Distribution and autecology of chrysophyte cysts from high Arctic Svalbard lakes: preliminary evidence of recent environmental change*

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Abstract

Chrysophycean stomatocyst assemblages were analysed from the sediments of 17 lakes and ponds from Svalbard as one component of a multi-proxy investigation of recent environmental change in the high Arctic. Sediment cores and water chemistry were collected from each of the study lakes, and chrysophyte stomatocysts were investigated from the top 0.25 cm of sediment (present-day) and bottom (i.e. bottom of short sediment core, pre-industrial) sediment samples. This study represents the first undertaking of chrysophyte cyst morphology and distribution on Svalbard. A total of 153 cyst morphotypes were described with light microscopy and/or scanning electron microscopy, of which 21 are new forms.

Canonical correspondence analysis indicates that the present-day distribution of cysts is significantly related to pH ($p = 0.02$), altitude ($p = 0.02$), and Na^+ ($p = 0.04$). Marked shifts in chrysophyte cyst assemblages were recorded between the top and bottom sediment samples of most lakes. Rose et al. (2004) have demonstrated that Svalbard lakes receive atmospheric contaminants from both local and remote sources. The observed assemblage shifts may be the result of the combined effects of these point sources and long-range pollutants, or the effects of recent climate change, or both.

Figure 1. The Svalbard archipelago and (inset map) its position relative to the North Pole and mainland Norway. The locations of the 21 lakes (A-U) samples in 1995 are shown. Seventeen top and 'bottom' core samples were examined in this study but only sediments from A, B, D, G-K, M-O, Q, and S contained abundant cysts. Lake codes follow Birks et al. (2004a).

Introduction

In order to better understand the nature and extent of environmental change, it is necessary to determine the environmental conditions that existed prior to substantial anthropogenic impact (Smol 1992). High Arctic lakes and ponds respond rapidly to slight changes in environmental conditions (Douglas and Smol 1999). Consequently, these aquatic systems are sensitive indicators of environmental change, and they make ideal study sites for palaeoecological studies. The direction and extent of modification resulting from environmental changes, such as climatic warming and atmospheric pollution, are expected to differ between geographic regions as a result of processes unique to each area (Sommaruga-Woegrath et al. 1997; Andreev and Klimanov 2000; MacDonald et al. 2000). Therefore, it is critical that studies of past environmental change are initiated in a variety of geographic and climatic regions.

Svalbard lakes provide important opportunities for the study of environmental change in the high Arctic resulting from anthropogenic activities. This group of islands is physically isolated from the large industrial areas of Europe, Asia, and North America, and local development is minimal (Rose et al. 2004). It would therefore be expected that recent change to this environment would largely be the result of global processes such as climate change or long-range transport of atmospheric pollutants.

Unfortunately, knowledge of background conditions in the Arctic is limited, as high costs and logistical concerns have generally prohibited traditional monitoring programmes in these remote locations. Palaeolimnology can provide information about past environments that are otherwise unobtainable. In particular, the 'top and bottom' palaeolimnological approach (e.g. Cumming et al. 1992) allows us to infer a regional estimate of change in an area that is relatively unstudied.

Chrysophyte algae may be exceptionally useful environmental indicators in arctic environments. These algae typically dominate the phytoplankton and periphyton of northern regions (Moore 1979; Sheath 1986; Siver 1995; Duff et al. 1995; Wilkinson et al. 2001). Their success is most likely due to their diverse nutritional strategies and ability to produce resistant siliceous resting stages, termed stomatocysts. Unlike most other algal groups that are predominantly autotrophic, many chrysophytes are able to switch between autotrophy, heterotrophy, and even phagotrophy. This puts them at a distinct advantage in arctic systems, where nutrient concentrations are typically low and long periods of ice and snow cover may drastically reduce light penetration. Moreover, their ability to create a resilient resting stage provides them with a means to survive unfavourable conditions. These cysts, which are morphologically distinct and well preserved in a variety of lake environments, make ideal palaeolimnological indicators (Duff et al. 1995; Wilkinson et al 2001).

The objectives of this study are: (1) to document present-day and pre-industrial stomatocyst morphotypes from a suite of small lakes on Svalbard; and (2) to investigate whether cyst assemblages have changed between the present-day and pre-disturbance sediment samples in order to assess the magnitude and direction of any recent environmental changes.

Table 1. Collective categories of cyst morphotypes identified in Svalbard sediments.

Collective Category I.D.	***Cysts included in the category***
C1	Cysts 234, 53 & 152
C2	Cysts 123, 188 & large 51
C3	Cysts 110, 50 & small 51
C4	Cysts 146 & 156
C5	Cysts 117, 178 & 210
C6	Cysts 140 & 141
C7	Cysts 114, 115 & 218
C8	Cysts 154 & 199
C9	Cysts 167, 211, 212 & small 266
C10	Cysts 239 & 94
C11	Cysts 33 & 222
C12	Cysts 118 & 158

Description of study sites and sample collection

In late July and early August of 1995, 20 lakes (Jensenvatnet (L) is ignored here – see Birks et al. 2004a) were sampled along the west coast of Svalbard (Figure 1). A detailed discussion of the sites, as well as limnological and catchment variables measured at the time of sampling, can be found in Birks et al. (2004a). Briefly, these sites are small, shallow lakes (Z_{max} = 0.9 m

– 26.0 m), covering a moderately large range in conductivity (12 μS cm^{-1} – 367 μS cm^{-1}) and pH (5.6 – 8.4). Cores were collected from the deep area of each lake using a Glew (1989) gravity corer, and sectioned at lakeside using a vertical, high-resolution extruding device. The top 0.25 cm and the bottom 1 cm of the sediment core were subsampled and retained for analysis from 17 of the 20 lakes using the 'top and bottom' sediment sampling approach. Using this approach, indicators deposited in surface sediments (the so-called 'top' samples) are presumed to represent present-day conditions, whilst sediment deposited deeper in the core (the so-called 'bottom' samples; mean depth of 21 cm in this study) are presumed to be archive indicators deposited before the period of any potential anthropogenic impacts.

Methods

Sample preparation and microscopy

Sediment subsamples (top and bottom) from each of the 17 sites were weighed (~ 0.5 g) and placed in scintillation vials. To digest the organic matter, the samples were treated with an acid solution (50% nitric acid, 50% sulphuric acid). The samples were placed in a hot water bath for approximately three hours to accelerate the digestion process. Once the digestion was complete, the supernatant was removed by aspiration and the residue was washed several times with distilled water. The resulting slurries were used to prepare slides for light microscopy (LM) and stubs for scanning electron microscopy (SEM). For each LM sample, the slurries were diluted with distilled water and pipetted onto coverslips. The coverslips were allowed to dry overnight on a slide warmer, and then mounted onto glass slides using Naphrax®, a permanent mounting medium with a high refractive index (RI = 1.74). The slurries from 12 of the samples were similarly used to prepare SEM stubs. Diluted aliquots of the slurries were pipetted onto aluminium foil, allowed to dry, and then mounted on aluminium SEM stubs using double-sided tape. Each stub was then sputter coated with approximately 20 nm of gold, using a Denton Vacuum Desk II Cold Sputter Etch Unit.

Stomatocysts were identified and enumerated under oil immersion (1000x magnification) using a Leica (Leitz DMRB) light microscope with interference optics equipped with a WILD Photoautomat MPS45 camera. A minimum of 200 cysts were identified and counted on each slide along parallel transects, and light micrographs were routinely taken to ensure taxonomic consistency and accuracy. Cyst morphotypes that were indistinguishable with the light microscope were 'grouped' into collective categories (Table 1). Duff et al. (1995), Zeeb et al. (1996), Wilkinson et al. (1997, 2001), Gilbert et al. (1997), and Wilkinson and Smol (1998) were used as the primary references for stomatocyst identification. To further ensure taxonomic consistency and for identification of new morphotypes, SEM stubs were examined using a Hitachi S-2500 SEM operating at 15 kV, and a working distance of 5 mm. SEM micrographs were taken using a Quartz PCI digital slowscan device.

Data analysis

The relative abundance of each cyst morphotype was determined, and only those forms which were present in at least 1% abundance in at least one surface sample were included in subsequent analyses. Furthermore, sites with low cyst abundances (i.e., fewer than 200 cysts in 1000 fields of view) were excluded. As a result of this screening, 71 cyst morphotypes, and 13 lakes were included in final data analyses.

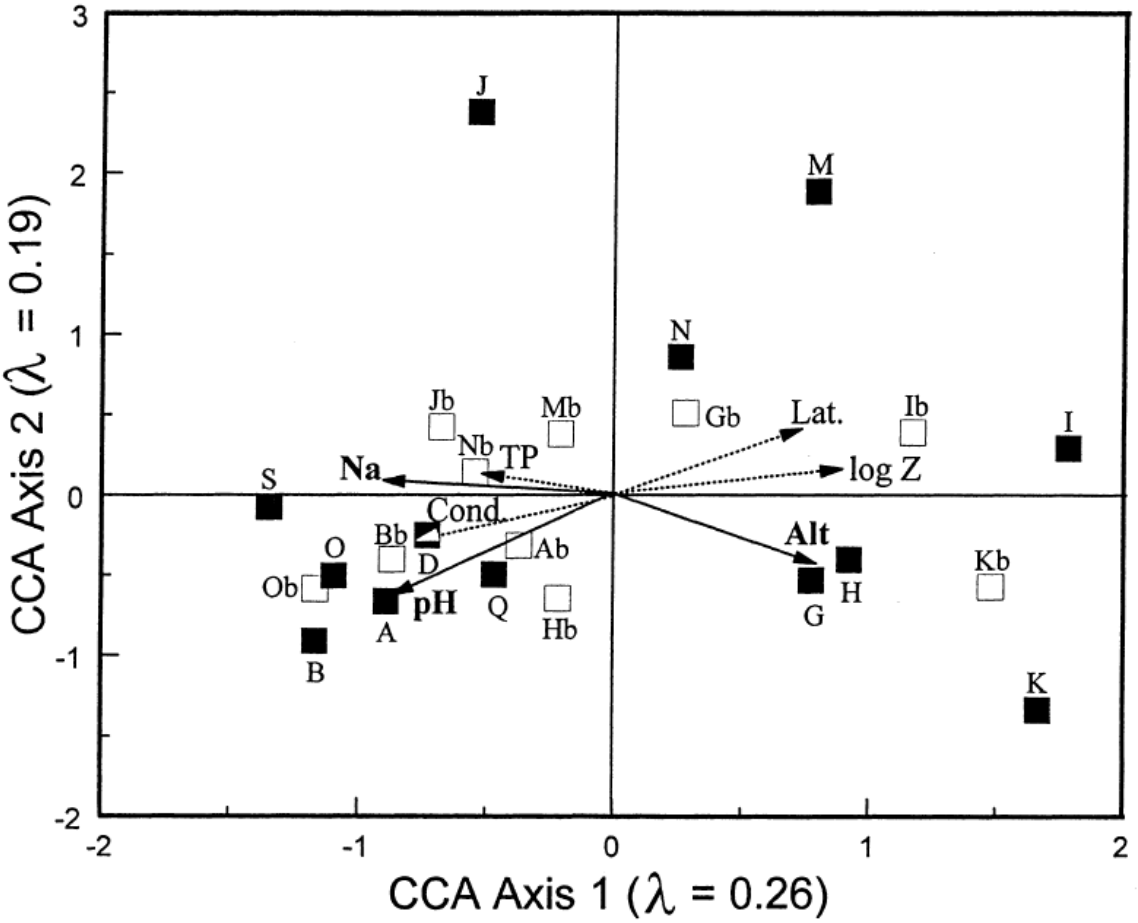

Figure 2. Canonical correspondence analysis (CCA) biplot of sites and environmental variables. Solid squares indicate present-day samples and open squares represent pre-industrial samples that are plotted passively. Sites are indicated by their letter codes. 'Bottom' samples are indicated by b.

A series of multivariate ordinations were performed on the modern samples using the program CANOCO, version 3.12 (ter Braak 1988, 1990). A preliminary detrended correspondence analysis (DCA) of the surface-sediment cyst data was used to determine the major compositional gradient lengths and to determine whether to use linear or unimodal statistical methods (ter Braak 1990). The measured limnological and catchment variables were screened for normality, and consequently, calcium (Ca^{2+}), chlorophyll *a* (Chl *a*), potassium (K^{+}), total dissolved phosphorus (TP), and maximum depth (Z) were log-transformed prior to analysis. The cyst data were not transformed; however, downweighting was performed to reduce the influence of rare morphotypes (ter Braak 1988). Due to the small number of sites and large number of measured variables, highly collinear variables were identified and removed prior to forward selection. Collinear variables were identified as those with high variance inflation factors (i.e. VIF > 20) in canonical correspondence analysis (CCA) (ter Braak 1990). The removed variables included Ca^{2+}, Mg^{+}, latitude, longitude, extent of bird activity in the catchment, the geological and landform categories (granite, carbonate rock, strandflat), and the catchment variables percent vegetation and percent snow in the catchment (see Birks et al. 2004a for details). Monte Carlo permutation tests (999 unrestricted permutations) under the null model in CCA (ter Braak 1988, 1990) were used to determine which of the remaining non-collinear environmental variables had a significant influence on the present-day distributions of cyst morphotypes. CCA was performed using solely the forward-selected variables. Other ecologically important variables were analysed and plotted passively (i.e., they were not used in creating the ordination). The significance of the first two

canonical axes was determined using Monte Carlo permutation tests. CCA ordinations were used to evaluate relationships between cyst morphotypes and environmental variables (Figure 2), and sites and environmental variables (Figure 3). Bottom samples for ten of the 13 lakes, for which there was a sufficient number of stomatocysts, were plotted passively in the ordination space of the sites and environmental variables (Figure 3) to detect how chrysophyte assemblages have changed in these lakes in recent times. The change in cyst assemblages from pre-disturbance conditions to present was also demonstrated through the production of profiles of dominant (Figure 4) and subdominant (Figure 5) cyst morphotypes.

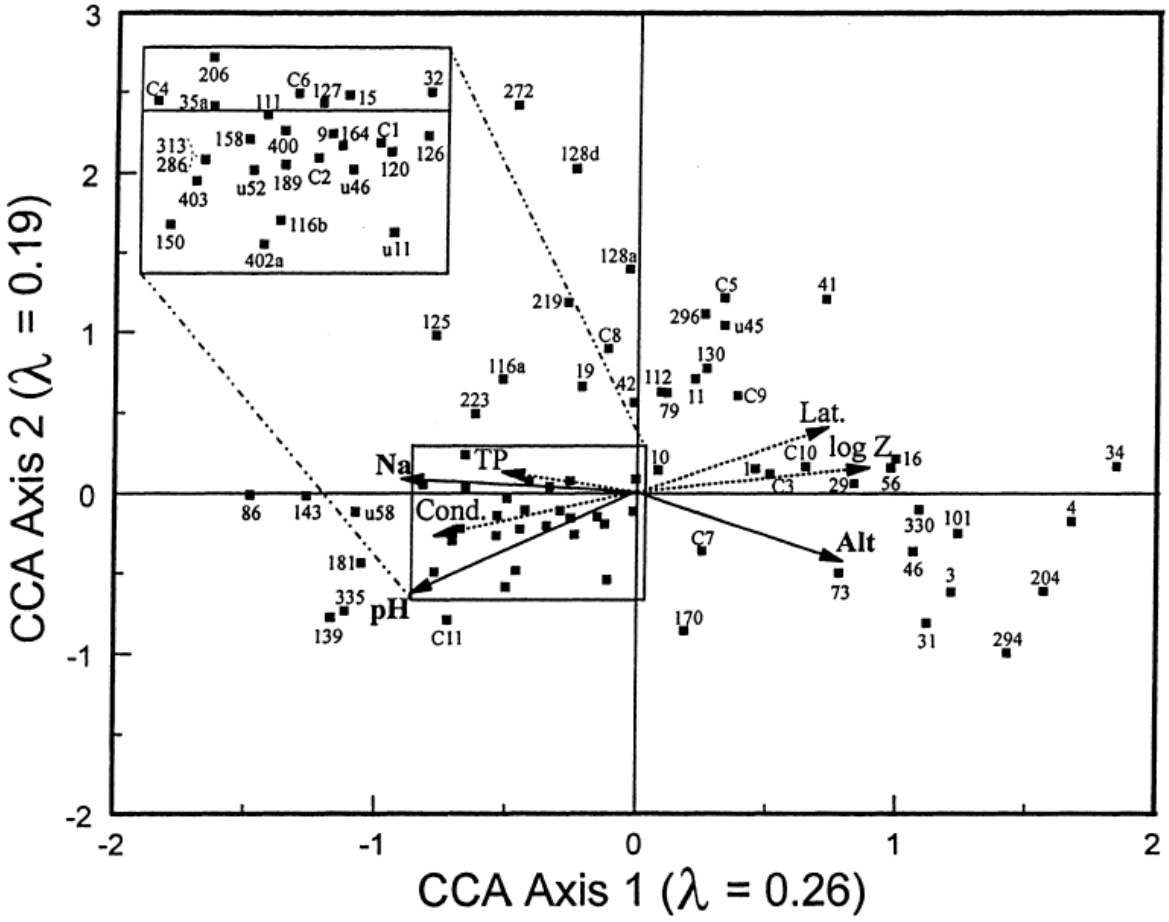

Figure 3. Canonical correspondence analysis (CCA) biplot of chrysophyte morphotypes and environmental variables. Solid lines indicate statistically significant environmental variables and passive environmental variables are represented by dotted lines. Collective categories of similar cysts are identified by CX, where X defines the number of the group. A complete list of these collective categories is provided in Table 1. Unidentified stomatocysts (i.e., cysts that have not been identified with SEM) are identified on the ordination by U followed by a number.

Results & Discussion

Svalbard stomatocyst flora

Cysts were abundant and well preserved in the surface sediments of 13 lakes and bottom sediments of ten lakes. An insufficient number of cysts for enumeration were found in the sediment of lakes E, P, R, and T, as well as from the bottom of the cores at lakes D, Q, and S. SEM work revealed partial dissolution at some of these sites, indicated by degradation of delicate features such as small spines and narrow ridges. However, as even the most lightly silicified cysts were present, albeit in low abundance, it seems unlikely that the poor representation of cysts in these samples was solely the result of dissolution. With respect to

the absence of cysts in bottom samples (D, Q, S), one explanation is that under cooler and perhaps drier conditions in the past, these shallow lakes may have had lower nutrient concentrations and a longer duration and extent of ice cover, precluding most chrysophyte growth. Preservation problems may, of course, also be important.

A total of 153 cyst morphotypes were identified with the light and/or scanning electron microscope (Appendix), of which 21 (14%) are believed to be new morphotypes. This is similar to Jones and Birks (2004) who report that ca. 15% of the diatom flora in 23 lakes could not be assigned to described forms. The number of cyst morphs represented in the Svalbard sediments demonstrates relatively high diversity considering the small number of samples. By comparison, a total of 181 morphotypes were identified from 71 lakes in Adirondack Park, USA (Duff and Smol 1995), 137 morphs from 35 ponds on Ellesmere Island in the Canadian high Arctic (Wilkinson et al. 1997), and 126 morphotypes from 50 Central European lakes (Facher and Schmidt 1996). This diversity was not particularly surprising, however, as even though there were only a small number of sites, they covered a relatively wide range of limnological variables (Birks et al. 2004a). The number of new morphotypes discovered seems somewhat low, given that this was the first taxonomic undertaking of chrysophyte subfossils from Svalbard. This preliminary study suggests that there may not be a distinct Svalbard chrysophyte flora, but rather the most common taxa are those that are typical of cold environments or are considered cosmopolitan.

Two new cyst morphotypes (402 *forma a* and 403) were found in greater than 5% abundance in at least one site; however, the majority of new morphotypes were very rare (i.e., <1%), and typically found in only one or two sites. The most abundant cyst morphotypes were unornamented (e.g., 1, 9, 15, 120), or had minimal surface ornamentation (e.g., C1, C2, C4, 189). This dominance of unornamented cysts has been observed in a number of studies of clear water, oligotrophic lakes (Betts-Piper 2001; Wilkinson et al. 1997; Stewart et al. 2000). It is possible that the majority of these unornamented forms are produced by more than one species of chrysophyte (Duff et al. 1995). In lumping these forms together, it appears that one group is dominant. However, it may be that two, three, or perhaps more chrysophyte species are producing similar cysts. Regardless, the dominance of unornamented over ornamented forms appears to be emerging as a characteristic of arctic environments.

Ordinations

DCA indicated that the primary axis was greater than 2.0 standard deviation units (SD) in length (DCA axis 1, gradient length = 2.69 SD). Thus, cyst distributions along the first axis were assumed to be unimodal (Birks 1995) and canonical correspondence analysis (CCA), a direct gradient analysis, was used (ter Braak 1990). CCA with forward selection indicated that altitude ($p = 0.02$), pH ($p = 0.02$), and $[Na^+]$ ($p = 0.04$) explained significant amounts of the variability observed in the cyst distributions between the sites. Axes 1 and 2 ($\lambda_1 = 0.26$; $\lambda_2 = 0.19$) accounted for 79% of the variance in the cyst data, and both axes were statistically significant (axis 1; $p = 0.01$, axis 2; $p = 0.05$) (Figures 2 and 3). The acute angles made by the three significant environmental arrows to the first canonical axis indicate that these variables contribute most strongly to the first axis (Jongman et al. 1995). Little of the variability associated with the secondary canonical axis is accounted for by these variables (Figures 2 and 3). CCA basically divides the suite of lakes and cysts into two groups, which are broadly delineated by the secondary axis. The first group, including the two left quadrants of the ordination, includes lakes A, B, D, O, Q, and S (Figure 2). This group is similar to Jones and Birks (2004) diatom TWINSPAN group 2, characterised by shallow, strandflat lakes dominated by *Fragilaria* species. Lakes in cyst group 1 are relatively shallow, calcium-rich,

high conductivity, relatively high dissolved TP, and predominantly high pH sites located on carbonate bedrock. Cysts 9, 189, 120, C1, and C2 typically dominate these sites (Figures 3 and 4). The presence of McVitiepynten (D) in this cluster may initially appear as an outlier, as one might expect it to be more closely related to the other group in terms of pH, conductivity, and ionic concentrations. However, its high dissolved TP and shallow depth appear to be the main reasons it clusters with this group.

The second cyst group is similar to diatom group 3 of Jones and Birks (2004), and forms a much less cohesive cluster on the right side of the ordination (Figure 2), and consists of lakes located on granite bedrock (G, H, I, K, M, N). These lakes are generally acidic and oligotrophic, with low conductivity and ionic concentrations. Dominant cysts common to this group include cysts 1, 29, 56, and C3 (Figures 3 and 4). Differences in the cyst assemblages between these sites, particularly M and N, do not appear to be associated with any of the measured variables.

Lake J is most similar to lakes on the right side of the ordination diagram, with respect to its morphology and measured limnological variables. However, its cyst assemblage was unique in that it was dominated by cysts 272 and 128 *forma d*, both of which were absent from other lakes in this study. The peculiar assemblage (Figures 2 and 3) and the position of this site on the edge of the ordination (Figure 2) suggest that some other unmeasured variable is strongly influencing the cyst flora of this particular lake. At the time of sampling, a distinct purple-coloured layer was identified at the sediment water interface of this lake (Birks et al. 2004a). This purple layer may have been a mat of sulphur bacteria. Although speculative, the chrysophyte algae that produce cysts 272 and 128 *forma d* may possibly use this mat as a substrate.

A detailed comparison of the groupings of the lakes based on water chemistry, the modern diatom, chrysophyte cyst, chironomid, and pollen assemblages, and the modern flora of the lake catchments is presented in Birks et al. (2004b). There is a perfect correspondence between the cyst- and diatom-based classification and high correspondence between the cyst- and chironomid-based classifications, but not such a high correspondence between the cyst- and water chemistry-based classifications.

Cyst autecology

CCA identifies relationships between cyst morphotypes in surface sediments and the significant forward-selected variables (Figure 3). Cysts clustered near the centre of the ordination (cysts 42, 1, 9, 10, 32, C1, C7, unid. 11, and 126) show no strong relationship to any of the measured variables. Most of these are simple cysts with little or no surface ornamentation. These and other unornamented cysts are widely distributed across a variety of geographical and ecological gradients. They appear to be generalists and/or they may be produced by more than one chrysophyte species. Alternatively, these simple forms may represent early developmental stages of other more ornamented cysts (Duff et al. 1995). Two ornamented forms, C7 and cyst 32, were also generalists for our measured environmental variables. C7 was found in three sites (G, I, Q; Figure 5), which differed greatly with respect to lake morphometry and water chemistry. In all likelihood, more than one of the cysts in this group was present in these sites, leading to its apparent ‘patchy’ distribution. Cyst 32 has previously been described as acidic to circumneutral (Duff and Smol 1989), circumneutral (Pla 2001), or acidophilic (Rybak et al. 1991); however, in Svalbard lakes, this cyst was present in several of the lakes across the pH gradient.

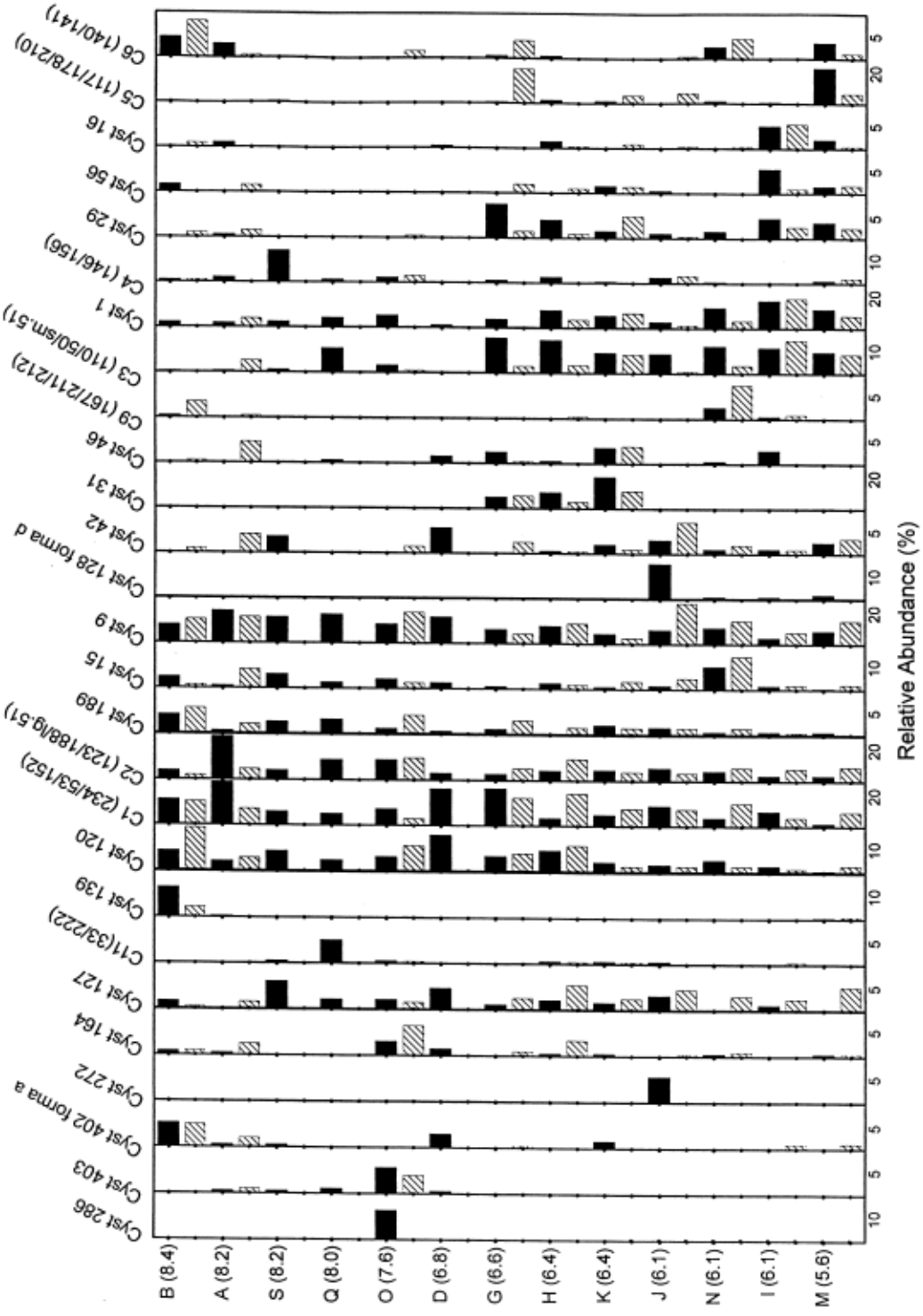

Figure 4. Relative abundances of dominant (>5%) cyst morphotypes. Solid bars represent the percentage abundance of each cyst in surface sediments, and hatched bars indicate the relative abundance in pre-industrial 'bottom' sediments. Sites are arranged in order of decreasing pH, and cyst morphotypes are arranged in order from highest (left) to lowest (right) CCA species scores. Sites are indicated by their letter codes.

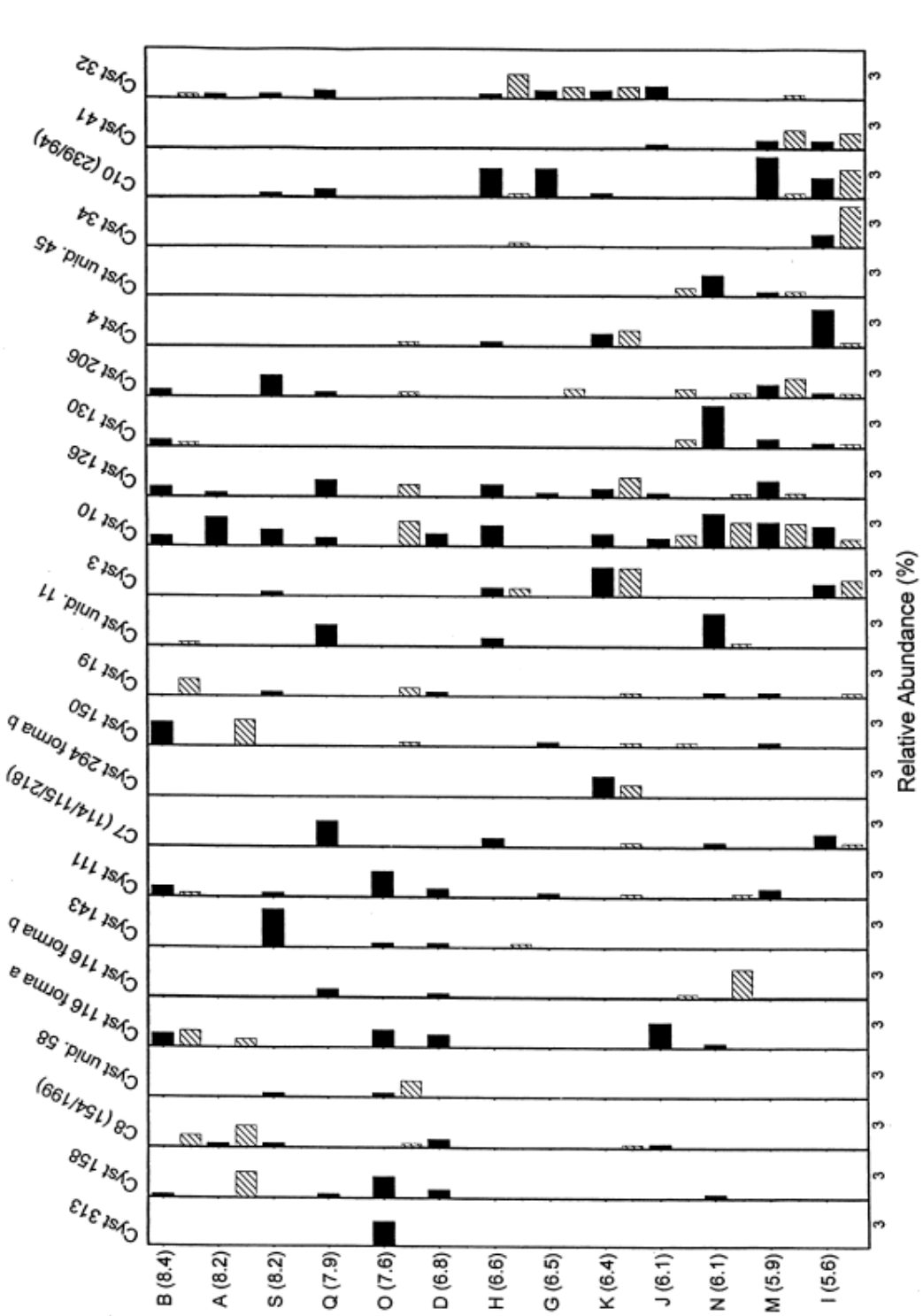

Figure 5. Relative abundances of sub-dominant (2–5%) cyst morphotypes. Solid bars represent the abundance of each cyst in surface sediments, and hatched bars indicate the relative abundance in pre-industrial 'bottom' sediments. Sites are arranged in order of decreasing pH, and cyst morphotypes are arranged in order from highest (left) to lowest (right) CCA species scores.

Cysts on the right side of the ordination (Figure 3) include morphotypes that are more typical of sites G, H, I, K, M, and N (Figures 2, 4, and 5). Many of these cysts have known preferences for acidic conditions (e.g. 73, 204, 101) (Duff 1994; Duff and Smol 1991; Smol 1988; Rybak et al. 1991). *Dinobryon sociale* var. *americanum* (cyst 79) is most likely an acidophilic species (Duff and Smol 1991; Smol 1988). In this study, as well as in a survey in Ontario (Wilkinson et al. 1999), this cyst showed an affinity for lakes with low Na^+ and dissolved TP values (Figure 3). Wilkinson et al. (1999) observed the same relationship with

Na^+ and dissolved TP for *Dinobryon cylindricum* (cyst 41), which is corroborated by this study (Figure 3). *D. cylindricum* has formerly been described as typical of cool, oligotrophic to mildly eutrophic waters (Rybak 1986; Rybak et al. 1987; Eloranta 1989; Siver 1995) and appears to be fairly representative of arctic environments (Duff and Smol 1989). There is, however, some debate about its pH optimum. Several studies have shown cyst 41 to be typical of alkaline conditions (Rybak et al. 1991; Carney et al. 1992; Duff 1994; Wilkinson et al. 1999); however, Facher and Schmidt (1996) estimate its pH optimum to be 5.93. In Svalbard, it was restricted to acidic lakes, and Pla (2001) reports a circumneutral pH of 6.94 in lakes of the Pyrenees (Spain). Cyst 41 likely exhibits a fairly wide tolerance for pH.

Collective category C5 reaches its highest abundance in the most acidic of the study lakes (Figure 4), and in this survey appears to be indicative of lower pH lakes (Figure 2). As a collective category, C5 (117/178/210) has been both positively (Wilkinson et al. 1999) and negatively (Duff 1994) correlated to pH. This is most likely a consequence of the grouping of three distinct morphotypes produced by different taxa with different ecological preferences. Individually, cyst 178 is reported to be alkaliphilic (Sandgren and Carney 1983; Rybak 1987), whereas cyst 210 has been described as an acidophilic, circumneutral, or pH-indifferent indicator (Adam and Mahood 1979, 1980; Adam and Mehringer 1980; Carney et al. 1992; Pla 2001). There is no information yet regarding the pH tolerance of cyst 117 (Zeeb et al. 1990). The strong preference exhibited by C5 for lower pH lakes (Figures 3 and 4) in combination with taxonomic work with the SEM suggests that, in Svalbard lakes, C5 is solely represented by cyst 210.

Our results suggest that cyst 16 is produced by a chrysophyte that is tolerant of low pH conditions, and may be more common in oligotrophic and low conductivity environments (Figures 3 and 4). This is similar to the distribution reported by Wilkinson et al. (1999).

Cysts 11, 294, and 296 appear to exhibit a preference for lower pH environments (Figure 3). These three morphotypes were associated with a Cyperaceae and *Sphagnum* dominated peat core from Siberia, Russia (Gilbert et al. 1997), suggesting that acidophilic and perhaps epiphytic algae produce these cysts.

Other cysts found on the right side of the ordination (Figure 3) have been previously recorded as typical of arctic or alpine environments, characterized by oligotrophic and/or cold water (e.g. cyst 112-*Ochromonas globosa*, C3, 3, 29, C10, 130-*Chrysococcus furcatus*, 31) (Carney and Sandgren 1983; Zeeb et al. 1990; Smith and White 1985; Duff and Smol 1988, 1989, 1991, 1994; Duff et al. 1992; Duff 1994; Wilkinson et al. 1999; Zeeb and Smol 1993). C3 (110/50/sm.51) was more common in acidic and low conductivity lakes (Figure 3), as indicated also by Duff (1994). Rybak (1987) and Zeeb et al. (1990) suggest that C3 is indicative of oligotrophy. This is consistent with our ordination data (Figure 3). In this study, cyst 29 appears to favour lower pH lakes (Figure 4), and cyst 3 shows some preference for deeper lakes (Figure 5; Table 1 in Birks et al. 2004a). Cyst 170 is also somewhat more common in deeper lakes, having reached its highest relative abundance in Kobberfjorden (K), the deepest (Z_{max} = 12.5 m) and most oligotrophic (TP = 2.7 μg/L) lake in our data.

Chrysococcus furcatus and cyst 31 apparently have a wide tolerance for pH (Duff 1994; Duff and Smol 1989, 1994; Duff et al. 1992; Zeeb and Smol 1993). Cyst 31 was also suspected of having a wide tolerance for trophic status (Duff and Smol 1988, 1989; Zeeb et al. 1990; Duff 1994). In the Svalbard lakes, cyst 31 was apparently restricted to lakes G, H, and K. These three sites were similar with respect to pH (6.4 – 6.6), conductivity (26 μS cm^{-1} – 76 μS cm^{-1}), TP (2.7 μg l^{-1} – 5.1 μg l^{-1}) and major ion concentrations (e.g., Ca^{2+} 44.9 – 49.9 μeq l^{-1}).

Cyst 4, a well-documented cold-water morphotype (Duff and Smol 1988, 1989, 1991; Duff 1994), was relatively more common in circumneutral to acidic lakes (Figure 5). This is consistent with Pla's (2001) work in the Pyrenees where cyst 4 was found in circumneutral lakes (pH = 6.70), but inconsistent with earlier studies (Duff 1994; Wilkinson et al. 1999) that have found cyst 4 to be more characteristic of alkaline environments. This could suggest a wider tolerance for pH than was previously thought.

Cysts on the left side of the ordination are more common in lakes A, B, D, O, Q, and S. Many of these cysts are typical of circumneutral to alkaline lakes, including cysts 35-*Mallomonas doignonii*, 143, 150, 120-*Chrysosphaerella longispina*, 164, C4, 116, 125-*Paraphysomonas antarctica*, 206 and 189 (Figure 3) (Carney et al. 1992; Sandgren and Carney 1983; Pla 2001; Rybak 1986; Rybak et al. 1991; Duff 1994; Duff et al. 1992; Zeeb and Smol 1993; Pienitz et al. 1992; Wilkinson et al. 1999).

Chrysosphaerella longispina (cyst 120), cyst 164 and C4 (146/156) were present in many sites, across a broad range of pH, but were relatively more common in the intermediate to higher pH lakes (Figure 4). C4 reached its greatest abundance in site S, which has a present-day pH of 8.2 (Figure 4). This distribution follows others that have described these cysts as having a wide tolerance for pH, but a preference for alkaline conditions (Rybak et al. 1991; Duff 1994; Zeeb and Smol 1993). Our data indicate that cysts 116 and 125 (*Paraphysomonas antarctica*) are probably tolerant of high conductivity (Figure 3) (Duff et al. 1992; Duff 1994; Pienitz et al. 1992; Wilkinson et al. 1999) and may be more common in mesotrophic to eutrophic lakes (Figure 3) (Rybak et al. 1987; Zeeb et al. 1990, 1994; Zeeb and Smol 1993).

Collective category C2 (123/188/lg.51) was common to most lakes, but appears to have an affinity for higher conductivity lakes (Figures 3 and 4). The distribution of cyst 206 in Svalbard lakes provides further support to the suggestion by Wilkinson et al. (1999) that this cyst exhibits a circumneutral to alkaline distribution, and favours higher TP environments. The association of cyst 127 with shallow, high pH, high conductivity Svalbard lakes (Figure 3) parallels that observed in lakes in British Columbia, Canada (Duff 1994).

Cyst 189 is reportedly strongly associated with oligotrophic, alkaline lakes (Duff et al. 1992; Duff 1994), and was present in all our sites, although it was more common at higher pH.

Spiniferomonas trioralis (cyst 111) has been identified across a wide range of pH from acidic (Eleoranta 1989; Zeeb et al. 1990), circumneutral (Pla 2001), to alkaline waters (Hartmann and Steinberg 1989; Wilkinson et al. 1999). It was found in most of the Svalbard lakes spanning a wide range of pH, but reached its highest abundance in 'Draba Pond' (O) (TP = 395.7 $\mu g\ l^{-1}$). Earlier studies have suggested that this morphotype is characteristic of eutrophic conditions (Carney and Sandgren 1983; Zeeb et al. 1990, 1994). Other cysts that may potentially be indicators of eutrophy include cysts 158, 313, 286, and 403, some of which have previously been associated with high productivity (158, 286; Kristiansen 1985; Zeeb and Smol 1993; Wilkinson et al. 1999). The abundance of these cysts, as well as cysts 313 and 403 in lake O, suggests that they are tolerant of and perhaps competitive in high TP waters. This is somewhat intriguing as chrysophytes are usually less common in high TP environments, where they are often out-competed by other algal groups such as cyanobacteria and chlorophytes (Sandgren 1988).

Cyst 15, which has been described as eutrophic (Kristiansen1985), exhibited a fairly widespread distribution in Svalbard lakes with no clear preference for high dissolved TP lakes. Very little is known about cysts 19 (*Epipyxis tubulosa*), 139, C6 (140/141), or C11 (33/222), other than that they are typical of arctic environments (Rybak 1986; Duff and Smol 1988, 1989, 1994; Duff 1994; Duff et al. 1992). Cyst 139 was only present in the highest pH lake (B: pH = 8.4), and may prefer high alkalinity or high pH conditions (Figure 4). Cyst 128 may

be fairly cosmopolitan (Cronberg and Kristiansen 1980), but has been reported to be more common in alkaline, high conductivity and productive lakes (Rybak 1986; Duff and Smol 1995; Zeeb and Smol 1993, 1995). In this study, cyst 128 was most common in lake J (Figure 4), a moderately acidic, low conductivity, oligotrophic lake. Cyst 272 was also dominant in this lake and, together, these two cysts comprised more than 23% of the cysts in lake J. It is not clear what environmental factors are influencing these taxa.

There are little or no existing autecological data for the remaining Svalbard cysts (46, 56, 86, 181, 219, 223, 330, 335, 400, 402, unid. 45, unid. 46, unid. 52, unid. 58, C8 (154/199), or C9 (167/211/212), and low abundances of many of these morphotypes preclude any ecological characterisations at this time.

Recent environmental change on Svalbard

Previous studies have shown that chrysophytes respond to a variety of environmental changes; including shifts in pH (Duff and Smol 1991; Facher and Schmidt 1996; Wilkinson et al. 1999), trophic status (Zeeb et al. 1990, 1994; Wilkinson et al. 1999), salinity (Pienitz et al. 1992; Zeeb and Smol 1995), and climate (Zeeb and Smol 1993). Thus, if there have been environmental changes on Svalbard since pre-industrial times, it would be expected that chrysophyte species would respond to these changes.

Dating of a number of cores from this suite of lakes indicated that ^{210}Pb reached equilibrium with supported ^{226}Ra between 7 and 11 cm (Appleby 2004). As most of the 'bottom' samples were well below this depth (core length: 12 - 35 cm; mean: 21 cm), we are confident that they are all of pre-industrial age. However, as sedimentation rates are quite variable in this region, it is likely that the bottom samples are of different ages.

Percentage abundance diagrams of common cyst morphotypes in both present-day and pre-industrial sediments (Figures 4 and 5) reveal striking differences in stomatocyst assemblages over time in most of the lakes. High variability in the assemblages between Svalbard lakes, and limited data on the specific optima and tolerances of chrysophyte stomatocysts to environmental variables, make it difficult to draw conclusions about the nature of these changes from the cyst data alone. However, the CCA ordination, with bottom samples plotted passively (Figure 3), indicates that lakes located on granite bedrock, which are presently acidic, may have become more acidic over time (G, H, I, J, K, M, N). Conversely, lakes located on carbonate bedrock that are presently alkaline appear to have increased their pH (A, B) in recent times. The remaining three lakes (D, Q, S) did not have sufficient cysts in pre-industrial sediments for enumeration, making it impossible to infer any changes.

Meteorological records show that precipitation and temperatures have generally increased at Spitsbergen in the years since 1912 (Førland et al. 1997), and it is widely known that some acid precipitation resulting from industrial activities impact Arctic regions via long-range transport mechanisms (Rose et al. 2004).

Warmer temperatures and increased precipitation, and in particular acid precipitation, may explain the apparent decrease in pH of many of the Svalbard lakes. All of the lakes that indicate a decrease in pH (Figure 2) are located on acid, granitic bedrock. This type of rock has a low capacity for reducing acidity as it is highly resistant to weathering and provides little buffering capacity. Svalbard lakes are located on deep permafrost, and are likely to be particularly sensitive to acid precipitation, as there is little groundwater interaction. Additionally, increased melting of snow and ice in spring due to warmer temperatures may result in a sudden pulse of acidic meltwater to the lake causing a decrease in both pH and conductivity. The effect of this 'spring shock' may be short-lived. However, many

chrysophytes are spring-blooming and would be sensitive to this sudden drop in pH. Interestingly, Jones and Birks (2004) find no changes in lake-water pH inferred from the diatom assemblages from five sites on Svalbard but these sites were not examined for chrysophyte cysts or cysts were not present in sufficient quantities in the 'bottom' sediments at lakes Q and S (Birks et al. 2004a).

Under warmer and wetter conditions, we would expect that chemical weathering and mineral dissolution would be augmented (Psenner and Schmidt 1992; Rühland and Smol 1998). Highly weatherable carbonate bedrock provides considerable buffering capacity to lakes subjected to acid precipitation. An increase in the contribution of base cations from enhanced weathering of carbonate bedrock in the catchments of lakes A and B may explain why these lakes appear to have increased in pH and conductivity over their recent histories (Figure 3) despite an apparent increase in acid precipitation.

Conclusions

The Svalbard chrysophyte flora is similar to that of other Arctic regions with a large proportion of collective cyst morphotypes, simple unornamented cysts, and cold-tolerant taxa (Duff and Smol 1988; Douglas and Smol 1994; Wilkinson et al. 1997). Although there does not appear to be a distinct Svalbard flora, several new morphotypes are identified. Chrysophytes exhibit strong relationships to limnological variables, and knowledge of chrysophyte ecology and distribution is expanded by our study. The small number of lakes we investigated, however, precludes a quantitative interpretation of the extent of recent environmental change on Svalbard. Nonetheless, qualitative interpretations can still be made. Chrysophyte cysts in most lakes showed obvious changes between pre-industrial and present-day assemblages. We present preliminary evidence that presently acidic lakes may have become more acidic over recent time, and that alkaline lakes may have become more alkaline. Although our conclusions are tentative, these changes may be directly or indirectly related to acidic precipitation and climate warming. There is clearly a need for further work on both modern and fossil chrysophyte cyst assemblages on Svalbard, to test these conclusions.

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Appendix. Stomatocyst morphotypes present in Svalbard lakes and the primary reference in which this cyst is described.

Stomatocyst Morphotypes (PEARL)	Reference
Smol cyst 1	Smol, 1984
cyst 1	Duff & Smol, 1988 emend. Zeeb & Smol, 1993
cyst 3	Duff & Smol, 1988
cyst 4	Duff & Smol, 1988
cyst 6	Duff & Smol, 1988
cyst 9	Duff & Smol, 1988 emend. Zeeb & Smol, 1993
cyst 10	Duff & Smol, 1988 emend. Wilkinson & Smol in Wilkinson et al., 1997
cyst 11	Duff & Smol, 1988 emend. Gilbert & Smol in Gilbert et al., 1997
cyst 15	Duff & Smol, 1988 emend. Zeeb & Smol, 1993
cyst 16	Duff & Smol, 1988
cyst 17 forma a, b	Duff & Smol, 1988
cyst 19	Duff & Smol, 1988
cyst 20	Duff & Smol, 1988
cyst 29	Duff & Smol, 1988
cyst 31	Duff & Smol, 1989
cyst 32	Duff & Smol, 1989
cyst 33/222	Duff & Smol, 1989; Duff & Smol, 1994
cyst 34	Duff & Smol, 1989
cyst 35	Duff & Smol, 1989
cyst 41	Duff & Smol, 1989
cyst 42	Duff & Smol, 1989
cyst 46	Duff & Smol, 1991
cyst 56	Duff & Smol, 1991
cyst 59	Duff & Smol, 1991
cyst 62	Duff & Smol, 1991
cyst 64	Duff & Smol, 1991
cyst 71	Duff & Smol, 1991
cyst 73	Duff & Smol, 1991
cyst 75	Duff & Smol, 1991
cyst 76	Duff & Smol, 1991
cyst 79	Duff & Smol, 1991
cyst 83	Duff & Smol, 1991
cyst 86	Duff & Smol, 1991
cyst 91	Duff & Smol, 1991
cyst 93	Duff & Smol, 1991
cyst 101	Duff & Smol, 1991
cyst 110/50/sm51	Zeeb et al., 1990; Duff & Smol, 1991
cyst 111	Zeeb et al., 1990
cyst 112	Zeeb et al., 1990 emend. Duff & Smol, 1994
cyst 113	Zeeb et al., 1990
cyst 114/115/218	Zeeb et al., 1990; Duff & Smol, 1994
cyst 116 forma a	Zeeb & Smol in Zeeb et al., 1990 emend. Brown & Smol in Brown et al., 1997
cyst 116 forma b	Zeeb & Smol in Zeeb et al., 1990 emend. Brown & Smol in Brown et al., 1997
cyst 117/178/210	Zeeb et al., 1990; Zeeb & Smol, 1993; Duff & Smol, 1994
cyst 118/58	Zeeb et al., 1990; Duff & Smol, 1991
cyst 120	Duff & Smol in Duff et al., 1992 emend. Zeeb & Smol, 1993
cyst 121	Duff & Smol in Duff et al., 1992
cyst 123/188/lg 51	Duff & Smol in Duff et al., 1992; Brown et al., 1994; Duff & Smol, 1991
cyst 125	Duff & Smol in Duff et al., 1992
cyst 126	Duff & Smol in Duff et al., 1992
cyst 127	Duff & Smol in Duff et al., 1992
cyst 128 forma a, d	Duff & Smol in Duff et al., 1992 emend Duff & Smol, 1994
cyst 130	Duff & Smol in Duff et al., 1992 emend. Duff & Smol, 1994
cyst 131	Duff & Smol in Duff et al., 1992

cyst 133 forma a, b, c	Duff & Smol in Duff et al., 1992 emend. Wilkinson & Smol in Wilkinson et al., 1997
cyst 134	Duff & Smol in Duff et al., 1992
cyst 139	Duff & Smol in Duff et al., 1992
cyst 140/141	Duff & Smol in Duff et al., 1992
cyst 143	Duff & Smol in Duff et al., 1992
cyst 146/156	Zeeb & Smol in Pienitz et al., 1992; Zeeb & Smol, 1993
cyst 149	Zeeb & Smol, 1993
cyst 150	Zeeb & Smol, 1993
cyst 151	Zeeb & Smol, 1993
cyst 153	Zeeb & Smol, 1993
cyst 157	Zeeb & Smol, 1993
cyst 158	Zeeb & Smol, 1993
cyst 161	Zeeb & Smol, 1993
cyst 162	Zeeb & Smol, 1993
cyst 164	Zeeb & Smol, 1993
cyst 167/211/212/sm.266	Zeeb & Smol, 1993; Duff & Smol, 1994; Zeeb et al., 1996
cyst 169	Zeeb & Smol, 1993
cyst 170	Zeeb & Smol, 1993
cyst 174	Zeeb & Smol, 1993
cyst 181	Brown & Smol in Brown et al., 1994
cyst 182	Brown & Smol in Brown et al., 1994
cyst 185 forma a	Brown & Smol in Brown et al., 1994
cyst 186	Brown & Smol in Brown et al., 1994
cyst 189	Zeeb & Smol in Zeeb et al., 1996
cyst 194	Zeeb & Smol in Zeeb et al., 1996
cyst 198	Duff & Smol, 1994
cyst 199	Duff & Smol, 1994
cyst 203	Duff & Smol, 1994
cyst 204	Duff & Smol, 1994
cyst 206	Duff & Smol, 1994
cyst 207	Duff & Smol, 1994
cyst 208	Duff & Smol, 1994
cyst 215	Duff & Smol, 1994
cyst 219	Duff & Smol, 1994
cyst 223	Duff & Smol, 1994
cyst 224	Duff & Smol, 1994
cyst 231	Duff & Smol, 1994
cyst 232 forma b	Duff & Smol, 1994
cyst 233	Zeeb et al., 1994
cyst 234/53/152	Duff et al., 1995; Duff & Smol, 1991; Zeeb & Smol, 1993
cyst 238	Duff et al., 1995
cyst 239/94	Duff et al., 1995
cyst 242	Duff et al., 1995
cyst 243	Duff et al., 1995
cyst 272	Gilbert et al., 1997
cyst 286	Gilbert et al., 1997
cyst 288	Gilbert et al., 1997
cyst 294 forma a, b	Gilbert et al., 1997
cyst 296	Gilbert et al., 1997
cyst 297	Gilbert et al., 1997
cyst 300	Gilbert et al., 1997
cyst 308	Brown et al., 1997
cyst 310	Brown et al., 1997
cyst 312	Brown et al., 1997
cyst 313	Brown et al., 1997
cyst 314	Brown et al., 1997
cyst 327	Wilkinson & Smol, 1998
cyst 329	Wilkinson & Smol, 1998
cyst 330	Wilkinson & Smol, 1998

cyst 334	Wilkinson & Smol, 1998
cyst 335	Wilkinson & Smol, 1998
cyst 342	Wilkinson & Smol, 1998
cyst 348	Wilkinson & Smol, 1998
cyst 355	Taylor, 1997
cyst 379	Wilkinson et al., 2001.
cyst unid. 11	Wilkinson et al., 1996
cyst unid. 40	Wilkinson & Smol, 1998
cyst unid. 41	Wilkinson & Smol, 1998
cyst unid. 45	Taylor, 1997
cyst unid. 46	Taylor, 1997
cyst unid. 48	Taylor, 1997
cyst unid. 50	Taylor, 1997