime. Despite the oligotrophic nature of most arctic and mountain lakes, oxygen depletion is a common feature of their seasonal cycle (SCHINDLER *et al.*, 1974; CATALAN *et al.*, 2002).

Lake water chemistry in Lake Saanajärvi had similar trends to ultraoligotrophic Canadian Char Lake (74°42′ N, 94°52′ W), where in early spring most chemical elements have highest values both at the sediment-water interface and at the ice-water interface (SCHINDLER *et al.*, 1974). In Lake Saanajärvi there seems to be an interannual variation in springtime water chemistry, especially in nutrient levels and pH. These are most likely linked to differences in winter weather conditions such as depth of the snow cover, which seems to be further connected to changes in the Arctic Oscillation.

Usually in Arctic areas the dilute meltwaters run into the lake in late spring and, together with the melting lake ice and snow, form a light and dilute water layer in the lake surface. Because of the differences in temperature and conductivity, this light water mass does not mix effectively with the lake water, but forms a major part of the outflow. In the catchment area of Arctic lakes most of the melting occurs while the lake is still ice-covered. Similar to Lake Saanajärvi, mixing of the different water masses is further hindered because the ice cover prevents wind-induced mixing (BERGMANN and WELCH, 1985). HOBBIE et al. (1983) used rhodamine dye in Toolik Lake in Alaska to show that stream water under the ice did not mix with most of the lake, but was flushed from the lake before the ice had melted. A similar kind of flushing has also been observed in boreal forest lakes from Finland (SIMILÄ, 1988). The influence of snowmelt was also seen in the springtime oxygen isotope values of 1997 (Fig. 6): clearly lower values than during the rest of the season were detected, but the decline was restricted to the surface water. During the years when pH depression was observed in Lake Saanajärvi, it seemed to affect only the surface layer (0-4 m) and only for a relatively short period (one to two weeks). These results are consistent with our second research hypothesis of the constricted effects of the acid pulse.

4.3. Effects of Spring Events on Plankton

Springtime phytoplankton biomass in Lake Saanajärvi was very low, compared to the biomass usually observed later in the season (Fig. 8) (FORSSTRÖM *et al.*, 2005). Phytoplankton consisted mostly of small unicellular flagellates, dinoflagellates, cryptophytes, and chrysophytes, all of which have been previously reported to be common in winter communities of phytoplankton in temperate and arctic lakes (KALFF, 1967; AGBETI and SMOL, 1995; PHILLIPS and FAWLEY, 2002). Many of these winter and spring taxa are heterotrophic or mixotrophic and survive well in low temperatures and low light (SANDGREN, 1988; HOLEN and BORAAS, 1995). Motility allows these algae to move freely in the water column, which is important especially under ice where wind-induced mixing is not taking place.

The biggest change in algal biomass and species structure during the study period occurred at the time of ice break. After ice-out small unicellular flagellates were outcom-

peted by taxa with larger cell-size or colony-formation. Based on partial RDA results the occurrence of ice was the main factor explaining the phytoplankton community structure and biomass during spring. The ice cover does not directly affect the algal communities, but together with snow it blocks most of the solar radiation and prevents wind-induced mixing of the water (SMOL, 1998).

The springtime plankton community in Lake Saanajärvi differs from the classical seasonality model designed especially for temperate lakes, where phytoplankton have a distinct spring maximum consisting of small fast-growing algae and small, centric diatoms, and where herbivorous zooplankton populations increase thereafter (SOMMER et al., 1986). In addition to temperate areas, a phytoplankton spring bloom, occurring either when lakes are still ice-covered or just after ice-out, has been recorded also in many subarctic and alpine lakes (KALFF and WELCH, 1974; MILLER et al., 1986; WELCH et al., 1989; JÓNASSON et al., 1992; O'BRIEN et al., 1997). In Arctic Toolik Lake the main reason for increased primary production and algal biomass during the spring was the nutrient load that flushed into the lake at ice melt (MILLER et al., 1986). In Lake Saanajärvi the meltwaters have low nutrient concentrations and do not bring any marked external nutrient load into the lake. The springtime phytoplankton growth in Lake Saanajärvi might be further hindered because of rapid changes in the light regime, dilution, and flushing, which have been shown to inhibit phytoplankton spring bloom in some cases (SIMILÄ, 1988; JONES, 1991; SCHMITT and NIXDORF, 1999). In addition, there is a relatively high grazing pressure since the dominant zooplankton species, *E. graciloides*, has its peak abundance during early spring. These potentially important factors could not be included in the statistical analysis, since no quantitative data were available.

Generally, zooplankton communities usually have their maxima in summer (SOMMER et al., 1986; AGBETI and SMOL, 1995; AGBETI et al., 1997). However, in high-latitude lakes, cold temperatures and limited resources prolong the life-cycle length of zooplankton. As a consequence, only a few species are able to benefit from the warmer summer months to produce several generations or cohorts that would account for the summer maximum of zooplankton typical of lower-latitude lakes. In Lake Saanajärvi, only the cladocerans and rotifers have more than one cohort per year. At least for *Daphnia umbra* the cohort cycles seem to be synchronous resulting in the ups and downs in species abundances during summer when the reproduction is fastest (RAUTIO et al., 2000). The dominant copepod Eudiaptomus graciloides is monovoltine, the nauplia hatching in February and resulting in a density maximum during the polar winter (RAUTIO et al., 2000). The hatched nauplia survive with their oil reserves until spring phytoplankton makes faster growth possible and initiates development that culminates in late autumn with adults full of lipid drops ready to reproduce. In addition to optimum resource utilisation, the winter hatching and resultant maximum of E. graciloides might be advantageous due to lowered predation pressure and lack of harmful UV radiation during the ice-covered period.

It is probable that plankton are not much affected by the acid pulse: the acid pulse is short and is mostly restricted to the uppermost surface waters. However, after the polar winter, the vulnerability of Arctic aquatic biota to acid and toxic impacts is high because many stressors (e.g. low temperature, low nutrient concentration and high solar radiation) operate simultaneously and many aquatic species are in early sensitive life stages (RAUTIO and KORHOLA, 2002; CATALAN *et al.*, 2002).

5. Conclusions

In unpolluted areas, like in NW Finnish Lapland, it seems that the dilution effect of melting snow is the main mechanism behind the acid pulse. This study shows that the magnitude of the acid pulse and its intensity can have considerable interannual variability which is linked to winter precipitation, and to some extent, to the AO. The spring processes, such as melting of snow, flushing and ice-break up, were responsible for most of the annual limno-chemical variation within Lake Saanajärvi. During the spring, most of the chemical parameters showed their highest and/or lowest concentrations. Phytoplankton and zooplankton had an atypical succession in Lake Saanajärvi compared to many temperate and arctic lakes. The lack of phytoplankton spring maxima is most probably affected by low inputs of external nutrient load (especially in NO₂ + NO₃–N and in NH₄–N) in addition to low water temperature. Low temperatures and limited food resources resulting in long life cycles of zooplankton may be the main factors controlling the succession of zooplankton in Lake Saanajärvi. This study clearly shows that arctic aquatic ecosystems have exceptional functional features compared to aquatic ecosystems from other regions, making these ecosystems distinct.

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