Available online at www.sciencedirect.com
ScienceDirect
Polar Science 3 (2009) 147–161
http://ees.elsevier.com/polar/

Bacterial dominance of phototrophic communities in a High Arctic lake and its implications for paleoclimate analysis

Dermot Antoniades [a,*], Julie Veillette [a], Marie-Josée Martineau [a], Claude Belzile [b], Jessica Tomkins [c], Reinhard Pienitz [a], Scott Lamoureux [c], Warwick F. Vincent [a]

[a] *Centre d'études nordiques, Université Laval, Québec, QC G1V 0A6, Canada*
[b] *Institut des sciences de la mer, Université du Québec à Rimouski, Rimouski, Québec, QC G5L 3A1, Canada*
[c] *Department of Geography, Queen's University, Kingston, Ontario K7L 3N6, Canada*

Received 19 November 2008; revised 6 May 2009; accepted 12 May 2009
Available online 7 July 2009

Abstract

The phototrophic communities in meromictic, perennially ice-covered Lake A, on Ellesmere Island in the Canadian High Arctic, were characterized by pigment analysis using high performance liquid chromatography. Samples were taken to determine the vertical changes down the water column as well as a variation between years. These analyses showed that Lake A had distinct phototrophic communities in its oxic and anoxic layers. The pigment analyses indicated that phototrophic biomass in the upper, oxic waters was dominated by picocyanobacteria, while in the lower, anoxic layer photosynthetic green sulphur bacteria were dominant. Interannual variation in pigment concentrations was related to the penetration of photosynthetically active radiation in the water column, suggesting that light availability may be limiting the net accumulation of photosynthetic bacterial biomass in Lake A. Pigment analysis of the surface sediments indicated that deposition was dominated by the photosynthetic sulphur bacterial contribution. The sedimentary record of bacterial pigments in polar meromictic lakes offers a promising tool for the reconstruction of past changes in ice cover and therefore in climate.

Keywords: Arctic; HPLC; Meromictic lake; Photosynthetic bacteria; Pigments

1. Introduction

Polar ecosystems are highly susceptible to disturbance by environmental change (ACIA, 2005). Climate models predict that warming over the next century will be amplified in the polar regions, with the most extreme temperature increases in spring and autumn (Anisimov et al., 2007; Turner et al., 2007). As a result of their sensitivity to perturbation, Arctic lakes will likely experience substantial future changes in their ecosystem properties including ice cover, light conditions, hydrological regimes, seasonality, trophic status and biological community structure (Rouse et al., 1997; Anisimov et al., 2007; Vincent and Laybourn-Parry, 2008).

The lakes of northwestern Ellesmere Island in the Canadian High Arctic are subject to pronounced

* Corresponding author. Centre d'Études Nordiques (Centre for Northern Studies), Université Laval, Québec City, QC G1V 0A6, Canada. Tel.: +1 418 656 2131x8298; fax: +1 418 656 2978.
E-mail address: dermot.antoniades@cen.ulaval.ca (D. Antoniades).

1873-9652/$ - see front matter © 2009 Elsevier B.V. and NIPR. All rights reserved.
doi:10.1016/j.polar.2009.05.002

annual extremes in their physical conditions, including temperature and photoperiod, that profoundly alter the conditions for lake biota. The severity of conditions in this region is comparable to polar desert sites in Antarctica such as the McMurdo Dry Valleys and the Vestfold Hills (Wharton et al., 1993; Gibson, 1999), with thick, perennial ice covers, annual precipitation below 150 mm, year round surface water temperatures near the freezing point, and several months per year without sunlight. Accordingly, there are numerous analogies between lakes from northern Ellesmere Island and these Antarctic regions (Vincent et al., 2008a). Meromictic lakes (i.e., lakes that are perennially stratified as a result of salt-dependent density gradients) have been identified from both polar regions, including several on northern Ellesmere Island (Hattersley-Smith et al., 1970; Pienitz et al., 2008) that formed after isostatic rebound caused the separation of fiord basins from the Arctic Ocean (Ludlam, 1996). These lakes are characterized by the presence of ice cover through all or most of the year, which controls mixing regimes, the penetration of solar radiation, and maintenance of stratification, among other properties (Doran et al., 1996; Gibson, 1999; Belzile et al., 2001). Presently, the ice thickness of northern Ellesmere Island lakes is on the order of 1.5–2 m, although nearby Ward Hunt Lake has an ice cover of ~4 m (Antoniades et al., 2007), and ice covers exceeding 5 m have been observed elsewhere on Ellesmere Island (Blake, 1989). While ice is seasonal in the majority of Arctic lakes, and typical Ellesmere Island lakes are ice-covered for over 10 months per year, several northern Ellesmere Island lakes including Lake A have perennial ice cover. It has, however, been hypothesized that even these lakes are now in transition to seasonal ice regimes due to climate warming (Van Hove et al., 2006).

Past research in Lake A has focused on its geochemistry (Jeffries et al., 1984; Jeffries and Krouse, 1985; Gibson et al., 2002), physical properties (Belzile et al., 2001; Van Hove et al., 2006), biology (Van Hove et al., 2001, 2008) and, more recently, on modelling patterns of thermal stratification (Vincent et al., 2008b) and sedimentology in the lake basin (Tomkins et al., 2009). This research has revealed that Lake A has a deepwater thermal maximum, both sharp and diffuse deepwater peaks in geochemical profiles, the presence of photosynthetic sulphur bacteria and the sedimentation of inorganic pyrite framboids. While Lake A has been more extensively studied than the large majority of polar lakes, many details of its biological and physical processes remain unknown.

Signature pigments from anaerobic photosynthetic bacteria have been applied in numerous paleoecological studies, including in polar lakes (Hodgson et al., 2004). Although they have largely been used to reconstruct variability in past oxic status and productivity, these changes often have climatic implications. Okenone, a marker pigment for purple sulphur bacteria, has been used to infer periods of stratification and meromixis in temperate and high latitude sites (e.g., McIntosh, 1983; Guilizzoni et al., 1986; Schmidt el al., 1998; Anderson et al., 2008; McGowan et al., 2008). Pigments from green sulphur bacteria, primarily isorenieratene, have been used to reconstruct past oxic and trophic characteristics in both marine and freshwater environments (McIntosh, 1983; Repeta, 1993; Mallorquí et al., 2005; Squier et al., 2005; Tani et al., 2009). Transformation products of isorenieratene and okenone have been used in studies of the evolution of ocean oxygen content (Brocks and Pearson, 2005), and have been identified from samples as old as the Paleoproterozoic (Brocks et al., 2005). In Lake A, we tested the hypothesis that bacterial photopigments might be reflective of the degree of ice cover, given the ice-dominated character of the lake and the role of ice in determining light penetration (Belzile et al., 2001). We further hypothesized that bacterial pigments preserved in the sediments might be developed as a new indicator of past ice cover in paleoecological reconstructions, a method that could then be applied in other ice-dominated meromictic lakes.

Our objectives, therefore, were to understand the phototrophic characteristics of Lake A's water column through high performance liquid chromatography (HPLC) examination of photosynthetic pigments, and to study the sedimentary deposition of photosynthetic pigments in order to evaluate the utility of this new application for the reconstruction of past ice cover and climate.

2. Materials and methods

2.1. Physical setting

Lake A is located along the northern coast of Ellesmere Island in Quttinirpaaq National Park (83°00′ N, 75°30′ W; Fig. 1). It lies approximately 4 m above sea level, with a maximum known depth of 128 m, a surface area of 4.9 km^2, and a catchment of 37 km^2 (Jeffries et al., 1984; Van Hove et al., 2006). Lake A is perennially ice-covered. Previous studies have shown that ice thickness was stable between 1969 and 1999, with early summer thickness measurements of ~2 m

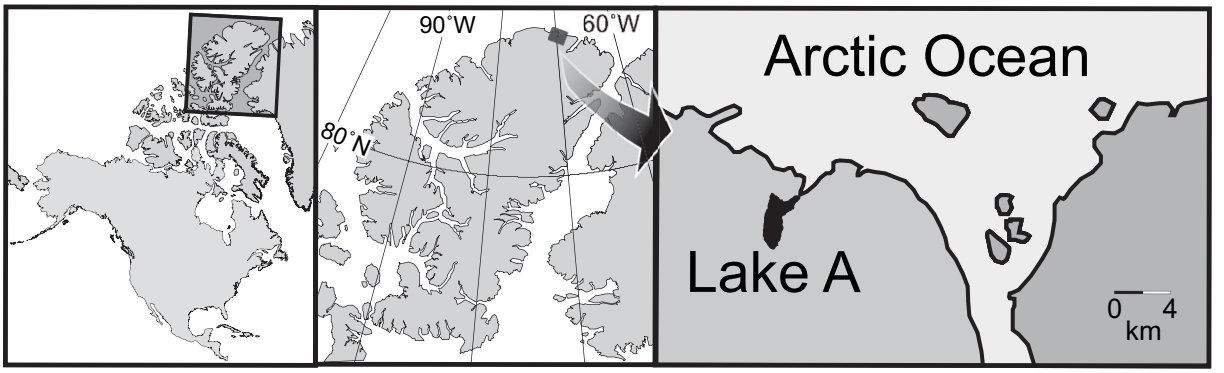

Fig. 1. Location map of Lake A, Ellesmere Island.

(Hattersley-Smith et al., 1970; Jeffries and Krouse, 1985; Belzile et al., 2001). Lake A's ice cover broke up during the warm summer of 2000, and our data indicate that ice thickness is now lower, with recent measurements of 1.5 m (May 2005) and 1.3 m (May 2006). Snow depth on the lake surface was also relatively stable, with early season values ranging from 42 to 52 cm in the 1980s through 1999 (Belzile et al., 2001; Mueller et al., in press), and measured snow covers of 60 cm in 2005 and 50 cm in 2006.

Lake A is meromictic and, due to lack of mixing in the strongly stratified water column, the oxic layer and the anoxic monimolimnion have developed strikingly different characteristics. Oxic freshwater is present at the surface, with a gradual halocline present between 10 and ~30 m, a sharp oxycline located at 10–16 m depth, and the anoxic monimolimnion below 16 m (Fig. 2). Lake A has a complex thermal profile with a slight peak immediately below the ice cover, and an overall maximum of 8.45 °C at 18 m (in 2006), below which the temperature drops gradually to 4 °C at depth (Fig. 2). The water in the surface oxic layer is oligotrophic, with surface concentrations in 1999 of 5 μg L^{-1} total phosphorus (TP), 118 μg L^{-1} total nitrogen (TN), and 0.32–0.52 μg L^{-1} Chl-*a* (Van Hove et al., 2006). However, nutrient and ionic concentrations in the anoxic monimolimnion far exceed those found in the upper fresh waters (Gibson et al., 2002; Van Hove et al., 2006).

Climate data from Lake A were recorded by a 3 m automated weather station that has been in operation since August 2004 as part of the SILA climate network of the Centre d'Études Nordiques. Climate normals from the ~55 year record from Alert (~175 km to the east) indicate that daily mean temperatures exceed the melting point for only 2 months of the year (i.e., July = 3.3 °C, August = 0.8 °C), and the summer (June–July–August) mean temperature is 1.1 °C (Environment Canada, 2008). For the period 2004–2006, monthly mean temperatures were significantly correlated with those from Alert ($n = 29$, $r^2 = 0.994$, $p < 0.0001$), but values were, on average, 2.7 °C below Alert. This suggests that overall trends in Lake A's climate prior to the 2004 opening of the Lake A weather station can be reasonably inferred from the Alert record. At Lake A, July was the only month for which mean air temperatures exceeded zero (1.4 °C), and the summer (June–July–August) mean temperature was 0.2 °C.

2.2. Water column and sediment sampling

Sampling for our study took place in late May 2005 and late May–early June 2006. Profiles of salinity, temperature, dissolved oxygen, and pH in the Lake A water column were measured with an RBR XR-420 conductivity-temperature-depth probe and a Hydrolab Surveyor 3. Water samples for HPLC analyses were taken with a 6.2 L Kemmerer sampler and transferred to acid-washed opaque plastic containers. In 2005, water was sampled at 2 m intervals up to 10 m depth, and at 2.5 m intervals to 35 m (15 samples), while in 2006, samples were taken each 2 m until 16 m and then at 29 and 32 m (10 samples). Samples were filtered in the field using Whatman GF/F glass microfiber filters (nominal pore size 0.7 μm, to capture all phytoplankton size fractions) that were frozen immediately and subsequently transferred to a −80 °C freezer until analysis. Sample sizes ranged from 0.2 to 1.5 L, with volumes below 1.5 L representing the maximum volume of water that could be passed through a single filter before it became clogged with particulate matter. Sediments were collected with a 68 mm diameter gravity corer (Aquatic Research Instruments, Hope, Idaho) from the anoxic bottom at approximately 50 m water depth. These

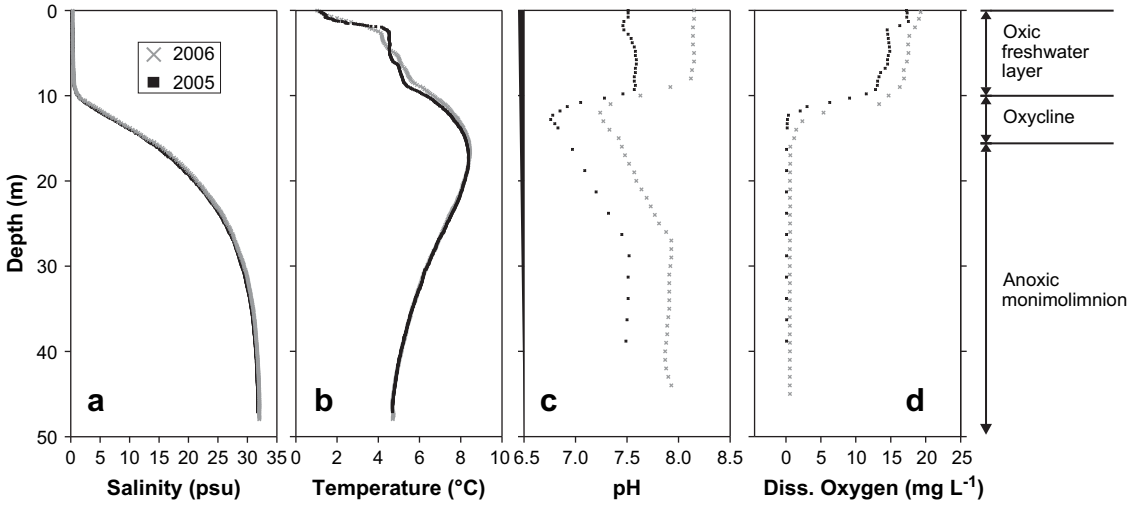

Fig. 2. Salinity, temperature, pH and dissolved oxygen profiles from the Lake A water column. Black symbols represent 2005 profiles, and grey symbols represent 2006 values.

sediments were stored cold and in the dark before and during transport to the laboratory, where they were kept at −80 °C until analyzed. A 1 mm thick layer of sediment was removed with a microtome and prepared for photosynthetic pigment analysis.

2.3. HPLC pigment analysis

Phytoplankton pigments were extracted by sonication in 2 mL of 95% methanol, cleared by centrifugation, filtered with PTFE syringe filters (pore size 0.2 μm) and placed under argon. For extraction of sedimentary pigments, samples were freeze-dried and then extracted by sonication in 2 mL 100% acetone. Samples were placed under argon and left to complete the extraction in a freezer for 24 h before filtering following the same steps as for phytoplankton samples. Serial sediment extractions were prepared to verify that no pigments remained in the sediments after the original application of acetone.

Immediately after extraction, pigment extracts were injected into a Varian ProStar high performance liquid chromatography (HPLC) system equipped with a Symmetry C8 column (3.5 μm pore size), a photodiode array (PDA) and a programmable fluorescence detector, and analyzed using a reverse-phase technique. Phytoplankton pigment analyses followed the solvent protocol of Zapata et al. (2000), while sedimentary pigment analyses followed the same method, but with a flow rate of 0.8 ml min^{-1} and a run time of 60 min to better separate the complex mixture of pigments and degradation products found in these samples. For all HPLC analyses, chlorophylls were detected by fluorescence (excitation, 440 nm; emission, 650 nm) and carotenoids by diode-array spectroscopy (350–750 nm) set to a slit width of 2 nm. Absorbance chromatograms were obtained at 450 nm for carotenoids and at 476 nm for bacteriochlorophylls. Standards for the identification and quantification of pigments were obtained from Sigma Inc. (St. Louis, MO, USA) (chlorophylls-*a* and -*b*, β,β-carotene) and DHI Water & Environment (Hørsholm, Denmark) (chlorophyll-*c*2, canthaxanthin, diadinoxanthin, echinenone, fucoxanthin, lutein, myxoxanthophyll, violaxanthin, zeaxanthin) to calibrate our HPLC. Where pigment identifications could not be confirmed by commercial standards (i.e., bacteriochlorophyll-*e*, isorenieratene and β-isorenieratene), the identifications and quantifications were made by comparison with PDA spectra, retention times, and extinction coefficients from literature (Hurley and Watras, 1991; Borrego and Garcia-Gil, 1994; Jeffrey et al., 1997; Borrego et al., 1999; Airs et al., 2001; Hirabayashi et al., 2004; Mallorquí et al., 2005). Concentrations of unidentified carotenoids were calculated using the extinction coefficient for β,β-carotene, while those of chlorophyll degradation products were calculated using our calibration coefficients for their respective undegraded chlorophylls. Sedimentary pigment concentrations are expressed relative to the organic matter content of sediment (i.e., μg g^{-1} OM) as determined by loss-on-ignition (LOI; Dean, 1974).

2.4. PAR reaching the water column

Incoming photosynthetically active radiation (PAR) was measured hourly by our Lake A climate

station. We summed the daily totals to calculate cumulative annual PAR up to the date of water column sampling. To then calculate the amount of PAR transmitted to the water column, we assumed the snow albedo and ice attenuation coefficients to be constant, and used the values measured by Belzile et al. (2001) together with measured snow depths and ice thicknesses of 0.6 and 1.5 m in 2005, and 0.5 and 1.4 m in 2006.

3. Results

3.1. Properties of the water column

Profiles of the Lake A water column reflected the lack of mixing between the oxic freshwater and anoxic saline layers and, with minor exceptions, indicated stable conditions between 2005 and 2006. Salinity was low from 0 to 10 m and increased to levels approaching that of seawater at ~30 m (Fig. 2a). The temperature profile was complex, with a minimum immediately below the ice-water interface, stepwise changes in the oxic layer, and maxima of 8.41 and 8.45 °C at 18.35 and 18.04 m depth in 2005 and 2006, respectively (Fig. 2b). pH varied little within the upper 10 m, beyond which it dropped sharply to a minimum between 12 and 13 m, rose again to a maximum at 29 m, and then dropped slightly in deeper waters (Fig. 2c). The shift in pH between 2005 and 2006 almost certainly results from issues of pH meter calibration, rather than a shift of 0.5 pH units throughout the water column. Dissolved oxygen had a maximum immediately below the ice-water interface, declined gradually until 10 m depth, and then sharply until the top of the anoxic monimolimnion (Fig. 2d). The transition to anoxic conditions through the oxycline (10–15 m) was more gradual in 2006 than in 2005 (Fig. 2d).

3.2. Pigments in the oxic zone

Pigment concentrations were low in the upper, oxygenated section of the water column (0–16 m, Figs. 3a and 4a). There were, however, notable differences between pigment concentrations in the 2 years sampled. Mean total pigment (Pig_{tot}) concentrations in the oxic zone were 0.16 and 0.35 μg L^{-1} in 2005 and 2006, respectively, while mean chlorophyll-*a* (Chl-*a*) concentrations were 0.07 (range 0.03–0.18 μg L^{-1}) and 0.13 μg L^{-1} (range 0.05–0.23 μg L^{-1}). Chlorophyll-*b* (Chl-*b*) concentrations were low throughout the oxic zone with the exception of the upper 2 m, where they increased both in absolute concentrations and relative to Chl-*a* in 2005 and 2006 (Fig. 5). In both years, maximum oxic zone concentrations of almost all pigments occurred immediately beneath the ice, at 2 m depth (e.g., Pig_{tot}/Chl-*a* = 0.49/0.18 μg L^{-1} in 2005; 0.58/0.23 μg L^{-1} in 2006, Fig. 4a). The ratios of undegraded chlorophylls to degradation products in the oxic zone were high (mean = 8.5/9.0 in 2005/2006). Four carotenoids were identified in the oxic layer (i.e., β,β-carotene, fucoxanthin, lutein and zeaxanthin; Table 1). There were differences in the profiles and concentrations of each pigment between 2005 and 2006 samples. In 2005, only zeaxanthin and β,β-carotene were consistently identified from the oxic layer, as fucoxanthin and lutein were found in one and two samples, respectively. Echinenone was below detection limits at most depths, but present in low concentrations at 17.5 m. Carotenoid concentrations were typically higher in 2006, when β,β-carotene, zeaxanthin and fucoxanthin were present throughout the oxic zone, and lutein was identified at 2 m depth (Table 1).

3.3. Pigments in the anoxic zone

Pigment assemblages in the anoxic bottom layer of Lake A were distinct from those in the oxic zone, and concentrations in the anoxic waters greatly exceeded those of the surface waters (Fig. 3). The most concentrated pigment by far was bacteriochlorophyll-*e* (BChl-*e*). Fifteen homologs of BChl-*e* were identified from monimolimnion samples. All 15 were present in 2005 samples, of which 12 were identified in 2006. Numerous other unidentified pigments that were likely of bacterial origin were found in the anoxic strata of the water column. In addition to isorenieratene and β-isorenieratene, two pigments that were likely *cis*-isomers of isorenieratene (Hopmans et al., 2005) and six unidentified carotenoids were present only in anoxic samples, including four whose concentrations were significantly correlated with those of isorenieratene ($r = 0.66–0.83$, $p = <0.001–0.03$, $n = 11$). All ten bacterial carotenoids were present in 2005, while isorenieratene and β-isorenieratene were the only bacterial carotenoids present during 2006.

Several non-bacterial pigments also reached their maximum water column concentrations in the monimolimnion. The overall maxima of Chl-*a* and -*b* in the water column occurred between 25 and 30 m depth, while β,β-carotene had a broad maximum between 22.5 and 32.5 m. In addition, chlorophyll derivatives, including pheophytin-*a*, pyropheophytin-*a*, and chlorophyllide-*a* all reached their maximum concentrations below 16 m depth (Table 1).

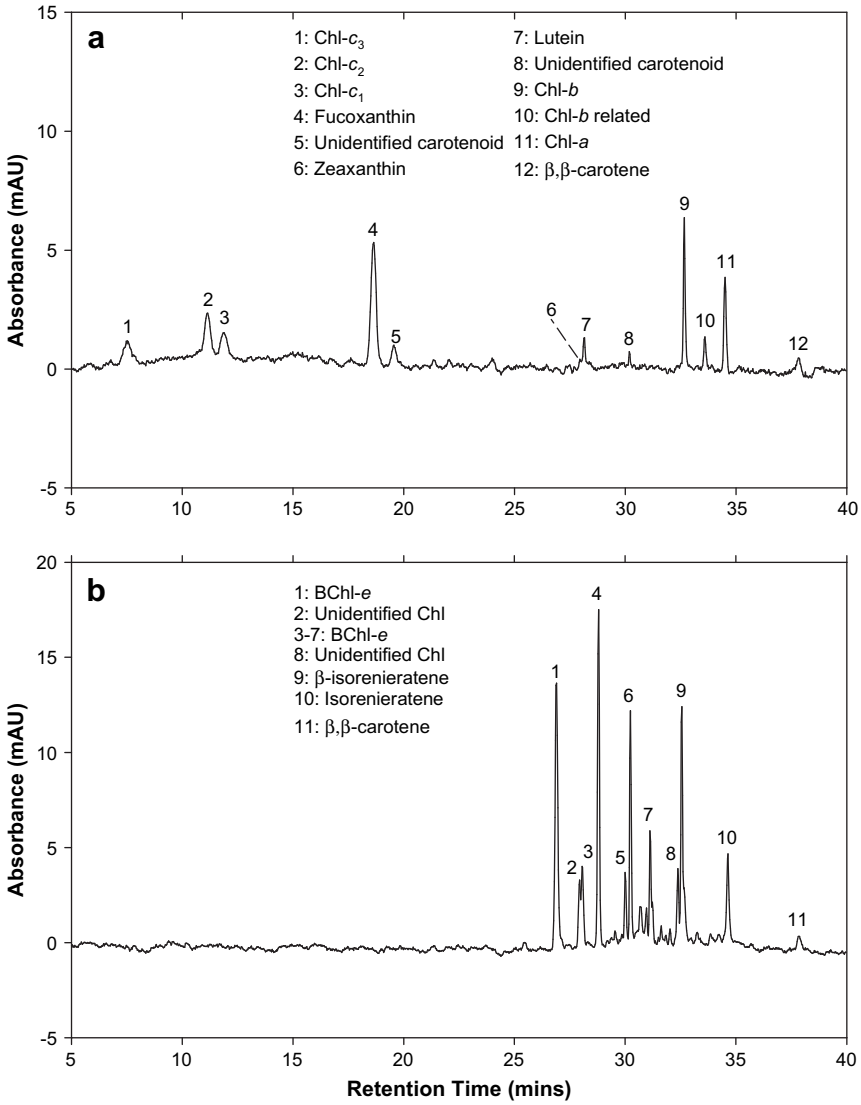

Fig. 3. Typical HPLC (PDA) chromatograms from (a) the oxic freshwater layer (2 m depth, 2005) and (b) the anoxic monimolimnion (17.5 m depth, 2005).

3.4. Pigments in the sediments

The surface sediments of Lake A contained a complex pigment mixture, of which the majority were bacterial in origin (Table 1). Pigments in the surface sediments of Lake A were highly concentrated (i.e., total BChl-*e* concentration = 789.2 μg g^{-1} OM; max. water column total BChl-*e* = 10.2 μg L^{-1}). Sixteen homologs of BChl-*e* were identified from the surface sediments, along with isorenieratene, β-isorenieratene, and one *cis*-isomer of isorenieratene. The only pigments identified from the sediments that were of oxygenic origin were Chl-*a*, pheophytin-*a*, and β,β-carotene, as well as other chlorophyll degradation products, all of which were present in low concentrations (Table 1).

3.5. PAR reaching the water column

The measured values of cumulative annual incoming PAR up to the date of sampling were 69,579 and 67,077 W m^{-2} in 2005 and 2006, respectively, while the calculated values of PAR transmitted through the ice and snow were 267 and 351 W m^{-2} PAR in 2005 and 2006, respectively.

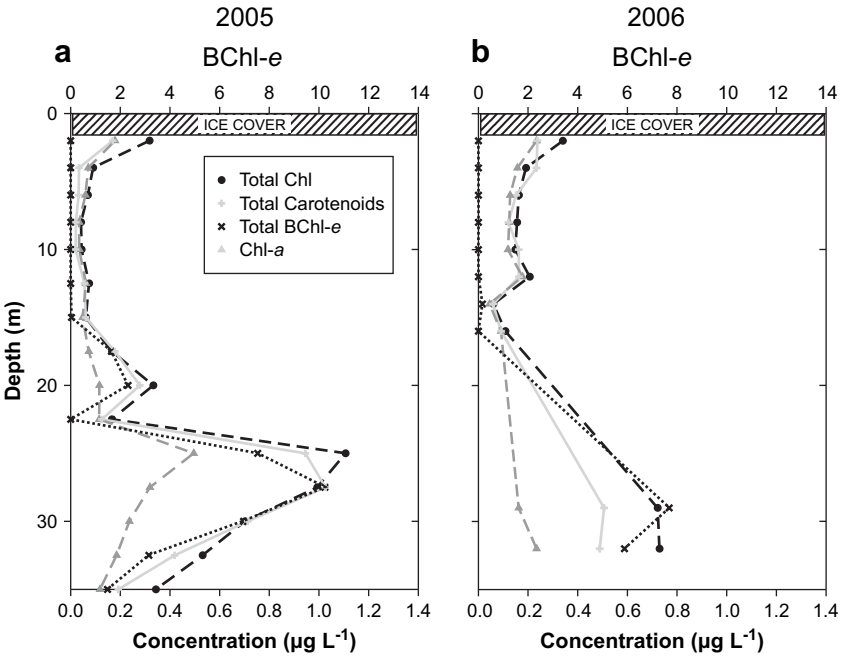

Fig. 4. Lake A HPLC water column pigment concentrations for (a) 2005, and (b) 2006. Note the different scale for BChl-*e*.

4. Discussion

4.1. Stability of the Lake A water column

The salinity profiles of Lake A were nearly identical in 2005 and 2006 (Fig. 2). Salinity in Lake A has been largely stable over the last 50 years (Vincent et al., 2008b), demonstrating the strong resistance to mixing in the water column produced by density stratification. However, during years of low ice cover, the oxic freshwater layer can become isohaline due to wind-induced mixing that may reach the top of the halocline (Van Hove et al., 2006). The general form of Lake A's thermal profile appears largely unchanged during recent decades, although temperatures in the oxic freshwater layer can also be affected by mixing events in low ice years (Van Hove et al., 2006), and the exact position of the thermal maximum has varied somewhat on decadal time scales. Between 2003 and 2006, the temperature and depth of the thermal maximum ranged between 8.41−8.72 °C and 18.04−18.96 m ($n = 5$). Earlier measurements taken between 1969 and 2001 indicated thermal maxima ranging from 7.61 to 8.78 °C at depths between 15.43 and 17.5 m (Hattersley-Smith et al., 1970; Jeffries et al., 1984; Jeffries and Krouse, 1985; Ludlam, 1996; Van Hove et al., 2006), and there were significant increases over time of the temperature ($r^2 = 0.61$, $p < 0.001$) and depth ($r^2 = 0.55$, $p < 0.001$) of the thermal maximum. Absorption of solar radiation and the absence of wind-induced mixing have been shown to permit the gradual accumulation of heat in Lake A during periods of stable perennial ice (Vincent et al., 2008b).

Pigment concentrations have been demonstrated to be a reliable proxy for algal biomass, although they may not be directly equivalent to biomass because of potential shifts in cellular pigment concentrations that can result from physiological adjustments (e.g., Veldhuis and Kraay, 1990; Schlüter et al., 2006). Lake A pigment data indicated that, similar to trends in physical and chemical variables, patterns of phytoplankton biomass and community composition were stable in the monimolimnion and showed interannual variability in the oxic zone. Waters below Lake A's halocline are isolated from physical forcing such as turbulence and advection due to inflowing water, wind-induced mixing around the ice margins and the effect of air temperature, as well as chemical changes due to nutrient inputs or differences in the ionic content of melt water. These changes would, however, affect conditions in the oxic zone and likely play a role in the interannual variability of pigment concentrations that we observed (Table 1). The chemical conditions in the monimolimnion appear to be stable, with major annual variation limited only to the amount of in situ irradiance that fluctuates in response to changes in the thickness and optical properties of the ice and snow cover as well as variations in meteorological conditions.

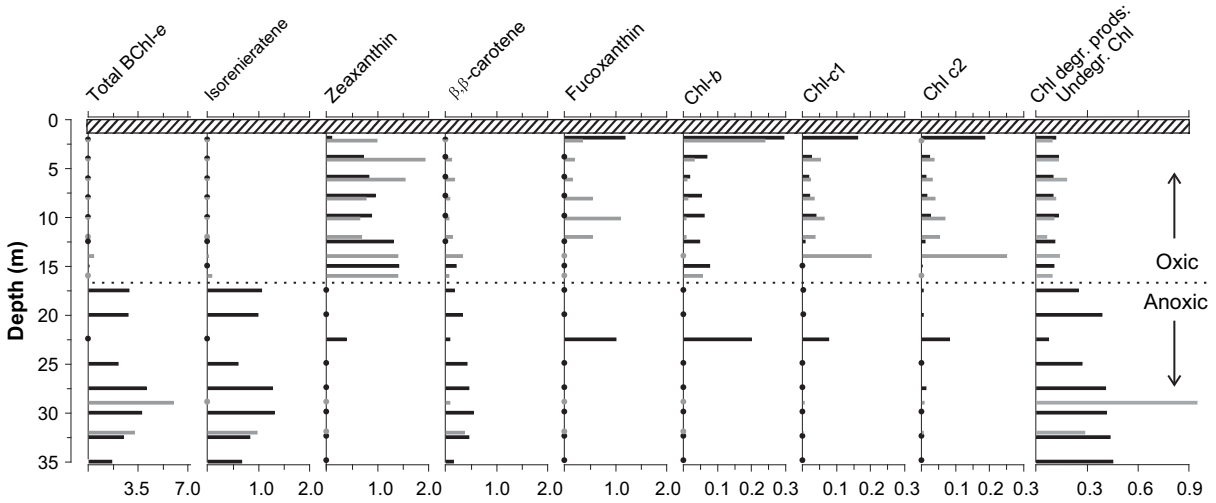

Fig. 5. Lake A HPLC pigment concentrations expressed as molar ratios to Chl-*a*. Black/grey symbols represent 2005/2006 ratios, respectively. Circles represent data points with zero values. Note the x-axis scales. The hatched box represents the ice cover, while the dotted line indicates the oxic/anoxic transition. The outlying data at 22.5 m may result from premature tripping of the sampling bottle higher in the water column.

4.2. Dynamics of the oxic zone

The waters of the oxic zone had low concentrations of all pigments, reflecting the oligotrophic nature of Lake A. The relatively low diversity pigment assemblage may also be indicative of the exclusion of certain algal groups due to other water column characteristics, including lack of turbulence, low solar radiation, and cold temperatures. The relatively higher concentrations of chlorophylls recorded just below the ice likely reflect the immediate absorption by phytoplankton of the limited available solar radiation. Given that diatoms are largely absent from the water column of Lake A (Van Hove, 2005) and rare in its sediments (Antoniades, unpubl. data), it is likely that the Chl-*c* related pigments and fucoxanthin that reach their peak concentrations at the surface are derived from dinoflagellates or flagellated chrysophytes. The Chl-*b* concentrations in the surface waters could result from communities of Chlorophyta, Prasinophyta or prochlorophyte cyanobacteria. Chlorophytes and prasinophytes are well known from Antarctic ice-covered meromictic lakes (e.g., Vincent, 1981), however prochlorophytes tend to be typical of warm marine waters (Waleron et al., 2007). Chl-*b* has been measured in high concentrations relative to Chl-*a* in lakes with thick perennial ice cover due to the increased densities of Chlorophyta in such low light environments (Morgan-Kiss et al., 2006). The decrease in the ratio of Chl-*b* to Chl-*a* in 2006 vs. 2005 may therefore result from the increase in transmitted PAR between these years and an accompanying reduction of these Chlorophyta communities. Prasinoxanthin was not detected in Lake A, suggesting that prasinophytes were likely absent, although this carotenoid is absent in some prasinophyte groups that have pigment signatures resembling those of green algae (Latasa et al., 2004).

Several lines of evidence suggest that picocyanobacteria represent a large proportion of phototrophic biomass stocks in the oxic layer of Lake A. Picocyanobacteria from the genus *Synechococcus* have been identified from Lake A using both epifluorescence microscopy and molecular techniques (Van Hove et al., 2008), a diagnosis supported by the presence of zeaxanthin in the oxic zone (Table 1). *Synechococcus* and *Synechocystis* populations have been observed in Antarctic meromictic lakes, sometimes in high concentrations (Powell et al., 2005). However, despite a broad peak in picocyanobacterial abundance centred around 20 m depth in Lake A (Van Hove et al., 2008), zeaxanthin in our study fell below the limits of detection in all but one sample below 16 m. Chl-*a* and zeaxanthin concentrations were correlated in the oxic layer ($r = 0.77$, $p = 0.02$), but uncorrelated in the anoxic layer, as zeaxanthin was largely absent and Chl-*a* was identified in every sample. As zeaxanthin is a marker pigment for *Synechococcus*, their correlation suggests that the majority of Chl-*a* in the oxic zone is derived from these picocyanobacteria. This pigment can also occur in Chlorophytes, although generally in the presence of the epoxidation products neoxanthin, violaxanthin and antheraxanthin, which were not detected in the present study. In 1999, the <2 μm fraction contributed an average of 62% of total Chl-

Table 1
HPLC pigment concentrations from water column (μg L^{-1}) and surface sediment (μg g OM^{-1}) samples. Isr = isorenieratene.

Water depth	Chl *a*	Phphy-*a* (x 10^{-3})	Pyroph-*a* (x 10^{-3})	Chl-ide *a* (x 10^{-3})	MgDVP (x 10^{-3})	Chl *c* 1 (x 10^{-3})	Chl *c* 2 (x 10^{-3})	Chl *c* 3 (x 10^{-3})	Chl *b* (x 10^{-3})	Chl deg products	BChl-*e* & homologs
2005											
2	0.179	0.387	0	1.100	0.807	20.200	23.100	1.940	53.900	0.033	0
4	0.071	0.151	0	0.948	0	1.410	1.300	0.143	5.100	0.011	0
6	0.060	0.132	0	1.070	0	0.892	0.680	0	1.270	0.007	0
8	0.034	0.095	0.059	0.725	0	0.575	0.408	0.044	1.960	0.004	0
10	0.035	0.170	0	0.825	0	1.030	0.670	0	2.250	0.005	0
12.5	0.062	0.774	0.124	0	0.377	0.398	0.609	0	3.220	0.008	0
15	0.049	0.559	0	0.451	0	0.124	0.202	0	3.880	0.006	0.036
17.5	0.073	1.160	0	0.239	0.131	0.179	0.339	0	16.800	0.019	1.644
20	0.116	2.330	0.332	0.173	0.193	0.187	0.692	0.399	30.700	0.046	2.313
22.5	0.115	0.345	0	1.810	0	6.370	6.730	0.614	23.700	0.013	0.000
25	0.496	9.910	0.561	0.424	0	0.275	1.010	0.496	92.900	0.138	7.531
27.5	0.319	5.790	0.359	0	0	0.385	3.600	1.450	104.000	0.135	10.238
30	0.237	3.690	0	0	0	0.425	0	0	79.200	0.100	6.965
32.5	0.185	3.050	0	0	0	0	0	0	43.500	0.081	3.153
35	0.118	1.930	0	0	0	0	0	0	25.200	0.054	1.486
2006											
2	0.234	0	0	4.640	0	8.700	4.780	0.812	57.400	0.030	0
4	0.157	0	0	5.390	0	2.220	2.930	0.154	5.310	0.023	0
6	0.128	0	0	9.220	0	3.070	3.490	0.169	1.740	0.025	0
8	0.124	0	0	2.710	0	5.510	5.820	0.364	1.910	0.017	0
10	0.119	0	0	2.650	0	6.060	6.260	0.416	1.390	0.015	0
12	0.177	0	0	0.779	0	6.320	7.810	0.357	2.100	0.013	0
14	0.045	0.251	0	0	0	0	0	0	1.600	0.007	0.167
16	0.091	0.438	0	0.252	0	1.020	1.150	0.084	5.420	0.010	0
29	0.163	2.490	0	0	0	0.792	1.360	0	79.100	0.158	7.682
32	0.234	3.140	1.110	0	0	0	1.410	0	61.700	0.089	5.882
Surface sediment											
	8.943	2.235	0	0	0	0	0	0	0	139.593	789.194

Water depth	β,β-car	Fucox	Echin.	Zeax.	Lutein	Isr	β-Isr	Bacterial carot 1	Bacterial carot 2	Chl_{tot}	$Carot_{tot}$	Pig_{tot}
2005												
2	0	0.158	0	0.005	0.005	0	0	0	0	0.318	0.169	0.487
4	0	0	0	0.034	0	0	0	0	0	0.091	0.034	0.124
6	0	0	0	0.032	0	0	0	0	0	0.069	0.032	0.102
8	0	0	0	0.021	0	0	0	0	0	0.042	0.021	0.063
10	0	0	0	0.020	0	0	0	0	0	0.044	0.020	0.064
12.5	0	0	0	0.052	0	0	0	0	0	0.074	0.056	0.130
15	0.007	0	0	0.045	0.006	0.003	0	0	0	0.061	0.061	0.158
17.5	0.008	0	0.003	0	0	0.094	0.047	0.018	0	0.166	0.178	1.988
20	0.024	0	0	0	0	0.144	0.069	0.026	0.001	0.333	0.279	2.924
22.5	0.007	0.088	0	0.030	0	0	0	0	0	0.166	0.125	0.291
25	0.132	0	0	0	0	0.447	0.184	0.072	0.009	1.107	0.945	9.583
27.5	0.091	0	0	0	0	0.532	0.246	0.093	0.013	0.993	1.026	12.257
30	0.082	0	0	0	0	0.366	0.186	0.061	0.009	0.702	0.713	8.380
32.5	0.053	0	0	0	0	0.228	0.093	0.045	0	0.532	0.419	4.103
35	0.012	0	0	0	0	0.098	0.048	0.033	0	0.343	0.192	2.021
2006												
2	0.012	0.065	0	0.150	0.010	0	0	0	0	0.340	0.238	0.578
4	0.015	0.026	0	0.194	0	0	0	0	0	0.191	0.234	0.426
6	0.008	0.016	0	0.127	0	0	0	0	0	0.162	0.152	0.314
8	0.006	0.051	0	0.063	0	0	0	0	0	0.156	0.121	0.277
10	0.013	0.098	0	0.051	0	0	0	0	0	0.149	0.163	0.312
12	0.010	0.074	0	0.080	0	0	0	0	0	0.207	0.164	0.371
14	0.005	0	0	0.041	0	0.008	0.005	0	0	0.060	0.059	0.286

(*continued on next page*)

Table 1 (*continued*)

Water depth	β,β-car	Fucox	Echin.	Zeax.	Lutein	Isr	β-Isr	Bacterial carot 1	Bacterial carot 2	Chl_{tot}	$Carot_{tot}$	Pig_{tot}
16	0.010	0	0	0.082	0	0	0	0	0	0.109	0.091	0.200
29	0.054	0	0	0	0	0.315	0.137	0	0	0.722	0.506	8.910
32	0.070	0	0	0	0	0.283	0.136	0	0	0.729	0.489	7.100
Surface sediment												
	8.798	0.000	0.000	0.000	0.000	61.860	16.507	34.074	0.000	150.772	121.239	1061.205

a in the upper 12 m of Lake A (range 39–97%; Belzile et al., 2001), consistent with picocyanobacterial dominance of the oxic phototrophic community.

Molar ratios of zeaxanthin:Chl-*a* varied between 0.46–1.44 in 2005 and 0.67–1.93 in 2006 in the oxic zone, below which they dropped to values at or near zero (Fig. 5). Our HPLC system has lower limits of detection for Chl-*a* than for zeaxanthin, which may partially explain the apparent absence of zeaxanthin in chlorophyll-containing waters. However, decreases in irradiance have also been shown to reduce the zeaxanthin:Chl-*a* ratio by up to five times (Kana et al., 1988; Schlüter et al., 2000, 2006). The decrease in zeaxanthin concentration and the corresponding shift in zeaxanthin:Chl-*a* ratios occurred at a depth where less than 0.05% of incident PAR remains and below a peak in light attenuation (Belzile et al., 2001). This decrease may thus reflect shifts in *Synechococcus* pigment production with reduced availability of solar radiation. This is further supported by the interannual differences in zeaxanthin:Chl-*a* ratios, given the estimated higher incident radiation at Lake A in 2006 relative to 2005.

4.3. Dynamics of the anoxic zone

The change in pigment assemblages across the oxycline reflected the shift toward anoxygenic photosynthesis in the monimolimnion. Chl-*a* and β,β-carotene reached their maximum overall concentrations in the anoxic waters at the base of the oxic freshwater layer. However, these higher concentrations likely consist of detrital pigments that settle from the water column above and accumulate at the pycnocline. This hypothesis is supported by the shift in the molar ratio of degradation products to undegraded chlorophylls across this horizon (i.e., 16–18 m, Fig. 5), as pigments are exposed longer to degradation when they accumulate due to the change in water density. In addition, the shift in this ratio suggests that most, if not all, of the *in situ* production of chlorophyll occurs in the upper 16 m of the water column.

BChl-e and β-isorenieratene, two pigments diagnostic of brown-coloured green sulphur bacteria (Overmann, 2008), were the most highly concentrated chlorophyll and carotenoid, respectively, in the Lake A water column. Each was absent in the oxic strata and each reached its maximum concentration in the anoxic monimolimnion (i.e., BChl-*e* 10.24 μg L^{-1}, β-isorenieratene 0.53 μg L^{-1}; Table 1). The maximum concentration of BChl-*e* exceeded that of Chl-*a* by a factor of 20, and β-isorenieratene exceeded zeaxanthin (the next most concentrated carotenoid in Lake A) by a factor of 2.5. While purple sulphur bacteria frequently occur in association with green sulphur bacteria in meromictic lakes (Pfennig, 1989), we did not identify the characteristic pigments bacteriochlorophyll-*a* or okenone at any point in the water column or sediment to suggest that purple sulphur bacteria were present in Lake A. Extremely low light levels in the anoxic layer may preclude the existence of purple sulphur bacteria, as the green sulphur bacteria can survive at much lower light intensities (Overmann, 2008). Okenone concentrations have also been observed to diminish during oligotrophic phases in some meromictic lakes (McIntosh, 1983), and so the absence of okenone in Lake A may reflect its extremely low trophic status. The pigment assemblage at 22.5 m that lacked bacterial pigments was distinct from all other depths in the anoxic monimolimnion. Given the overall similarity of this sample to those from the oxic zone (i.e., the absence of bacterial pigments, the presence of algal pigments, and low total pigment concentration), it is likely that the sampling bottle closed accidentally while in the oxic portion of the water column.

Although green sulphur bacteria have been shown to produce different homologs of BChl-*e* under different irradiances (Borrego and Garcia-Gil, 1995), individual homologs in our samples did not show directional vertical trends, with maximum concentrations of almost all bacterial pigments between 25 and 30 m depth (Table 1). Hirabayashi et al. (2004) similarly showed that the cellular concentrations of numerous carotenoids

in the green sulphur bacterium *Chlorobium phaeobacteroides* varied with changing irradiance, however our bacterial carotenoid concentrations again showed no linear trends, with pigments reaching maxima between 25 and 30 m. This may result from the very low irradiance at all levels of the water column, or because trends have been obscured by the vertical diffusion of pigments within the anoxic zone.

Two calanoid copepod taxa identified from Lake A (*Limnocalanus macrurus* and *Drepanopus bungei*) were shown to live both adjacent to and within the anoxic layers of the water column (Van Hove et al., 2001). Moreover, adult populations of *L. macrurus* reached their maximum between 15 and 17.5 m, and *D. bungei* between 20 and 25 m (Van Hove et al., 2001), suggesting that zooplankton may be entering the anoxic layers of Lake A either in search of food or for refuge from predators. Zooplankton have been shown to dive into anoxic strata to graze on phototrophic bacteria in other meromictic lakes (Sorokin, 1999; van Gemerden and Mas, 1995), and the dense layer of bacteria between 27.5 and 29 m in Lake A may therefore serve as a food source for these copepods. It is unlikely, however, that zooplankton enter the toxic, sulphide-bearing waters (Overmann, 2008). H_2S was present in measurable concentrations only below 32 m in the water column (Gibson et al., 2002). This depth was just below the depth of peak in BChl-*e* concentrations, implying that the H_2S is completely oxidized by the green sulphur bacteria communities, which thereby act as a barrier to H_2S diffusion to depths higher in the anoxic water column (Gibson et al., 2002).

The depth of the peak in bacterial pigments recurred at the same depth in the water column in both 2005 and 2006 (Fig. 4). In 1999, the maximum occurred at the same depth (i.e., 27.5–30 m), however the peak appeared to be more diffuse, with a secondary peak centered around 50 m, and diminishing to near zero concentrations near 60 m depth (C. Belzile, unpubl. data). The maximum concentration of the peak was higher in 2006 than 2005, and both were high relative to 1999. Lake A's thermal and geochemical profiles were largely unchanged between these years, and therefore these differences in peak characteristics are unlikely to be the result of turbulent mixing, and more likely represent interannual differences in photosynthetic bacterial growth and biomass accumulation. However, it is unclear whether analytical differences may account for part of this discrepancy, given that different methodologies were used to calculate bacteriochlorophyll concentrations in samples from 1999 (spectrophotometry of ethanol extracts) and 2005/2006 (HPLC).

Changes in the pH profile of Lake A coincided with community shifts in the water column. pH was stable near 8.2 throughout much of the oxic layer. A sharp decrease in pH began at 10 m, just above a peak of Crenarchaeota at 12 m depth where there was a high concentration of the archaeal ammonium monooxygenase (amoA) gene (Pouliot et al., 2009). This decrease in pH could therefore result from the liberation of protons during nitrification by archaea. Increases in pH began only below 15 m, the depth of the onset of anoxygenic photosynthesis, as inferred from the first occurrence in the water column of BChl-*e*. pH increased through a secondary peak at 29–30 m, below which it dropped slightly. This secondary pH peak likely represents the base of the zone of active bacterial photosynthesis, a hypothesis supported by the absence of sulphide above 32 m (Gibson et al., 2002).

4.4. Light limitation in the water column

While cumulative incident PAR at Lake A decreased by 4% between 2005 and 2006, the amount of light transmitted to the water column actually rose by 31% due to the reduction of both snow depth and ice thickness during that time and the strong control of ice and snow cover on light attenuation. Although the albedo and transmissivity of the ice and snow may also vary on an interannual basis, our calculations provide a first order approximation of the magnitude of change in available PAR. Pigment concentrations in the water column also rose between 2005 and 2006, with increases in the oxic zone of 86% of mean Chl-*a* and over 300% of mean zeaxanthin, while in the anoxic zone, peak BChl-*e* concentrations increased from 10 to 86%. While nutrients and other factors likely also play a role in determining water column productivity, due to the lack of interaction between the fresh and saltwater layers of Lake A, light availability is likely the sole factor that varies simultaneously both above and below the oxycline. The corresponding increases in available PAR and pigment concentrations in both the oxic and anoxic layers of Lake A suggest that light penetration plays a strong role in limiting both algal and bacterial photosynthesis. The persistently higher nutrient concentrations present in the anoxic waters suggest that the photosynthetic bacteria are unable to exhaust completely these resources. The higher pigment concentrations that accompany greater light penetration (due to thinner ice cover) indicated that under higher light conditions, bacteria could increase their production per unit biomass and access the higher nutrient concentrations present at deeper points in the anoxic layer.

4.5. Bacterial pigments in lake sediment and their paleoecological implications in ice-covered lakes

The dominance of bacterial pigments in Lake A sediment reflected the high ratio in the water column of bacterial pigments to those from algal and cyanobacterial sources. Bacterial pigments may be more efficiently deposited in the sediments due to the extracellular deposition of elemental sulphur during the reduction of H_2S (Overmann, 2008). The relatively lower concentrations of Chl-*a*, zeaxanthin, and β,β-carotene in the sediments may also indicate increased degradation within the oxic zone prior to sedimentation and the longer distance for transportation of pigments to the sediments. Pigment degradation in the water column is dependent on site-specific characteristics such as depth and basin morphometry. Estimates suggest that in typical lakes over 90% of pigments are degraded in the water column (Leavitt, 1993; Guilizzoni and Lami, 2002). While the anoxic conditions, low temperatures and extremely low irradiance in Lake A's water column may reduce decomposition rates, the relatively great depth and thus residence time of algal pigments in the water column (i.e., >100 m from the base of the oxic zone to the sediment surface at the lake's deepest point) could favour their degradation. Moreover, studies concerned with bacterial pigments have shown that they are often preferentially preserved due to the strictly anoxic nature of their depositional environment (Villanueva et al., 1994; Itoh et al., 2003).

Bacterial pigments were highly concentrated in the surface sediments (Table 1), and only one homolog of BChl-*e* was identified from the sediments that was not present between 15 and 35 m in the water column. This, combined with the lack of systematic increase of any BChl-*e* homolog either with depth in the water column or in the sediment relative to water samples, suggests that pigment decomposition within the anoxic monimolimnion is limited. Although there were several unidentified pigments in the sediments, none could be linked to aerobic pigments as degradation products (cf. Jeffrey et al., 1997), and they were present at sufficiently low concentrations that it was impossible to obtain reproducible absorption spectra for conclusive identifications.

The relationship between incident radiation and bacterial phototrophic biomass, as measured by pigment concentrations, strongly implies that the communities of photosynthetic bacteria in Lake A are light limited. Light availability was also inferred to constrain bacterial photosynthesis in an ice-covered lake from Spitsbergen (Guilizzoni et al., 2006). Due to high albedo and light attenuation, Belzile et al. (2001) calculated that in 1999 only 0.45% of incident PAR was transmitted through Lake A's ice and snow cover, which rose to ~6% when the snow was removed. The importance of light availability in the water column is reinforced by the phototrophic maximum immediately below the ice surface, indicated by pigment concentrations and diversity, as well as by oxygen supersaturation. Moreover, only 0.03% of incident PAR reached the depth where phototrophic bacterial pigments appeared (16 m), and less than 0.003% arrived to the depth of peak concentrations of green sulphur bacteria at 27.5–29 m (Fig. 4; Belzile et al., 2001). Peak bacterial concentrations did not occur at the top of the anoxic zone, which implied that resource limitation also played a role in controlling these communities, particularly the absence of H_2S (cf. Gibson et al., 2002). However, even small changes in ice and snow thickness have strong effects on the absolute amount of solar radiation reaching the bacterial plate, thus changing bacterial standing stocks over time. While changes in the penetration of UV radiation have been inferred from variations in sedimentary concentrations of pigments from benthic cyanobacteria (Hodgson et al., 2005; Verleyen et al., 2005), paleoecological inferences based on bacterial photopigments have been largely restricted to the occurrence of anoxic conditions and changes in stratification, and not applied to reconstructions of changes in the degree of ice cover.

Photosynthetic green sulphur bacteria communities are present in numerous ice-covered, polar lakes (e.g., Tominaga and Fukui, 1981; Burke and Burton, 1988; Squier et al., 2005), and BChl-*e* and isorenieratene have been identified in the sediments of meromictic Ace Lake in Antarctica (Hopmans et al., 2005). The favourable environment for pigment preservation in such lakes (i.e., low light penetration, low temperatures, bottom anoxia) implies that there is a considerable number of high latitude sites whose sediments contain well-preserved bacterial pigment archives (Hodgson et al., 2004). While bacterial pigments in meromictic lakes can clearly be used to infer past anoxia, the particular characteristics of perennially ice-covered lakes should permit additional paleoecological information to be extracted from their sedimentary records. Changes in ice thickness caused by climate warming and cooling alter the amount of PAR reaching photosynthetic bacterial communities, due primarily to the control exerted on light attenuation by the ice and snow cover. For example, the complete removal of Lake A's ice cover would increase the amount of PAR

incident on the upper euphotic zone by a factor of more than 200. Given the demonstrated links between PAR penetration and bacterial biomass, sedimentary BChl-*e* concentrations should reflect bacterial production, mediated by ice cover, and therefore enable the reconstruction of contemporary ice conditions. Due to the control of climate on ice cover regimes, we therefore suggest that paleoecological reconstructions using bacterial photopigments such as BChl-*e* and isorenieratene may prove to be effective proxies for the reconstruction of past Arctic climates.

Acknowledgements

We are grateful to Parks Canada and Quttinirpaaq National Park for their continued co-operation and facilitation of our research. We thank the Natural Sciences and Engineering Research Council of Canada, the Canada Research Chairs Program, le Fonds québécois de la recherche sur la nature et les technologies, and the Network of Centres of Excellence of Canada program ArcticNet for research funding. Eric Bottos and Jérémie Pouliot provided able assistance in the field, and Denis Sarrazin helped with the meteorological data from Lake A. We also thank the Polar Continental Shelf Project for their excellent and essential logistic support; this is PCSP/ÉPCP contribution # 03109.

References

ACIA, 2005. Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.

Airs, R.L., Atkinson, J.E., Keely, B.J., 2001. Development and application of a high resolution liquid chromatographic method for the analysis of complex pigment distributions. J. Chromatog. A 917, 167–177.

Anderson, N.J., Brodersen, K.P., Ryves, D.B., McGowan, S., Johansson, L.S., Jeppesen, E., Leng, M.J., 2008. Climate versus in-lake processes as controls on the development of community structure in a low-Arctic lake (South-West Greenland). Ecosystems 11, 307–324.

Anisimov, O.A., Vaughan, D.G., Callaghan, T.V., Furgal, C., Marchant, H., Prowse, T.D., Vilhjálmsson, H., Walsh, J.E., 2007. Polar regions (Arctic and Antarctic). In: Parry, M.L., Canziani, O.F., Palutikof, J.P., Van Der Linden, P.J., Hanson, C.E. (Eds.), Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 653–685.

Antoniades, D., Crawley, C., Douglas, M.S.V., Pienitz, R., Andersen, D., Doran, P.T., Hawes, I., Pollard, W., Vincent, W.F., 2007. Abrupt environmental change in Canada's northernmost lake inferred from fossil diatom and pigment stratigraphy. Geophys. Res. Lett. 34, L18708. doi:10.1029/2007GL030947.

Belzile, C., Vincent, W.F., Gibson, J.A.E., Van Hove, P., 2001. Bio-optical characteristics of the snow, ice, and water column of a perennially ice-covered lake in the High Arctic. Can. J. Fish. Aquat. Sci. 58, 2405–2418.

Blake Jr., W., 1989. Inferences concerning climatic change from a deeply frozen lake on Rundfjeld, Ellesmere Island, Arctic Canada. J. Paleolimnol. 2, 41–54.

Borrego, C.M., Garcia-Gil, L.J., 1994. Separation of bacteriochlorophyll homologs from green photosynthetic sulfur bacteria by reversed-phase HPLC. Photosynth. Res. 41, 157–163.

Borrego, C.M., Garcia-Gil, L.J., 1995. Rearrangement of light harvesting bacteriochlorophyll homologues as a response of green sulfur bacteria to low light intensities. Photosynth. Res. 45, 21–30.

Borrego, C.M., Gerola, P.D., Miller, M., Cox, R.P., 1999. Light intensity effect on pigment composition and organization in the green sulfur bacterium *Chl. tepidum*. Photosynth. Res. 49, 159–166.

Brocks, J.J., Pearson, A., 2005. Building the biomarker tree of life. Rev. Mineral. Geochem. 59, 233–258.

Brocks, J.J., Love, G.D., Summons, R.E., Knoll, A.H., Logan, G.A., Bowden, S.A., 2005. Biomarker evidence for green and purple sulphur bacteria in a stratified Palaeoproterozoic sea. Nature 437, 866–870.

Burke, C.M., Burton, H.R., 1988. Photosynthetic bacteria in meromictic lakes and stratified fjords of the Vestfold Hills, Antarctica. Hydrobiologia 165, 13–23.

Dean, W.E., 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. J. Sediment. Petrol. 44, 242–248.

Doran, P.T., McKay, C.P., Adams, W.P., English, M.C., Wharton Jr., R.A., Meyer, M.A., 1996. Climate forcing and thermal feedback of residual lake-ice covers in the High Arctic. Limnol. Oceanogr. 41, 839–848.

Environment Canada, 2008. Canadian Climate Normals 1971–2000. [WWW document]. URL: http://climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html.

Gibson, J.A.E., 1999. The meromictic lakes and stratified marine basins of the Vestfold Hills, East Antarctica. Antarct. Sci. 11, 175–192.

Gibson, J.A.E., Vincent, W.F., Van Hove, P., Belzile, C., Wang, X., Muir, D., 2002. Geochemistry of ice-covered meromictic Lake A in the Canadian High Arctic. Aquat. Geochem. 8, 1–23.

Guilizzoni, P., Lami, A., 2002. Paleolimnology: use of algal pigments as indicators. In: Bitton, G. (Ed.), Encyclopedia of Environmental Microbiology. John Wiley & Sons, New York, pp. 2306–2317.

Guilizzoni, P., Lami, A., Ruggiu, D., Bonomi, G., 1986. Stratigraphy of specific algal and bacterial carotenoids in the sediments of Lake Varese (N. Italy). Hydrobiologia 143, 321–325.

Guilizzoni, P., Marchetto, A., Lami, A., Brauer, A., Vigliotti, L., Musazzi, S., Langone, L., Manca, M., Lucchini, F., Calanchi, N., Dinelli, E., Mordenti, A., 2006. Records of environmental and climatic changes during the late Holocene from Svalbard: palaeolimnology of Kongressvatnet. J. Paleolimnol. 36, 325–351.

Hattersley-Smith, G., Keys, J.E., Serson, H., Mielke, J.E., 1970. Density stratified lakes in northern Ellesmere Island. Nature 225, 55–56.

Hirabayashi, H., Ishii, T., Takaichi, S., Inoui, K., Uejara, K., 2004. The Role of carotenoids in the photoadaptation of the brown-colored sulfur bacterium *Chlorobium phaeobacteroides*. Photochem. Photobiol. 79, 280–285.

Hodgson, D.A., Doran, P.T., Roberts, D., McMinn, A., 2004. In: Pienitz, R., Douglas, M.S.V., Smol, J.P. (Eds.), Long-term

Environmental Change in Arctic and Antarctic Lakes. Developments in Paleoenvironmental Research. Paleolimnological studies from the Antarctic and Subantarctic Islands, Vol. 8. Springer Verlag, Dordrecht, pp. 419–474.

Hodgson, D.A., Vyverman, W., Verleyen, E., Leavitt, P.R., Sabbe, K., Squier, A.H., Keely, B.J., 2005. Late Pleistocene record of elevated UV radiation in an Antarctic lake. Earth Planet. Sci. Lett. 236, 565–572.

Hurley, J.P., Watras, C.J., 1991. Identification of bacteriochlorophylls in lakes via reverse-phase HPLC. Limnol. Oceanogr. 36, 307–315.

Itoh, N., Tani, Y., Soma, M., 2003. Sedimentary photosynthetic pigments of algae and phototrophic bacteria in Lake Hamana, Japan: temporal changes of anoxia in its five basins. Limnology 4, 139–148.

Jeffrey, S.W., Mantoura, R.F.C., Wright, S.W. (Eds.), 1997. Phytoplankton Pigments in Oceanography. UNESCO, Paris.

Jeffries, M.O., Krouse, H.R., 1985. Isotopic and chemical investigations of two stratified lakes in the Canadian Arctic. Z. Gletscherkunde 21, 71–78.

Jeffries, M.O., Krouse, H.R., Shakur, M.A., Harris, S.A., 1984. Isotope geochemistry of stratified Lake "A," Ellesmere Island, N.W.T., Canada. Can. J. Earth Sci. 21, 1008–1017.

Kana, T.M., Glibert, P.M., Goericke, R., Welschmeyer, N.A., 1988. Zeaxanthin and β-carotene in *Synechococcus* WH7803 respond differently to irradiance. Limnol. Oceanogr. 33, 1623–1627.

Latasa, M., Scharek, R., Le Gall, F., Guillou, L., 2004. Pigment suites and taxonomic groups in Prasinophyceae. J. Phycol. 40, 1149–1155.

Leavitt, P.R., 1993. A review of factors that regulate carotenoid and chlorophyll deposition and fossil pigment abundance. J. Paleolimnol. 9, 109–127.

Ludlam, S.D., 1996. Stratification patterns in Taconite Inlet, Ellesmere Island, N.W.T. J. Paleolimnol. 16, 205–215.

Mallorquí, N., Arellano, J.B., Borrego, C.M., Garcia-Gil, L.J., 2005. Signature pigments of green sulfur bacteria in lower Pleistocene deposits from the Banyoles lacustrine area (Spain). J. Paleolimnol. 34, 271–280.

McGowan, S., Juhler, R.K., Anderson, N.J., 2008. Autotrophic response to lake age, conductivity and temperature in two West Greenland lakes. J. Paleolimnol. 39, 301–317.

McIntosh, H.J., 1983. A paleolimnological investigation of the bacterial carotenoids of Sunfish Lake. M.Sc. Thesis, Queen's Univ., Kingston, 129 pp.

Morgan-Kiss, R.M., Priscu, J.C., Pocock, T., Gudynaite-Savitch, L., Huner, N.P.A., 2006. Adaptation and acclimation of photosynthetic microorganisms to permanently cold environments. Microbiol. Mol. Biol. Rev. 70, 222–252.

Mueller, D.R., Van Hove, P., Antoniades, D., Jeffries, M.O., Vincent, W.F. High Arctic lakes as sentinel ecosystems: cascading regime shifts in climate, ice cover and mixing. Limnol. Oceanogr., in press.

Overmann, J., 2008. Ecology of phototrophic sulfur bacteria. In: Hell, R., Dahl, C., Knaff, D., Leustek, T. (Eds.), Sulfur Metabolism in Phototrophic Organisms. Springer, Berlin, pp. 375–396.

Pfennig, N., 1989. Ecology of phototrophic purple and green sulphur bacteria. In: Schlegel, H.G., Bowien, B. (Eds.), Autotrophic Bacteria. Springer-Verlag, Berlin, pp. 97–116.

Pienitz, R., Doran, P.T., Lamoureux, S.L., 2008. Origin and geomorphology of polar lakes. In: Vincent, W.F., Laybourn-Parry, J. (Eds.), Polar Lakes and Rivers – Limnology of Arctic and Antarctic Aquatic Ecosystems. Oxford University Press, Oxford, pp. 25–41.

Pouliot, J., Galand, P.E., Lovejoy, C., Vincent, W.F., 2009. Vertical structure of archaeal communities and the distribution of ammonia monooxygenase A gene variants in two meromictic High Arctic lakes. Environ. Microbiol. 11, 687–699.

Repeta, D.J., 1993. A high resolution historical record of Holocene anoxygenic primary production in the Black Sea. Geochim. Cosmochim. Acta 57, 4337–4342.

Rouse, W.R., Douglas, M.S.V., Hecky, R.E., Hershey, A.E., Kling, G.W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B.J., Roulet, N.T., Smol, J.P., 1997. Effects of climate change on the fresh waters of Arctic and sub-Arctic North America. Hydrol. Process. 11, 873–902.

Schlüter, L., Møhlenberg, F., Havskum, H., Larsen, S., 2000. The use of phytoplankton pigments for identifying and quantifying phytoplankton groups in coastal areas: testing the influence of light and nutrients on pigment/chlorophyll a ratios. Mar. Ecol. Prog. Ser. 192, 49–63.

Schlüter, L., Lauridsen, T.L., Krogh, G., Jørgensen, T., 2006. Identification and quantification of phytoplankton groups in lakes using new pigment ratios – a comparison between pigment analysis by HPLC and microscopy. Freshwater Biol. 51, 1474–1485.

Schmidt, R., Wunsam, S., Brosch, U., Fott, J., Lami, A., Löffler, H., Marchetto, A., Müller, H.W., Pražáková, M., Schwaighofer, B., 1998. Late and post-glacial history of meromictic Längsee (Austria), in respect to climate change and anthropogenic impact. Aquat. Sci. 60, 56–88.

Sorokin, Y.I., 1999. Aquatic Microbial Ecology. Backhuys Publishers, Leiden.

Squier, A.H., Hodgson, D.A., Keely, B.J., 2005. Evidence of late Quaternary environmental change in a continental east Antarctic lake from lacustrine sedimentary pigment distributions. Antarct. Sci. 17, 361–376.

Tani, Y., Matsumoto, G.I., Somaa, M., Somaa, Y., Hashimotoa, S., Kawaic, T., 2009. Photosynthetic pigments in sediment core HDP-04 from Lake Hovsgol, Mongolia, and their implication for changes in algal productivity and lake environment for the last 1 Ma. Quatern. Int. doi:10.1016/j.quaint.2009.02.007.

Tominaga, H., Fukui, F., 1981. Saline lakes at Syowa Oasis, Antarctica. Hydrobiologia 82, 375–389.

Tomkins, J.D., Lamoureux, S.F., Antoniades, D., Vincent, W.F., 2009. Sedimentology of perennial ice-covered, meromictic Lake A, Ellesmere Island, at the northern extreme of Canada. Can. J. Earth Sci. 46, 83–100.

Turner, J., Overland, J.E., Walsh, J.E., 2007. An Arctic and Antarctic perspective on recent climate change. Int. J. Climatol. 27, 277–293.

van Gemerden, H., Mas, J., 1995. Ecology of phototrophic sulfur bacteria. In: Blankenship, R.E., Madigan, M.T., Bauer, C.E. (Eds.), Anoxygenic photosynthetic bacteria. Kluwer Academic Press, Dordrecht, pp. 49–85.

Van Hove, P., 2005. Limnologie du Nord d'île d'Ellesmere: Réponses et Sensibilité aux Changements de Climat dans les Environnements Extrêmes, Ph.D. Thesis, Université Laval, Québec, 119 pp.

Van Hove, P., Swadling, K.M., Gibson, J.A.E., Belzile, C., Vincent, W.F., 2001. Farthest north lake and fjord populations of calanoid copepods *Limnocalanus macrurus* and *Drepanopus bungei* in the Canadian high Arctic. Polar Biol. 24, 303–307.

Van Hove, P., Belzile, C., Gibson, J.A.E., Vincent, W.F., 2006. Coupled landscape-lake evolution in High Arctic Canada. Can. J. Earth Sci. 43, 533–546.

Van Hove, P., Vincent, W.F., Galand, P.E., Wilmotte, A., 2008. Abundance and diversity of picocyanobacteria in High Arctic lakes and fjords. Algological Studies 126, 209–227.

Veldhuis, M.J.W., Kraay, G.W., 1990. Vertical distribution and pigment composition of a picoplanktonic prochlorophyte in the subtropical North Atlantic: a combined study of HPLC analysis of pigments and flow cytometry. Mar. Ecol. Prog. Ser. 68, 121–127.

Verleyen, E., Hodgson, D.A., Sabbe, K., Vyverman, W., 2005. Late Holocene changes in ultraviolet radiation penetration recorded in an East Antarctic lake. J. Paleolimnol. 34, 191–202.

Villanueva, J., Grimalt, J.O., Dewit, R., Keely, B.J., Maxwell, J.R., 1994. Sources and transformations of chlorophylls and carotenoids in a monomictic sulphate-rich karstic lake environment. Org. Geochem. 22, 739–757.

Vincent, W.F., 1981. Production strategies in Antarctic inland waters: phytoplankton eco-physiology in a permanently ice-covered lake. Ecology 62, 1215–1224.

Vincent, W.F., Laybourn-Parry, J., 2008. Polar Lakes and Rivers – Limnology of Arctic and Antarctic Aquatic Ecosystems. Oxford University Press, Oxford.

Vincent, W.F., Hobbie, J.E., Laybourn-Parry, J., 2008a. Introduction to the limnology of high latitude lake and river ecosystems. In: Vincent, W.F., Laybourn-Parry, J. (Eds.), Polar Lakes and Rivers – Limnology of Arctic and Antarctic Aquatic Ecosystems. Oxford University Press, Oxford, pp. 1–23.

Vincent, A.C., Mueller, D.R., Vincent, W.F., 2008b. Simulated heat storage in a perennially ice-covered high Arctic lake: sensitivity to climate change. J. Geophys. Res. 113, C04036. doi:10.1029/2007JC004360.

Wharton Jr., R.A., McKay, C.P., Clow, F.D., Andersen, D.T., 1993. Perennial ice covers and their influence on Antarctic lake ecosystems. In: Physical and Biogeochemical Processes in Antarctic Lakes. American Geophysical Union, Washington, DC, Antarctic Research Series 59, pp. 53-70.

Zapata, M., Rodriguez, F., Garrido, J.L., 2000. Separation of chlorophylls and carotenoids from marine phytoplankton: A new HPLC method using a reversed phase C8 column and pyridine containing mobile phases. Mar. Ecol. Prog. Ser. 195, 29–45.