



Biogeography and ecology of freshwater chrysophyte cysts in Finland

Sanna Korkonen · Jan Weckström · Atte Korhola

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Abstract The occurrence of various chrysophyte cyst morphotypes is unknown in Finland, with the exception of a few isolated lake studies. We set out to chart which cyst types are found in Finland and what their ecological preferences are, focusing on cyst-air temperature relationships that could be further utilized in reconstructing past winter/spring air temperatures and ice-free periods from sedimentary cyst assemblages. Surface sediment samples from lakes across Finland were analysed for their chrysophyte stomatocyst assemblages. Multivariate ecological techniques (e.g. canonical correspondence analysis, principal component analysis) were used to identify the environmental variables that most strongly affected the

distribution of the cysts. This survey expanded the known geographical range for several cyst types. Lake water pH and ice-free periods (surrogate for air temperature) explained the statistically significant distribution and composition of the cyst assemblages studied. The results broaden our knowledge of cyst biogeography and strengthen the findings of previous studies of the environmental factors contributing to the occurrence of cysts. Highly variable and rich chrysophyte cyst assemblages in Finland are clearly associated with temperature, pH, electrical conductivity and total phosphorus, with good potential in contemporary and retrospective environmental assessment.

Keywords Lake sediments · Subarctic lakes · Statospore · Morphotype · Multivariate analysis

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S. Korkonen (✉)
Ecosystems and Environment Research Programme,
Faculty of Biological and Environmental Sciences,
University of Helsinki, 00014 Helsinki, Finland
e-mail: sanna.korkonen@helsinki.fi

J. Weckström · A. Korhola
Ecosystems and Environment Research Programme,
Faculty of Biological and Environmental Sciences and
Helsinki Institute of Sustainability Science (HELSUS),
University of Helsinki, 00014 Helsinki, Finland

Introduction

Chrysophytes, also known as golden algae or golden-brown algae (classes Chrysophyceae and Synurophyceae), usually form an essential part of algal communities in cool, high-latitude, oligotrophic lakes, such as the majority of lakes in Finland (Eloranta, 1995; Sandgren et al., 1995). All chrysophytes produce siliceous resting stages, often previously referred to as statospores, but now more properly called stomatocysts or simply cysts, to ensure the

survival of the population under unfavourable environmental conditions in the form of a seed bank. Many phytoplankton groups produce resting stages with long-term persistence, in some cases up to at least a century (Ellegaard & Ribeiro, 2018). Germination from chrysophyte cysts at least 60 years old has been reported in lake sediments from Sweden (Cronberg, 1982), but the exact longevity of chrysophyte cysts remains yet unknown (Ellegaard & Ribeiro, 2018).

Chrysophyte cysts are produced endogenously, either asexually or sexually, resulting in an identical-looking cyst whose morphology is considered to be species-specific (Sandgren, 1983, 1991). Chrysophyte cysts possess a hard siliceous cyst wall resistant to dissolution, a characteristic that, together with the sheer numbers of cysts produced, makes them ideal subjects in palaeolimnological investigations. To date, only a small percentage of chrysophyte stomatocysts have successfully been linked with their vegetative stages. This shortcoming led to the development of an artificial naming system created by the International Statospore Working Group (Cronberg & Sandgren, 1986). These guidelines have been extensively modified and revised in subsequent taxonomic treatments (Duff et al., 1995; Wilkinson et al., 2001).

During recent decades, several cyst floras from different geographical regions have been published, e.g. Central Europe (Facher & Schmidt, 1996), the Azores (Hansen, 2001), the Pyrenees (Pla, 2001), sub-Antarctica (van de Vijver & Beyens, 1997, 2000) and China (Pang & Wang, 2014, 2016; Bai et al., 2018). The most expansive floras are the Atlas of Chrysophycean Cysts (Duff et al., 1995) and the Atlas of Chrysophycean Cysts Volume II (Wilkinson et al., 2001), focusing largely on North American temperate and Arctic locations. In addition to cyst identification floras, several palaeolimnological studies throughout the world have successfully linked cyst morphotypes with various environmental variables in the form of cyst-based transfer functions, e.g. for pH (Rybak et al., 1991; Facher & Schmidt, 1996; Pla & Anderson, 2005), temperature (Kamenik & Schmidt, 2005; Pla-Rabes & Catalan, 2005; de Jong et al., 2016; Hernández-Almeida et al. 2015a), salinity (Zeeb & Smol, 1995) and water chemistry (Duff & Smol, 1995; Pla et al., 2003). However, chrysophyte cysts are not as widely used as diatoms or pollen in palaeolimnological research, mostly due to the challenges in linking chrysophyte species with the stomatocysts

they produce. The studies that have utilized cysts have revealed their great potential for reconstructing past environmental conditions, particularly winter- and spring-related climate parameters, which is a great advantage, since most other palaeobioindicators are related to summer conditions only (e.g. Kamenik & Schmidt, 2005; Pla-Rabes & Catalan, 2005).

Even though chrysophyte stomatocysts have even been associated with carnivorous plants (Wolowski et al., 2011) and have also been found in a thermal spring in Egypt (Piątek et al., 2009), there still remain geographic regions where no comprehensive knowledge of the cyst flora is available. One of these areas is Northern Continental Europe. This is the first large-scale study aiming to describe the distribution and ecological preference of various chrysophyte cyst types in Finland, ‘the land of a thousand lakes’.

Materials and methods

Study sites

The study sites comprised 59 lakes located throughout Finland, ranging from the clear-water ultraoligotrophic cold lakes in the Hemi-arctic Zone to the warmer, more nutrient-rich humic lakes in the Hemi-boreal Zone (Fig. 1). The ice-free period varies typically from approximately 8 months in the southern parts to only 4 months in northernmost Finnish Lapland (Table 1). Spring mixing usually occurs during May in the south, autumnal mixing in October. In northern Finnish Lapland, spring mixing has been observed in July and a longer autumnal mixing in September–October (Forsström et al., 2005). The study lakes were chosen according to their available water chemistry data (Oiva, 2015), with the main object of keeping the water pH close to neutral (pH 7), total phosphorus (tot-P) concentration below 20 µg/l and lakes with as little human influence in the drainage area as possible. Electrical conductivity values varied between 5 and 164 µS/cm.

The surface sediment chrysophyte cyst assemblages from 59 lakes were sampled in 2007 and 2008 with a Limnos-type sediment corer. The top 1 cm of sediment was retrieved from the deepest part of the lake and stored in the dark in Minigrip bags at + 4°C prior to laboratory analysis. Nineteen of the lakes are located in southern or central Finland (SF),

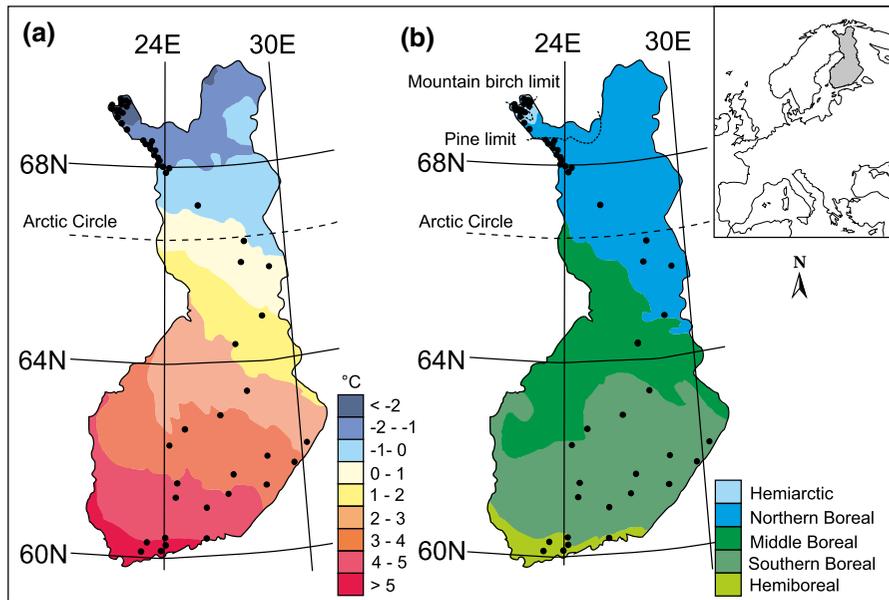


Fig. 1 Location of study lakes in Finland in relation to **a** average annual temperature and **b** vegetation zones and the location of Finland in Northern Europe

Table 1 Summary statistics of the environmental variables at the study sites

	Min	Max	Mean	Median	Range
Latitude (°N)	60.25	69.27	66.10	68.10	9.02
Longitude (°W)	20.67	30.39	24.10	23.40	9.72
Altitude (m a.s.l.)	25.2	987.2	347.9	254.0	962.0
Sampling depth (m)	1.5	25.0	7.4	5.3	23.6
Area (ha)	0.9	88700.0	2318.0	16.9	88699.1
Electrical conductivity (µS/cm)	5	164	36	30	159
Alkalinity (mmol/l)	0.0	0.4	0.1	0.1	0.4
pH	4.9	7.6	6.8	6.9	2.7
tot-N (µg/l)	54.0	1500.0	355.2	330.0	1446.0
tot-P (µg/l)	2.0	46.0	11.3	8.3	44.0
Ice-free period (days)	129.0	242.0	170.0	154.0	113.0
Spring mean (°C)	- 4.1	4.4	- 0.6	- 1.5	8.5
Summer mean (°C)	8.7	16.5	12.6	12.4	8.2
Autumn mean (°C)	- 2.5	6.1	1.0	- 0.5	8.6
Winter mean (°C)	- 12.8	- 3.6	- 10.0	- 11.9	9.2
July mean (°C)	10.4	18.3	14.5	14.3	8.0
January mean (°C)	- 13.6	- 3.9	- 10.7	- 12.4	9.7

seven in southern and eastern Lapland (SYKE) and 33, mostly in western Finnish Lapland (WFL), both above and below the tree line (Fig. 1).

Sample preparation

The sediment samples were cleaned according to the standard treatment for diatoms (Weckström et al., 1997; Battarbee et al., 2001), i.e. by digesting the sediment in hydrogen peroxide (H₂O₂) and adding a

few drops of hydrochloric acid (HCl, 37%) before repeated washing with distilled water. The cleaned chrysophyte cyst aliquot suspension was dried on scanning electron microscope (SEM) stubs and left uncoated. A minimum of 200 cysts per sample were counted and identified from SEM (JEOL JSM-840A, Hitachi S-4800) images. Unornamented cysts in which the pore morphology could not be observed were classified, using probabilistic counting, i.e. they were classified as a specific morphotype based on the percentage distribution of different morphotypes in the same sample. The cyst identification was based on Duff et al. (1995), Facher & Schmidt (1996), Pla (2001), Wilkinson et al. (2001) and Baumann et al. (2010).

Water chemistry data

The water chemistry data were retrieved from the Finnish Environment Institute's Oiva database (Oiva, 2015) for nationwide lake water chemistry information. The used data are average values of 1–51 in situ measurement conducted between years 1997 and 2008.

Climate data

The meteorological data are part of the Finnish Meteorological Institute's ClimGrid dataset described in Aalto et al. (2016), derived from the spatial data for research and teaching database (PaiTuli). The daily and monthly temperature data are based on a spatial resolution of 10×10 km. Due to the variable sediment-accumulation rates in lakes located in different vegetation/climatic zones, and thus a different temporal extent of the topmost 1-cm sediment sample, daily and monthly temperature data for 10 years were used for sites located in the Middle, Southern and Hemiboreal zones, 20 years for Northern Boreal Zone lakes and 30 years for lakes in the Hemiartic (Weckström et al., 2014). The temperature data for different seasons were based on the monthly mean temperatures of 3 months per season (i.e. March, April and May for spring; June, July and August for summer; September, October and November for autumn; and December, January and February for winter). The ice-free period for each lake was calculated, using the melting degree-day value of + 130 and a freezing degree-day value of – 30, based

on Thompson et al. (2005) and Weckström et al. (2014).

Numerical methods

In total, 17 environmental variables (altitude, alkalinity, conductivity, total nitrogen, total-phosphorus (tot-P), pH, surface area, sampling depth, spring mean temperature, summer mean temperature, autumn mean temperature, winter mean temperature, July mean temperature, January mean temperature, ice-free period, latitude, longitude) were used to study the relationship between the chrysophyte cysts and the environmental variables. All the environmental data except pH were \log_{10} -transformed prior to the statistical analyses.

Principal component analysis (PCA) was used to summarize the major patterns of variation within the 10 environmental variables screened (Fig. 2). The vegetation zones (Hemiartic, Northern Boreal, Middle Boreal, Southern Boreal and Hemiboreal) were added as supplementary, i.e. passive, variables. Species richness at constant sample counts was estimated by rarefaction, which is well suited for stratigraphical species data with different count sizes between individual samples (Birks & Line, 1992). The Shannon H' diversity index was used to evaluate the species diversity in the samples (Shannon & Weaver, 1949). Rarefaction and Shannon H' analysis were conducted, using Palaeontological Statistics (PAST) statistics software 3.1. (Hammer et al., 2001). A species abundance diagram (Fig. 3) was created, using the program C2 (version 1.7.2., Juggins, 2007). Due to the high species turnover rate (DCA axis one length of 2.3 SD) between the surface sediment assemblages, canonical correspondence analysis (CCA) was used to analyse the species distribution across the environmental gradients measured. Monte Carlo permutation tests with 999 permutations were used to assess the statistical significance of the primary ordination axis and overall models. To assess the sensitivity of the chrysophyte cysts to the climate variables (mean July temperature and ice-free period), pH, and tot-P, the optima and tolerances for independent chrysophyte cysts were calculated, using the weighted-averaging (WA) regression technique (ter Braak & van Dam, 1989) in the program C2. All cysts were transformed to percentage abundances and square-root-transformed prior to the statistical analyses, which were

Fig. 2 Principal component analysis of the study lakes and their environmental variables in Finland. The vegetation zones indicated with star symbols were added as passive variables. Lake symbols refer to the vegetational zones shown in Fig. 1, square = Hemiboreal, triangle = Southern Boreal, swirl = Middle Boreal, circle = Northern Boreal, diamond = Hemiarctic (Tot-N = total nitrogen, Tot-P = total phosphorus)

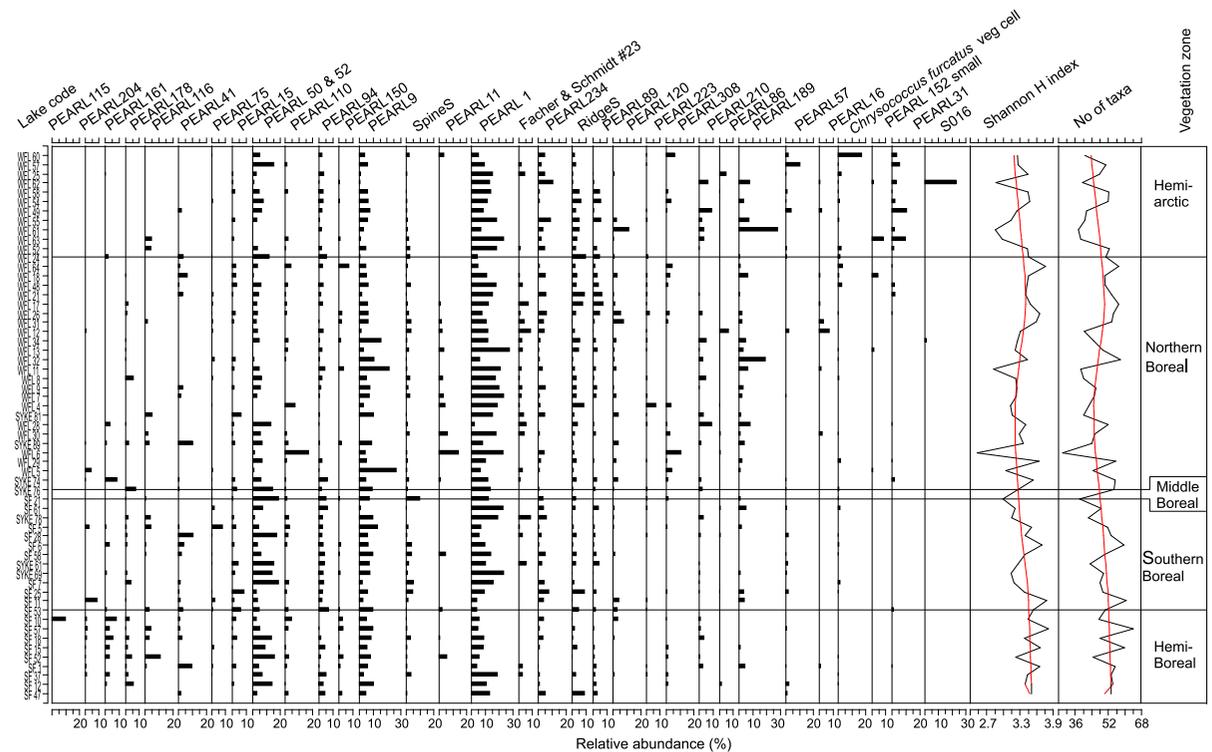
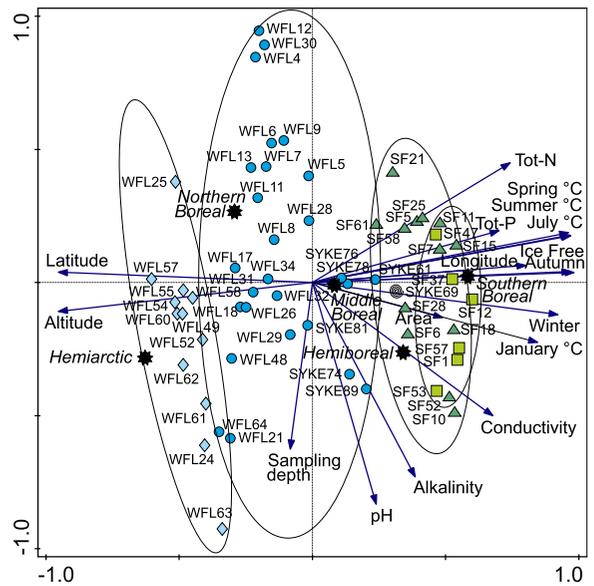


Fig. 3 The most commonly occurring (> 7%) cyst types in Finland, together with the Shannon index, number of taxa and vegetation zones. The lakes are ordered according to their altitude from the high altitudes at the top to the low altitudes at the bottom

performed using CANOCO 5.01 (ter Braak & Šmilauer, 2007–2012). All taxa were included in the PCA and CCA; however, only the most common taxa (the same as in Fig. 3) were plotted in Fig. 4.

Results

The study lakes are divided into three groups according to their location. The WFL lakes are mostly

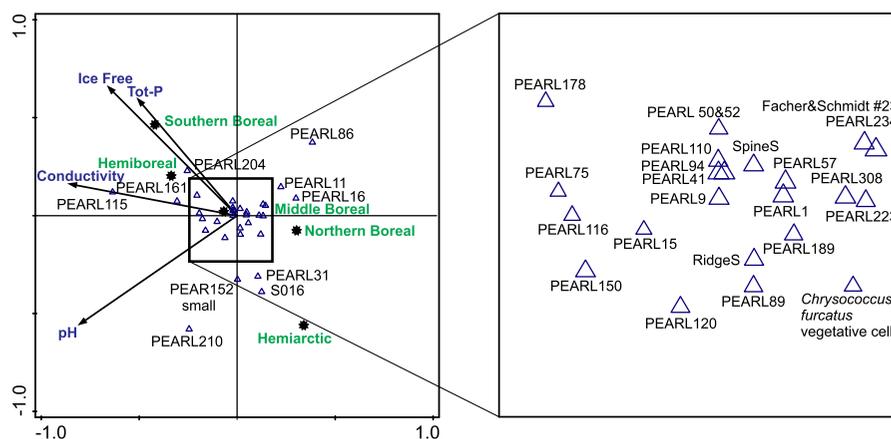


Fig. 4 Canonical correspondence analysis of the most common chrysophyte cysts in Finland (open triangles). The environmental variables are indicated with arrows and the vegetation zones are marked with star symbols

located in the Hemiarctic Vegetation Zone at a higher elevation, with the drainage area consisting of mountain birch (*Betula pubescens* ssp. *czerepanovii* (Orl.) Hämet-Ahti) forest or barren land if located above the treeline (Fig. 1). The PCA reveals that the WFL lakes are associated with low temperatures, low phosphorus concentrations, low conductivity and shorter ice-free periods (Fig. 2). The SYKE and SF lakes (Fig. 2) with coniferous forests or mixed vegetation in the drainage area belong to the Northern, Middle, Hemi- and Southern Boreal zones. These lakes are associated with higher temperatures for all seasons, higher tot-P concentrations, higher conductivity and longer ice-free periods. The SYKE lakes form a continuum between the WFL and SF lakes.

In all, 253 cyst morphotypes or collective categories were identified from the Finnish sediment material, 32 of which occurred at > 7% proportions in at least one lake (Fig. 3). SEM images of some of the most common cyst types found in Finland are shown in Online Resource 1. The number of morphotypes or collective categories per lake varied between 30 and 66; in general, the number of different morphotypes decreased from the southern lakes towards the northern lakes with barren drainage areas. A similar trend can be observed in the Shannon H' index. Unornamented cyst surfaces form the majority of all cyst ornamentation types in lake sediments from Finland, their relative occurrence ranging between 31% and 71% per sample, with an average of 54% of cysts counted per sample. No clear association between cyst

ornamentation type and the various vegetation zones was observed.

The majority of the cysts found are featured in the two cyst atlases; codes from PEARL 1 to PEARL 243 refer to Duff et al. (1995) and the rest of the PEARL codes refer to Wilkinson et al. (2001). The most common cyst types in Finland are PEARL 1, PEARL 9 and PEARL 50&52 (Duff et al., 1995). These are all collective categories: fairly small, unornamented and most likely produced by several different species of chrysophytes (Duff et al., 1995). Cysts that occur throughout Finland also include cyst types PEARL 15, 10, 116, 41 (*Dinobryon cylindricum* Imhof; Donaldson & Stein, 1984), 94, 234, 89 and 120. Of the most common cyst types only two, PEARL 115 and PEARL 75, are clearly linked with the Southern Boreal Vegetation Zone, with no particular cysts associated only with the narrow Hemiboreal Vegetation Zone. Cysts associated with vegetation zones spanning from the Hemiboreal to the Northern Boreal Zone include PEARL 204, 161 and 178. Cyst types preferring the Hemiarctic Vegetation Zone include S016 (Pla, 2001), PEARL 31, small PEARL 152 and PEARL 57.

The initial 17 environmental variables captured 36.9% of the total variance of the cyst data. Based on the known ecological preferences of the cysts, a subset of four environmental variables (pH, conductivity, ice-free period and tot-P) were chosen to further determine the relationship between the enumerated cysts and the environment. These four variables captured 14.4 of the total variance of the cyst data and 39% of the total variance explained by the initial

17 environmental variables, with sole explanatory power of 5.4% (pH), 5% (conductivity), 4.8% (ice-free period) and 4.1% (tot-P). All of these variables were statistically significant ($P < 0.001$). The CCA showed that the majority of the most common cysts were located close to the origin, i.e. they showed no clear preference for any of the environmental variables (Fig. 4).

The calculated optima show that the cysts PEARL 115, 204, 161, 178, 116, 75 and 50&52 prefer longer ice-free periods and higher tot-P concentrations (Fig. 5a, b). In contrast, *Chrysococcus furcatus* (Dol-goff) K.H. Nicholls vegetative cell, S016 (Pla, 2001), PEARL 31, 16, and small 152 favour short ice-free times and low tot-P concentrations. The cysts PEARL 86, 16, 11, 223 and 57 seem to prefer pH of 6.5 or less,

while PEARL 115, 161, 204, 178 and 116 prefer higher conductivity ($> 50 \mu\text{S}/\text{cm}$).

Discussion

The most frequently occurring cysts found in this study were mainly cosmopolitan types found commonly in many previous studies (e.g. Brown et al., 1997; Pla & Anderson, 2005). These cyst types were mostly collective categories, in which similar-looking cysts were most likely produced by different species, possibly with different environmental preferences. Many of these were unornamented, leaving only size and pore morphology as identification criteria. Cyst types in Finland concurred with previous observations that unornamented cysts seem to predominate in most

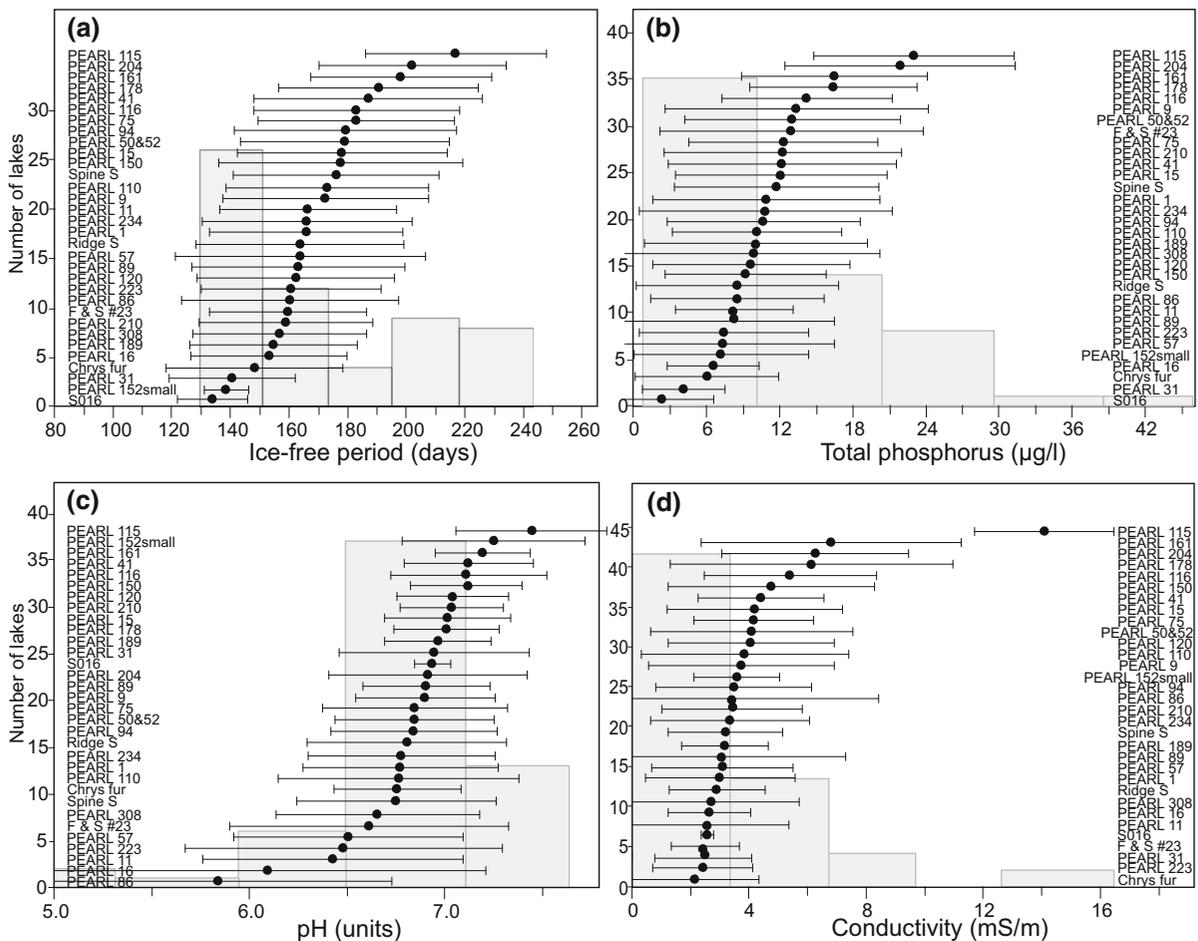


Fig. 5 Optima and tolerance values of the most common cyst types in Finland for **a** ice-free period (surrogate for air temperature), **b** total phosphorus, **c** pH and **d** conductivity. The grey bars represent the number of lakes within the range of the environmental variables

lakes and are common in all habitats (Duff et al., 1992; Wilkinson et al., 1997; Stewart et al., 2000; Betts-Piper et al., 2004; Pla & Anderson, 2005).

Cyst types in different vegetation zones

Of the most frequently occurring cysts, one type, PEARL 115, occurred only in the Southern Boreal Vegetation Zone. It has previously been associated with productive lakes and has been most abundant in slightly acidic to circumneutral lakes (Zeeb et al., 1990; Duff et al., 1995). Brown et al. (1997) have also found this cyst type in lakes with relatively high temperature in northwestern Canada. Our results show that this cyst type favours lakes with higher tot-P values and conductivity, long ice-free periods, but unlike in previous studies, it has been found in Finland in a slightly alkaline lake. This may also have been an artificial result, since PEARL 115 was only found in the sediment of one lake in Finland, causing the environmental range for this cyst to be somewhat limited.

PEARL 75 also occurred mainly in lakes located in the Southern Boreal Vegetation Zone. This cyst type is most likely produced by *Dinobryon bavaricum* Imhof, which has been found in Finland throughout the ice-free season and prefers clear oligotrophic lakes, although it has often also been found in mesotrophic lakes (Eloranta, 1989; Lepistö, 1999). Other cyst types preferring lakes located in the southern and central parts of Finland include PEARL 204 and 161 produced by *Uroglena volvox* Ehrenberg (Kristiansen 1980) and by *Dinobryon divergens* Imhof, respectively. In Finland, *Dinobryon divergens* is a common species in all but the most eutrophic lake types (Lepistö & Rosenström, 1998).

Cyst types occurring from the Hemiboreal to the Northern Boreal zones include PEARL 11, Facher & Schmidt # 23 (Facher & Schmidt, 1996), resembling PEARL 11 without the characteristic ridge extending from the collar, and PEARL 223. PEARL 11 has previously been observed at least in Svalbard (Betts-Piper et al., 2004) and in Arctic peat in Siberia, Russia (Gilbert et al., 1997). In a seasonality study of one particular lake in Finland (Korkkonen et al., 2017), PEARL 11 occurred in small numbers mainly in spring cyst assemblages. Cyst Facher & Schmidt # 23 was also found in high numbers in Central European

lakes with no clear ecological preference (Facher & Schmidt, 1996).

Cysts associated with northern boreal and hemiarctic lakes included PEARL 189 and PEARL 308. PEARL 189 has also been found in, e.g. Greenland and Ellesmere Island in the Canadian Arctic Archipelago and British Columbia, Canada, which may indicate that it is produced by cold-tolerant species (Duff et al., 1992; Brown et al., 1994; Duff & Smol, 1994). Brown et al. (1997) found and described PEARL 308 in lakes with relatively high temperature in northwestern Canada at relatively low latitudes.

PEARL 31 has also previously been considered to be produced by a cold-tolerant species. In our study, it was among the few that showed the optimum for an ice-free period of 140 days or less, which supports this hypothesis. S016 (Pla, 2001) has been described from lakes in the Pyrenees, and in the Finnish material it has mainly been found in hemiarctic lakes, i.e. lakes at high altitude in Western Finnish Lapland. S016 differs from PEARL 16 in collar-pore morphology and size. Both forms were among the most common cyst types in the Finnish material but they showed differences in their temperature and pH preferences. PEARL 16 prefers longer ice-free times and lower pH. Although also occurring in small numbers in other vegetation zones, PEARL 57 is found at greatest abundance in the Hemiarctic Zone. It has previously been found in oligotrophic locations (Duff & Smol, 1991; Rybak et al., 1991), which is also supported by this study (Fig. 5b). In Finland, it has previously been linked with the summer season in a mesotrophic lake (Korkkonen et al., 2017).

Cysts and environmental variables

Temperature, pH and conductivity were among the most important variables affecting chrysophyte communities and their resting stages in several studies (e.g. Siver & Hamer, 1992; Duff & Smol, 1995; Stewart et al., 2000). According to Hernández-Almeida et al. (2015b), the general trend with factors controlling cyst assemblages at different locations indicates that temperature is an important controller of cyst assemblages in alpine and subalpine lakes, while water chemistry, including conductivity, pH and nutrients plays a bigger role in low-lying lake assemblages (Kamenik & Schmidt, 2005; Pla & Anderson, 2005; Hernández-Almeida et al., 2015b; de Jong et al., 2016). Ice break-

up controlled by spring air temperatures affects stomatocyst assemblages (Kamenik & Schmidt, 2005; de Jong & Kamenik, 2011). Siver (1995) suggested that the ability of chrysophytes to survive under ice cover gives them a head start once the ice melts, while the low grazing pressure may add to the maximal biomass (Sandgren & Walton, 1995). The importance of chrysophyte cyst relationships to winter and spring conditions is highlighted in the scarcity of the palaeobioindicators available for reconstruction of past winter and spring temperatures.

In this study, pH, ice-free period (a surrogate for temperature), conductivity and tot-P were shown to statistically significantly explain the distribution of morphotypes in Finland (Fig. 4). Many of the morphotypes in Fig. 4 not showing clear preferences for the environmental variables, i.e. PEARL 1, 9, 15, 120, 150, 189, 234, PEARL 50&52, RidgeS and SpineS are collective categories produced by several different species (Duff et al., 1995). PEARL 115 stands out in the most commonly occurring cyst assemblages by displaying the highest optima (Fig. 5) for ice-free periods, pH, tot-P and conductivity. This may have been an artefact caused by the fact that this cyst type was only found in one lake, and the data range was therefore limited.

Chrysophytes are among the first algae to bloom in cold spring waters, some of the taxa even living under the ice (Cronberg, 1980; Siver & Hamer, 1992). The calculated ice-free period optima for cysts in Finland support previous studies in which a clear link has been found between spring temperatures/ice-cover times and cyst assemblages (Kamenik & Schmidt, 2005; Hernández-Almeida et al., 2015a). In the Pyrenees (Pla, 2001), S016 occurred only in low-elevation lakes, while in the Finnish lake material it displayed the shortest ice-free optimum and was mainly found in one lake in Western Finnish Lapland. A small version of PEARL 152 was found only in lakes in western Finnish Lapland thus displaying short ice-free period optimum. PEARL 152 was previously reported at least in Minnesota USA (Zeeb & Smol, 1993), where it was interpreted as an indicator of earlier springs, British Columbia in Canada (Duff & Smol, 1994) and Poland (in Rybak, 1987 as Cyst 2). PEARL 31 and 16 have also previously been interpreted as being produced by cold-tolerant species, as was the species *Chrysococcus furcatus*, whose vegetative cell in this study was

associated with low tot-P levels, low conductivity and short ice-free time (Duff et al., 1995).

Cysts that were more commonly reported in lakes with longer ice-free periods include PEARL 204, produced by *Uroglena volvox*, and PEARL 161, produced by *Dinobryon divergens*, a species commonly found in phytoplankton assemblages in lakes in Finland. *Dinobryon divergens* has also been known to bloom under the ice cover, with the highest stomatocyst formation just before the onset of ice cover under oligotrophic, low-light, high-bacterial abundance conditions (Watson et al., 2001). In Finland, the highest accumulations of the cyst PEARL 161 were reported during summer (Korkkonen et al., 2017). Our study indicates that in Finland, PEARL 116 prefers long ice-free periods, unlike in Elk Lake, Minnesota (Zeeb & Smol, 1993), where this cyst was suggested to be more common in lakes with later-than-average ice-out and deep snow.

Unlike many other phytoplankton groups in which a higher number of species can be observed in eutrophic habitats, chrysophytes usually thrive under oligotrophic conditions (Eloranta, 1986; Willén, 1987; Siver, 1995; Lepistö & Rosenström, 1998). Lakes with high phosphorus and nitrogen levels have been observed sustaining a decreased abundance of cysts (Smol, 1985; Wilkinson & Smol, 1998). The data range in our study for nutrients was not wide enough for this trend to be observed, since the lakes in this study are either oligotrophic or mesotrophic. PEARL 115 and 204 produced by *Uroglena volvox* and PEARL 116, 178 and 161 produced by *Dinobryon divergens* have also previously been associated with productive lakes (Duff et al., 1995; Lepistö, 1999). PEARL 116 has been linked with meso/eutrophy in palaeolimnological studies (Zeeb et al., 1990; Zeeb & Smol, 1993). PEARL 75, the cyst of *Dinobryon bavaricum*, however, has previously been linked with oligotrophic lakes (Duff et al., 1995; Eloranta, 1995). Lepistö (1999) showed that this chrysophyte species is also often observed in mesotrophic lakes. Our study on cysts associates PEARL 75 with slight mesotrophic conditions (Fig. 5b). Cysts associated with low phosphorus levels in this study include S016, originally described from material from Pyrenean lakes with low phosphorus content (Pla, 2001). PEARL 16 was also an indicator of low phosphorus in this study, the environmental preferences being similar to S016 regarding conductivity, but the pH and ice-free period

optima differed considerably. Duff et al. (1995) described PEARL 31 as having a wide range for trophic status. In Finland, PEARL 31 can be interpreted as an indicator for low phosphorus levels, the cyst being mainly found in oligotrophic and ultraoligotrophic cold, clear-water northern lakes.

Our research supports previous studies in which pH was one of the most important variables that controlled the distribution of chrysophytes and their cysts (Duff & Smol, 1991; Carney et al., 1992; Siver, 1995; Duff et al., 1997; Wilkinson & Smol, 1998; Hansen, 2001; Pang & Wang, 2014). The most diverse cyst assemblages have been found in neutral and slightly acidic lakes and ponds, as in most of the lakes in this study (Adam & Mahood, 1981; Hansen, 2001; Pang & Wang, 2014). PEARL 86, 11, 16 and 57, found in Finland, seem to be produced by chrysophyte species tolerant of lower-pH environments, which is also backed up by previous studies elsewhere (Rybak et al., 1991; Facher & Schmidt, 1996; Duff et al., 1997; Betts-Piper et al., 2004). A cyst similar to PEARL 86, S086 (Pla, 2001), has a higher pH optimum, but since its size is recorded as being considerably bigger than that reported by Duff et al. (1995), it could be produced by a different species. *Dinobryon divergens* has been found in many types of lakes in Finland, including very acidic, species-poor lakes (Lepistö & Rosenström, 1998). Our study, however, associates the cyst PEARL 161, produced by this species, at the higher end of our pH range.

Conductivity is one of the key factors controlling cyst assemblages (Duff et al., 1997; Pla & Anderson, 2005; Hernández-Almeida et al., 2015b; de Jong et al., 2016). Cumming & Smol (1993) and Duff et al. (1997) stated that conductivity (i.e. salinity) probably affects algal species through the cells' adaptability to external osmotic pressure changes in their surroundings. Most cysts in lakes in Finland prefer conductivity levels between 20 and 50 $\mu\text{S}/\text{cm}$. Our results show that the cysts PEARL 115, 161, 204, 178 and 116 could be considered as indicators of slightly higher conductivity values. PEARL 204 and 116 have also previously been associated with high conductivity values (Duff et al., 1995; Zeeb & Smol, 1995).

Conclusions

Highly diverse chrysophyte cyst assemblages are preserved in Finnish lake sediments, adding Northern Continental Europe to the areas where chrysophyte cysts have been surveyed on a larger scale. While many cyst types are common and found in various locations, our study expands the known geographical range for several of these cyst types to previously uncharted territory. Chrysophyte cyst assemblages in Finland are clearly associated with pH, ice-free periods (as a surrogate for temperature), electrical conductivity and tot-P, providing an additional tool with high potential for use in palaeolimnological environmental assessments, particularly in reconstructing past winter/spring temperatures, a challenging area due to the current scarcity of suitable palaeoproxies.

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