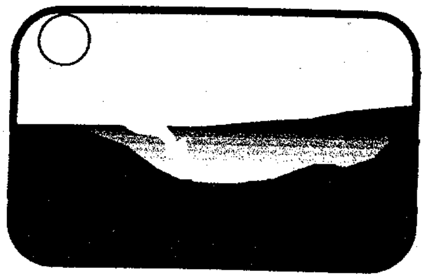

Sensitivity of High-latitude Freshwater Ecosystems to Global Change: Temperature and Solar Ultraviolet Radiation

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SUMMARY

Freshwater ecosystems are a major component of the northern environment. The application of new limnological technologies and approaches to these ecosystems is producing a revised perspective on their structure and dynamics, and is leading to insights into their potential response to global change processes. The planktonic communities of northern lakes are dominated by microbial food webs, with components that are highly sensitive to changes in temperature. North-south transects in Quebec, Yukon and the Northwest Territories show that lakes beyond the northern tree line have concentrations of UV-screening dissolved organic carbon less than 5 mg·l^{-1}, rendering them vulnerable to changes in incident UVB and to climatic effects on catchment hydrology. The coupling of studies on the modern-day limnology of northern freshwater ecosystems with paleolimnological approaches will allow the interpretation of short-term changes in these systems within the context of their historical variability.

RÉSUMÉ

Les écosystèmes d'eau douce sont une composante majeure du paysage nordique. L'application de nouvelles approches et technologies pour l'étude de ces écosystèmes est en voie de changer nos perspectives concernant leur structure, leur dynamique et leur réponse potentielle face aux changements globaux. Les communautés planctoniques des lacs nordiques sont dominées par le réseau alimentaire microbien dont les composantes sont très sensibles aux changements de température. Plusieurs recherches effectuées sur des lacs localisés le long de transects latitudinaux au Québec, au Yukon et dans les Territoires du Nord-Ouest, ont démontré que les lacs situés au-delà de la limite nord des arbres sont caractérisés par des concentrations en carbone organique dissous inférieur à 5 mg·l^{-1}. Ces lacs sont donc particulièrement vulnérables aux changements du rayonnement ultraviolet et aux effets des variations climatiques sur l'hydrologie de leurs bassins versants. La combinaison des études portant sur la limnologie actuelle et la paléolimnologie permettra l'interprétation des changements à court terme de ces écosystèmes dans le contexte de leur variabilité historique.

INTRODUCTION

Lakes, rivers and wetlands are major elements of the northern landscape, providing essential habitats for migratory wildlife (*e.g.*, snow geese and other water fowl) as well as resident species (*e.g.*, northern pike). Their limnological characteristics, however, remain poorly understood. Two high arctic lakes on Cornwallis Island were a focus of the International Biological Program in the 1970s (Rigler, 1978) and limnological research at these sites generated much information about their physical, chemical, as well as biological properties. Since that time there have been substantial advances in limnological theory and technology which have led to a revised understanding of many aspects of freshwater ecosystems at all latitudes, for example in lake mixing processes (Spigel and Imberger, 1987), bio-optics and underwater light regimes (Laurion *et al.*, 1997), aquatic food web structure and dynamics (Sherr and Sherr, 1991), the importance of organic chemicals in the aquatic environment (Wetzel, 1995) and the interactions between landscape and freshwater ecosystem processes. These new concepts and approaches have only recently been applied to lakes and streams in high northern latitudes. A much greater diversity of lakes has been discovered than was previously imagined, including permanently stratified (meromictic) lakes (*e.g.*, Ouellet *et al.*, 1989), and important new information has become available about seasonal waterbodies such as tundra ponds and thermokarst lakes (*e.g.*, Douglas *et al.*, 1994; Vézina and Vincent, 1996). The interactions and flow of materials and energy through tundra drainage basins has begun to receive increased attention (Kling *et al.*, 1991). The last 25 years have also seen significant advances in paleolimnology with new, quantitative approaches toward reconstructing the history of lakes and their catchments (Smol, 1990).

In this paper we briefly review the chemical, physical and biological characteristics of high-latitude freshwater ecosystems with emphasis on the eastern Canadian Arctic (northern Quebec and Nunavut) and the potential sensitivity of these systems to two aspects of global change, temperature and ultraviolet B radiation (UVB). We present new findings that link these effects and which show that freshwater ecosystems in the tundra zone may be more responsive to global change than those located within forested catchments further to the south.

GLOBAL CHANGE AT NORTHERN LATITUDES

During the past century, the Earth's climate has warmed 0.3°C to 0.6°C and atmospheric CO_2 concentration has increased by 25%, to more than 350 ppmv (McBean, 1994; IPCC, 1995). Anthropogenic impacts such as acid haze (see Wadleigh, 1996), acid snow, and other pollutants continue to affect Arctic regions, and the effects of global changes in climate are expected to be amplified in high-latitude regions (Luckman, 1989; Houghton *et al.*, 1990). For example, the CO_2-doubling scenarios of Manabe and Wetherald (1986) show summertime temperature increases of 7°C and soil moisture decreases of 50% for the subarctic area bordering on the west coast of Hudson Bay, while changes in these variables are likely to be much lower in the mid-latitude regions. The Hudson Bay prediction represents the most extreme change in all of North America (Bello and Smith, 1990). Long-term data sets, however, show that there are major regional differences in the current pattern of temperature change in the Arctic, with warming trends in western and central Canada, Alaska and Siberia, but pronounced cooling trends in the eastern Canadian Arctic and Greenland (Chapman and Walsh, 1993). At Iqaluit, for example, the number of freezing-degree days *per annum* between the late 1970s and the present increased from 3700 to 4900 (Allard *et al.*, 1995). Aquatic ecosystems in high-latitude regions, which have adapted to low natural energy flows, are expected to be particularly sensitive to a given change in the magnitude and timing of available energy, and to changes in physical and geochemical conditions, such as annual heat balance and nutrient loading. Evidence of these effects on diatom community structure may already be seen in arctic freshwater ponds and lakes (Douglas *et al.*, 1994).

Fauna and flora respond to environmental change through a complex combination of direct and indirect (including feedback) effects. A good knowledge of their modern ecology coupled with quantitative analysis allows reconstruction of the paleoenvironment (*e.g.*, lakewater temperature, acidity, salinity) from biological proxy data. Paleolimnology is the science that uses the physical, chemical and biological information contained in lake sediments to infer past environmental conditions. This window on the past plays a key role by extending the baseline of environmental observations, thereby establishing the envelope of natural variability and the potential for future change. These data may help determine how arctic freshwater ecosystems operated under boundary conditions substantially different from today (*e.g.*, at different atmospheric trace gas concentrations, insolation), and how accurately lake ecosystem processes can be simulated by models.

The observed increase in ultraviolet-B radiation (UVB) in high-latitude regions of both hemispheres has raised further concern about the response of northern freshwaters to global change. Solar UVB accounts for less than 1% of the total radiation reaching the surface of the Earth but it contains the most energetic wavelengths. This waveband is known to have a broad range of effects on aquatic ecosystems including the photoproduction of toxic compounds, mutagenesis and physiological stress (Vincent and Roy, 1993). In the subarctic region, spring time levels of UVB radiation reaching the surface of the Earth increased by 10-20% between the late 1970s and 1995 (International Arctic Science Committee, 1995).

CHEMICAL ENVIRONMENT

The transfer of materials from land to water strongly regulates the functioning of lake and river ecosystems (*e.g.*, Kling, 1995). These inputs include water, nutrients and organic matter which form the building blocks of aquatic food webs. Most northern lakes are highly transparent, oligotrophic (nutrient-poor) systems in which the productivity at the base of the food web is limited by nutrient supply. Bioassay experiments in lakes of northern Quebec (Smith *et al.*, 1984) and the high Arctic (Kalff and Welch, 1974) indicate a primary limitation by phosphorus availability, although inorganic nitrogen is also typically in short supply and may prevent a substantial phytoplankton response to P-only enrichment (Smith *et al.*, 1984). Recent experiments with microcosms (experimental enclosures) in Lac à l'Eau Claire, a large lake in the forest–tundra transition zone of subarctic Quebec, have shown that phosphorus enrichment causes a change not only in phytoplankton biomass but also in the relative abundance of different small-celled organisms within the microbial food web such as picocyanobacteria, heterotrophic bacteria and protozoa (Bergeron and Vincent, in press). The microbial community structure was modified by the presence of ultraviolet radiation, implying that there are likely to be interactions between the effects of rising UVB and nutrient enrichment.

The nutrient status of northern freshwater ecosystems is intimately linked to catchment processes, and changes in climate that affect the water table, soil moisture, mineralization and/or run-off processes will, in turn, influence the aquatic community structure and productivity (*e.g.*, Oechel and Vourlitis, 1994). There is evidence from the Canadian boreal forest that decreased precipitation has resulted in prolonged hydraulic residence times in the lakes of that region, leading to increased total phosphorus concentration and increased primary production (Schindler *et al.*, 1996). The productivity of northern lakes is likely to be similarly responsive to changes in precipitation, water balance and flushing rates.

There is a pronounced north-south trend in the organic carbon content of northern lakes. These materials occur primarily in the form of dissolved compounds (dissolved organic carbon, DOC) which are brought in by streams from the surrounding wetlands and catchment. A recent transect analysis in northern Quebec shows that DOC concentrations drop from 10-20 mg $C \cdot l^{-1}$ in the boreal forest lakes to less than 5 mg $C \cdot l^{-1}$ in tundra lakes (Fig. 1). Pienitz *et al.* (1996a, b) have found similar trends in two northern transects in the central and western part of the Canadian subarctic The greatest relative variability in DOC concentration occurs at the tree line where there are large differences in vegetation, even between adjacent catchments (fourfold variation in DOC values at 0 km in Fig. 1). Similarly, in another set of lakes from the forest–tundra transition zone in northern Quebec, Laurion *et al.* (1997) found lake DOC values ranging from 2

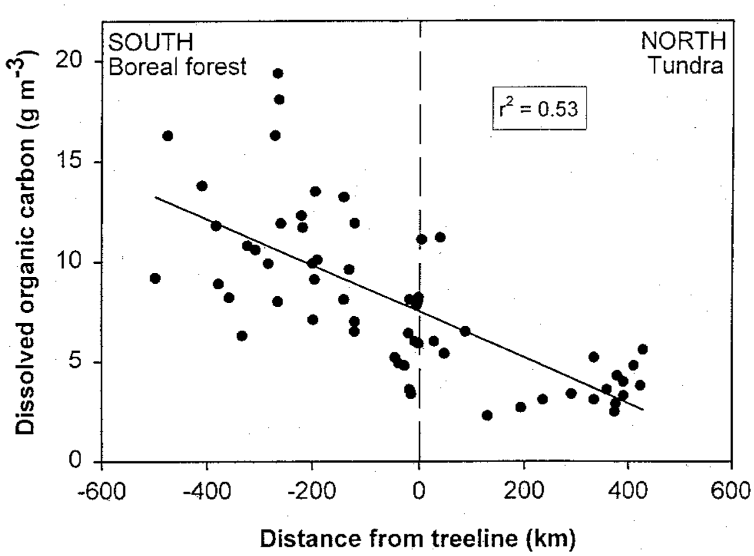

Figure 1 *DOC concentrations (July 1995) in 60 northern Quebec lakes in relation to distance from northern tree line (defined as 80% tree cover in catchment). The samples were taken by helicopter from the surface waters of each lake and then filtered through 0.45μm Sartorius membranes. The samples were stored in the dark at 4°C until subsequent analysis with a Beckman Carbon Analyzer.*

mg C·l⁻¹ to 11 mg C·l⁻¹.

A strong link between aquatic and terrestrial ecosystems was demonstrated by Pienitz and Smol (1993) in a calibration data set derived from surficial sediments of lakes from three vegetation zones (boreal forest, forest–tundra, and arctic tundra). The results showed that lakewater DOC concentrations (a function of external humus loading from catchment vegetation and soils; see Wetzel, 1983; Engstrom, 1987; and Kling, 1995) accounted for significant proportions of the variation in the distribution of the diatoms. Transfer functions were developed relating diatom distributions to measured DOC concentrations and water transparency. Diatom-based reconstructions of DOC in dated sediment cores may therefore provide information on vegetational change (such as tree line shifts) in response to long term climate variations (Pienitz, 1993; MacDonald *et al.*, 1993).

PHYSICAL ENVIRONMENT

Low temperatures and prolonged ice cover characterize lakes of the high Arctic and exert a controlling influence on habitat, biological productivity, and community structure. For example, Smol (1988) demonstrated that the extent of snow and ice cover on a lake may strongly affect the distribution of algae and invertebrates. Pienitz *et al.* (1995), studying modern diatom assemblages from 59 lakes along a transect that spanned boreal forest, forest–tundra and arctic tundra conditions in northwestern Canada, found that summer surface water temperature (independent of lake-water chemistry) was the main predictor of the species distribution of diatoms. This finding led them to conclude that fossil diatom data could be used to reconstruct relative temperature changes. It should be noted, however, that such reconstructions would be related to water rather than air temperature. Although these two variables are closely related, the timing and extent of stratification (which is dependent on timing of ice break-up), atmospheric circulation, and lake depth, also affect water temperature and must be considered in any extrapolation to air temperature.

Another important physical influence on northern lakes is the effect of low water temperature on stratification and mixing properties. At temperatures less than 4°C the water column does not stratify, and convective circulation extends to the bottom of the lake, even during late summer. At temperatures in the range 4-10°C, lakes stratify only weakly because the change in density per degree Celsius is small. For this reason, northern lakes may stratify only intermittently or not at all during summer. For example, in Lac à l'Eau Claire in northern Quebec, Milot-Roy (1994) found that the western basin was polymictic, the shallow side-arms were dimictic, while the deep (178 m) eastern basin remained unstratified and freely circulating throughout summer. These differences are important because they affect the availability of light for phytoplankton photosynthesis, and are likely to vary with changes in duration of ice cover and other climatic variables.

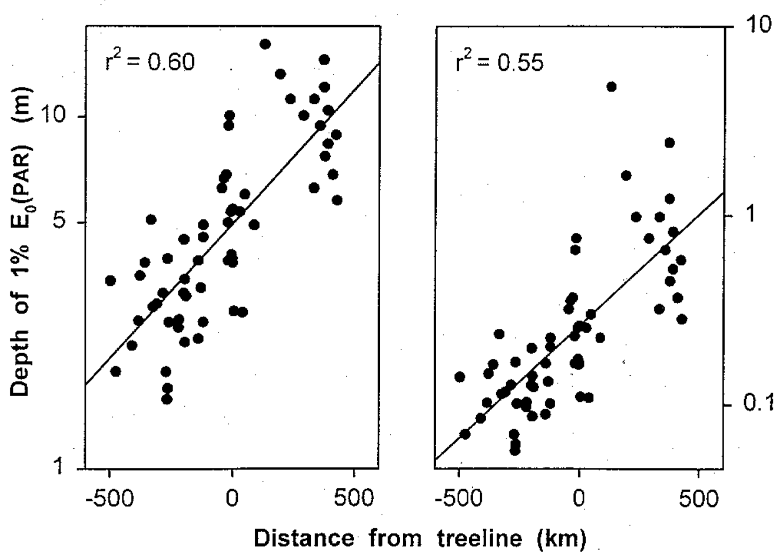

Figure 2 *The depth at which PAR (400-700 nm) or UV radiation at 320 nm is reduced to 1% of surface values (E_0) in relation to the distance from northern tree line. These values have been calculated from the DOC data in Figure 1 using the regression models of Laurion* et al. *(1997) which are based on estimates of downwelling irradiance for PAR and 320 nm ($E_d(320)$) using a Biospherical PUV-500 profiler.*

There is increasing evidence that the DOC content of lakes in the temperate zone influences many of their physical properties, and that such effects also operate at northern latitudes. DOC appears to control the underwater availability of light for photosynthesis in two ways, directly *via* the attenuation of photosynthetically available radiation (PAR) and indirectly by influencing the heating and mixing regime of the surface layer. In boreal forest lakes, DOC (and not phytoplankton) has been identified as the main variable responsible for differences in the underwater PAR attenuation (Schindler *et al.*, 1990, 1996). In a south-north transect of lakes from the boreal forest to the Arctic tundra, Pienitz *et al.* (1997a,b) found a strong inverse correlation between Secchi disk transparency and DOC. Similarly, 78% of the optical (PAR) variability between lakes in the forest–tundra region of northern Quebec could be attributed to variations in DOC concentration (Laurion *et al.*, 1997). Application of a regression model from this latter study to the northern Quebec DOC transect given in Figure 1 shows that the depth of the 1% PAR (typically used as a measure of the depth limit of the euphotic zone; Wetzel, 1983) becomes greater with distance northwards, and that this relationship is logarithmic (Fig. 2).

PAR accounts for about 45% of the total solar energy reaching the Earth's surface and absorption of this radiation by DOC can thus cause heating of surface waters (Fee *et al.*, 1996; Wetzel, 1983). This trapping of solar energy in the upper surface layer of northern lakes in turn gives rise to buoyancy fluxes (changes in density gradients) that cause temporary stratification. This so-called diurnal stratification can lead to phytoplankton communities being trapped in the brightly lit surface layer of lakes (Milot-Roy and Vincent, 1994). It may also result in the near-surface accumulation of potentially toxic photo-products that are generated by UV interactions with DOC (Scully and Vincent, 1996).

DOC also plays a pre-eminent role in controlling the underwater penetration of solar UV radiation, and recently it has been suggested that changes in lakewater DOC (through climate change or acidification) may have a greater impact on the UV-damage of aquatic biota than stratospheric ozone depletion (Schindler *et al.*, 1996; Williamson *et al.*, 1996; Yan *et al.*, 1996). The dissolved humic and fulvic acid fractions of natural DOC absorb strongly across the UV waveband, with increasing absorbance towards the shorter, most damaging wavelengths (Vincent and Roy, 1993; Scully and Lean, 1994). DOC thus acts as a natural sunscreen in lakes, protecting aquatic biota from the biologically most reactive components of UV radiation. DOC characteristics such as absorbance and fluorescence have proved to be an accurate guide to the underwater spectral composition of UV radiation in high arctic as well as subarctic lakes (Laurion *et al.*, 1997). This spectral balance is important because the short UVB wavelengths have a broad range of direct and indirect damaging effects on aquatic biota (Vincent and Roy, 1993) while the longer wavelength UVA and PAR wavebands have been implicated in natural repair mechanisms as well as damage (Quesada *et al.*, 1995). Applying the Laurion et al. (1997) model to the DOC data from the northern Quebec transect (Fig. 1) it is evident that, as for PAR, the 1% UVR level (320 nm) becomes logarithmically deeper towards the north (Fig. 2); *i.e.*, there is a sharp, non-linear rise in the transparency of lakes to UVR with increasing latitude. This suggests that northern lakes may be poorly protected against the rising UVB associated with stratospheric ozone depletion.

Laurion *et al.* (1997) have recently shown that the water column ratio of UVR to PAR, which may control the balance between biological damage and repair, is relatively stable across the DOC range 4-11 mg $C \cdot l^{-1}$, but rises precipitously with decreasing DOC below this range. Application of their water column model to the northern transect data in Figure 1 reveals a marked increase in this ratio for lakes located north of the treeline (Fig. 3). These results imply that the lakes of Nunavut may be highly sensitive to small changes in DOC, to a greater extent than lakes of the boreal forest.

The influence of climate change on DOC underscores the need to consider the interactive effects of UVB and variations in global temperature. An additional interaction is the impact of temperature on UV toxicity. For example, the sensitivity of high-latitude cyanobacteria to UV damage has been found to increase markedly at low temperatures (Roos and Vincent, unpubl.).

The potential for inferring past DOC levels from paleolimnological records (Pienitz and Smol, 1993) combined with the recent advances in bio-optical modelling in northern lakes (Laurion *et al.*, 1997) leads to the exciting prospect of reconstructing past underwater light regimes. Such analyses could include estimates of euphotic depth as well as spectral attenuation across the ultraviolet waveband. This new theme in paleolimnology, "lake paleo-optics," offers opportunities for integrating studies of the present day with historical properties of lakes. New techniques for measuring DOC concentrations and chlorophyll *a* from space (*e.g.*, Landsat colour imagery; lidar analysis of DOC fluorescence, Nieke *et al.*, 1997a; in press) are opening the way for estimating underwater spectral irradiance by remote sensing. This approach is of special interest for lakes in remote high-latitude regions.

MICROBIAL FOOD WEBS

Recent biological research on northern lake ecosystems has drawn attention to the role of minute organisms at the base of their aquatic food webs. These microbial communities include photosynthetic species, notably picocyanobacteria which are similar in size (*ca.*, 700 nm in diameter) to the wavelengths of light that they capture. Picocyanobacteria have been quantified in lakes of Yukon (Stockner and Shortreed, 1991), subarctic Quebec (Bergeron, 1996), Ellesmere Island (Vincent *et al.*, unpubl.) and Bylot Island (Vézina and Vincent, 1996). These minute cells typically dominate the phytoplankton community in terms of numerical abundance. They may also be important in terms of total phytoplankton biomass; for example, in samples from northern Quebec lakes, the median contribution of cells less than 2μm to total chlorophyll *a* was 43%, with half of all estimates in the range of 37% to 53% (Bergeron, 1996).

Small-celled heterotrophic organisms are also abundant in northern lakes and may be strongly dependent on DOC materials arriving from the catchment as well as organic carbon substrates that are generated by phytoplankton and benthic algae within the lakes. In northern Quebec lakes, Bergeron (1996) found that the biomass of heterotrophic bacteria often matched and sometimes exceeded the total phytoplankton community biomass. A large population of protozoa, including potentially mixotrophic species (organisms which can feed on particles as well as photosynthesize), such as *Ochromonas*, *Dinobryon* and other chrysophytes, were also recorded in these lakes (Bergeron, 1996) and are likely to be important intermediates in the transfer of energy and carbon from the picocyanobacteria and heterotrophic bacteria to larger zooplankton. A biologically diverse community of protozoa has also been discovered in high arctic lakes, including the original IBP sites, Char Lake, and Meretta Lake (Vincent *et al.*, unpubl.).

The morphological remains of chrysophytes, common in subarctic as well as arctic lakes and ponds (Smol, 1988, Bergeron, 1996), and certain protozoan groups provide a variety of paleolimno-

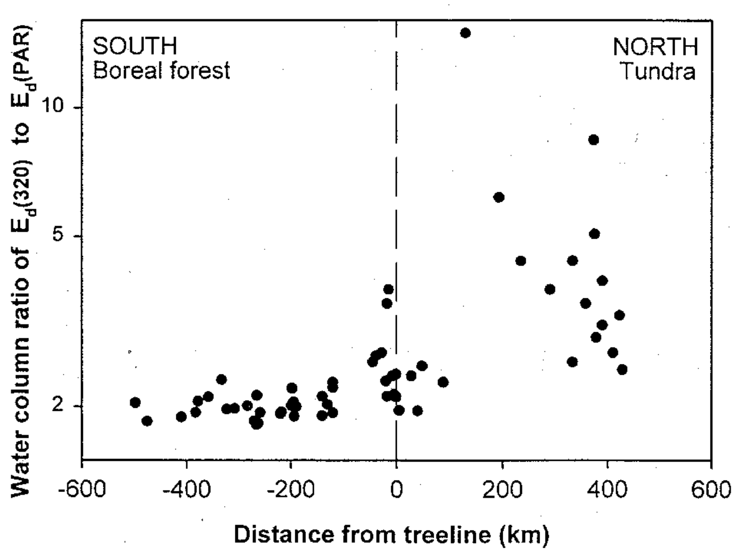

Figure 3 *Underwater spectral balance as a function of distance from northern tree line. The values for the water column ratio of ultraviolet radiation (as indexed by UVR at 320 nm, $E_d(320)$) to photosynthetically active radiation ($E_d(PAR)$) have been multiplied by 10^4 and were calculated from the DOC data in Figure 1 using the RI (ratio of integrals) model of Laurion* et al. *(1997).*

logical markers to hindcast changes in microbial food webs. The chrysophytes produce siliceous resting cysts or statospores which are generally well preserved in sedimentary and periphytic environments (*e.g.*, Duff *et al.*, 1992; Wilkinson *et al.*, in press). Such analyses can be coupled with indices that are part of the traditional aquatic food web such as diatoms and other algal groups (*e.g.*, Chlorophyta, cyanobacteria). The chitinous parts of zooplankton (*e.g.*, exuviae of Cladocera) and aquatic insects (*e.g.*, head capsules of chironomids) are also remarkably well preserved in high-latitude freshwater sediment records, and their analysis should also be included in paleolimnological studies.

Recent studies have begun to draw attention to the importance of bottom-dwelling communities in the overall ecology of northern lakes. A diverse assemblage of diatoms, green algae, and cyanobacteria occurs over the rocks in the littoral zone of subarctic lakes, with cyanobacteria and diatoms forming a sublittoral community beneath the surface of translucent sands (Maltais, 1994). At higher latitudes, mat-forming cyanobacteria are an especially important component. For example, in the abundant lakes and ponds on Bylot Island, filamentous cyanobacteria of the family Oscillatoriaceae produce benthic mats 5 mm to 50 mm thick, with chlorophyll *a* concentrations up to 35 $\mu g\ cm^{-2}$ (Vézina and Vincent, in press). These biomass-rich communities strongly resemble the benthic mats found in lakes and streams throughout the south polar region (Vincent and Quesada, 1993, 1996), and they are a major source of organic carbon for benthic invertebrates, as well as for planktonic heterotrophs in the overlying water column. Some of the mats contain nitrogen-fixing cyanobacteria, particularly *Nostoc commune*, which is a species known to be important for the overall nitrogen economy of the tundra (Henry and Svoboda, 1986; Chapin *et al.*, 1991).

The dominance of benthic as well as the planktonic communities of northern lakes by cyanobacteria is of special interest relative to the question of climate warming or cooling trends. This group of micro-organisms is often found in warm-water environments, and analyses of isolates from northern latitudes confirm that these species are currently living at temperatures well below their optima for growth (Tang *et al.*, 1997). With these organisms dominating the base of their food webs, northern ecosystems are likely to be highly responsive to changes in the ambient temperature regime.

CONCLUSIONS

We are within a period of rapid increase in our understanding of northern lake ecosystems. In part this derives from the availability of new measurement technologies, such as automated profilers, remote sensing systems, light and electron microscopy, molecular assays and analytical instrumentation. It is also the result of major conceptual advances in limnological knowledge.

The application of these new perspectives and technologies to northern lakes is providing insights into how these ecosystems respond to present and future climate change. These approaches can be strengthened by complementary paleolimnological studies based on the microscopic fossils contained in northern lake sediments. Such studies provide a window into the past and are beginning to show how these ecosystems have previously responded to variations in climate. This combination of approaches (*e.g.*, lake paleo-optics with modern day bio-optics) will allow the interpretation of short-term responses of northern freshwater ecosystems to global change within the context of their historical variability.

ACKNOWLEDGEMENTS

This work was supported financially by the Natural Sciences and Engineering Research Council of Canada and the Department of Indian and Northern Affairs. Logistic support was provided by Centre d'études nordiques and the Polar Continental Shelf Project (this is publication number PCSP/ÉPCP/27). We thank Nancie Allaire, Marie-Andrée Fallu and Patrick Tremblay for help with the field work, Dr. David Lean for facilitating water chemistry analyses at the National Water Research Institute (Burlington, Ontario), and John Cullen, Isabelle Laurion and Moire Wadleigh for helpful review comments on this manuscript.

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Accepted as revised 25 November 1996.