Polar Biol (1997) 17: 523–534

ORIGINAL PAPER

Sophie Vézina · Warwick F. Vincent

Arctic cyanobacteria and limnological properties of their environment: Bylot Island, Northwest Territories, Canada (73°N, 80°W)

Received: 3 June 19961 Accepted: 3 November 1996

Abstract Cyanobacteria were a major constituent of phototrophic communities in the lakes, ponds and streams of Bylot Island, in the Canadian high Arctic. The waters spanned a range of temperatures (1.8-16.8°C in late July), pH regimes (6.2-9.2) and conductivities (1.5-1700 μS cm^{-1}) but nutrient concentrations were consistently low (< 1 μg dissolved reactive Pl^{-1} at all sites; < 10 μg $N0_3$-N l^{-1} at most sites). Picoplanktonic species *(Synechococcus* spp.) were often the numerical dominants in the plankton, and periphytic filamentous species (Oscillatoriaceae) commonly formed thick (5-50 mm) benthic mats. Bloom-forming species of cyanobacteria were either absent or poorly represented even in Chla-rich ponds. The total community biomass ranged from 0.1 to 29.8 μg Chla l^{-1} in the plankton and from 1.1 to 34.8 μg Chla cm^{-2} in the benthos. The in vivo absorbance characteristics of isolates from these environments indicated a genetically diverse range of species in each group of Arctic cyanobacteria. Growth versus irradiance relationships were determined for each of the isolates and similarly revealed large genetic differences (maximum growth rates from 0.17 to 0.61 day^{-1}), even between morphologically identical taxa. A comparison of nutrients, pigment concentrations and species composition underscores the strong similarities between freshwater ecosystems in the north and south polar zones.

Introduction

Cyanobacteria are known to colonize a remarkably wide thermal range of habitats, from hot desert soils, geothermal pools and tropical rain forests to polar tundra environments, ice shelves and glacier surfaces (Fay 1983). They are a ubiquitous component of freshwater ecosystems in the temperate zone where they often form extensive mats and films that cover the bottom substrata, or within the water column as picoplankton or large bloom-forming species. In Antarctica, cyanobacteria often dominate the total ecosystem biomass and productivity of lakes, ponds and streams (Vincent 1988; Wynn-Williams 1990). These cold-water environments are characterized by extreme variations in energy supply, from continuous darkness in winter to the short growing season of continuous light during summer.

Although cyanobacteria are known to be important constituents of aquatic ecosystems in Antarctica, there are few reports of their presence in equivalent habitats of the north polar zone. This may suggest that the two poles fundamentally differ in their physical and chemical environments, or that there are biogeographical differences in species composition. Observations earlier this century strongly implied that there were such differences. McLean (1918) concluded that there was a predominance of cyanobacteria in the Antarctic benthic and soil ecosystems relative to the Arctic. Work during the Canadian IBP program drew attention to the apparently low proportional abundance of cyanobacteria in the plankton of Arctic lakes (Kalff et al. 1975).

More recent studies have begun to mention cyanobacteria as noteworthy constituents of the Arctic aquatic environment (e.g., Chapin et al. 1991; Sheath and Cole 1992) and the apparently sparse distribution of cyanobacteria may simply reflect the relative lack of research in microbial ecology in this region. Arctic freshwater studies have included investigations of the total periphyton (Stanley 1976; Moore 1979; Sheath and Cole 1992), benthic diatoms (Hickman 1974; Douglas and Smol 1993a,b), nano- and microplankton (Kalff and Welch 1974; Welch et al. 1989), filamentous chlorophytes (Hamilton and Edlund 1994), rotifers (Nogrady and Smol 1989) and eutrophication effects (Schindler et al. 1974). Croasdale (1973) noted that 10 of the 13 cyanobacterial species that she described from Ellesmere

S. Vézina · W.F. Vincent (✉)
Dépt de biologie et Centre d'études nordiques, Université Laval, Sainte-Foy, Québec G1K 7P4, Canada
fax: 1-418-656-2043; e-mail: warwick.vincent@bio.ulaval.ca

Island had been previously reported from northern Greenland; she also drew attention to the sparseness of taxonomic data from these northernmost regions. Nitrogen fixation by cyanobacteria has been studied in the Arctic (Henry and Svoboda 1986; Alexander et al. 1989); however, the distribution and abundance of cyanobacterial species have been little considered.

The present study was undertaken as a part of a broader program to examine the ecophysiology of highlatitude cyanobacteria. Our first objective was to measure the physical, chemical and biological properties of the abundant ponds and lakes on Bylot Island in the Canadian high Arctic. Secondly, we measured the distribution and abundance of cyanobacteria using methods that have been previously applied in Antarctica. Our final step in this project was to bring a range of Arctic cyanobacteria into culture to examine their genetic diversity and to compare their cellular characteristics with species from Antarctica. The relatively simple morphology of species in the two dominant groups (Chroococcaceae and Oscillatoriaceae) provides little information for distinguishing genetically distinct taxa; we therefore supplemented the microscopic analysis of cellular form and size with assays of cellular pigment composition (in vivo absorbance spectra) and analysis of the growth-irradiance relationship for each isolate.

Materials and methods

Study sites

The field study was undertaken from 23-28, July 1993 during the warm mid-summer period of maximum meltwater production.

Sampling and field measurements were conducted in freshwater lakes, ponds and streams located on the west side of Bylot Island (73°N, 80°W) (Fig. 1). Mean daily air temperatures over this period were within the range 1.5-8.5°C. Fifty-nine ponds and small lakes and two streams were sampled along a series of transects. The dimensions (length, width and depth) of each waterbody were noted, and then temperature, pH and conductivity were measured using a Corning multiple probe system.

Nutrient analysis

Ten ponds were selected at random for analysis of dissolved reactive nutrient concentrations. Water samples were collected in sampled-rinsed Nalgene bottles. Within 1-4 h of sampling, the water was filtered through Whatman (grade GF/F) glass fiber filters, transferred into 2-ml sample-washed cryovials, and stored in the dark at -20°C. All water analyses were subsequently carried out on an Alpkem model RFA-300 autoanalyzer system. Nitrate was measured by diazotization after cadmium reduction to nitrite, and was corrected for ambient nitrite (American Public Health Association 1976). Dissolved reactive phosphorus (DRP) was measured by the method of Whitledge et al. (1981), and silicate, after repolymerization at room temperature, was measured by the method of Truesdale and Smith (1975). The limits of detection were 2 µg DRP or $Si02\text{-}Si^{-1}$ and 1 µg $N03\text{-}N\ 1^{-1}$.

Pigment extraction

Subsurface samples for phytoplankton analysis were collected in Nalgene bottles, 1 m out from the margin of the ponds. The water samples were immediately filtered through Whatman (grade GF/F) glass fiber filters. The filters were kept frozen at -20°C for 8 weeks until extraction and analysis. Chlorophyll a (Chla) was subsequently extracted by placing the filters in boiling 95% ethanol for 5 min. Chla fluorescence was measured with a Shimadzu spectrofluorophotometer RF5000U before and after acidification, and the concentration of Chla of each sample was then estimated using the equation of Marker et al. (1980).

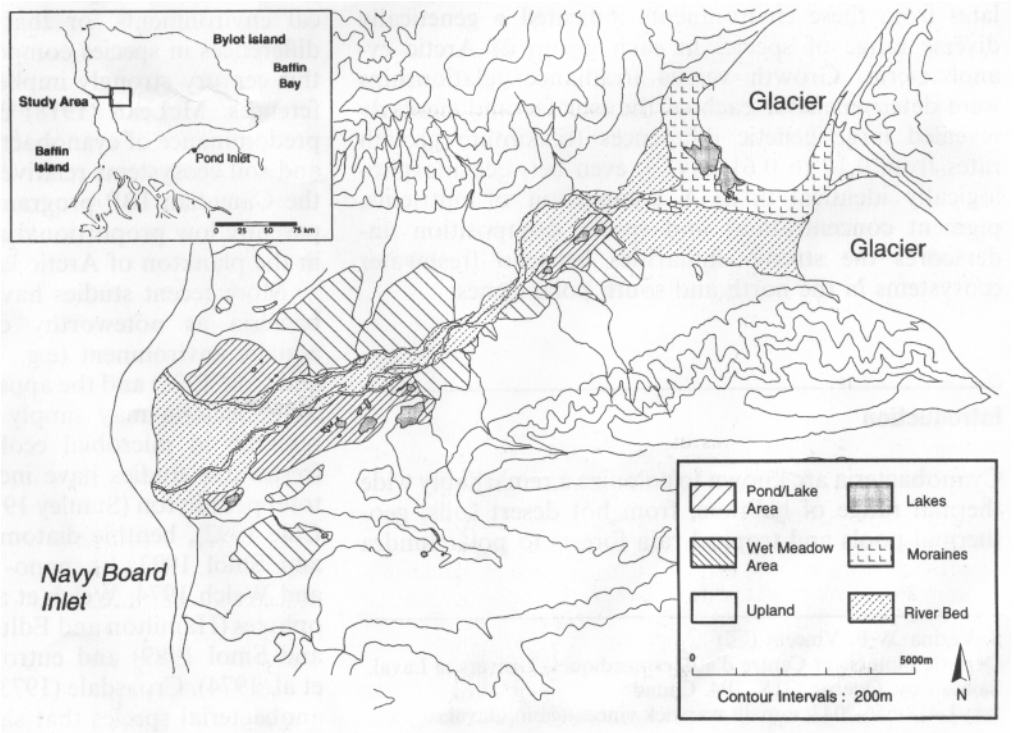

Fig. 1 Location map and geographic features of Bylot Island

Cores of 11 mm diameter were cut from representative sections of the benthic algal mats with a plastic tube. The cores were stored at -20°C for 8 weeks as for the planktonic samples. For the extraction of Chla and carotenoids, each sample was ground with a Teflon tissue grinder in 4-8 ml 90% acetone (10% water). The samples were left to extract at 4°C for 30 min. At the end of this period, the samples were shaken and cleared by centrifugation. A spectral scan of absorbance (190-820 nm) was then run for each of the extracts on a Hewlett Packard model HP-8452A diode array spectrophotometer before and after acidification (addition of three drops of 1 N HCl). The pigment concentrations were determined using the equations of Marker et al. (1980) for Chla, and Britton (1985) for carotenoids.

Taxonomic composition

Water samples of planktonic algae, as well as cores of benthic algal mats, were preserved with 10% (final concentration) glutaraldehyde/paraformaldehyde solution (Lovejoy et al. 1993). These were enumerated by the FNU method (Fluorescence, Nomarski, Utermôhl) (Lovejoy et al. 1993) for identification of the dominant species. Planktonic algae species in five ponds were identified and their relative abundance was estimated qualitatively (dominant, common, rare). For five ponds, an estimate was made of the abundance of species in the benthic mat communities. Random fields were enumerated to give a total count of 300 individuals or colonies in each sample.

Culture of cyanobacteria

Small quantities of additional planktonic and benthic samples were transferred to tubes containing liquid BG-11 culture medium (Rippka et al. 1979) or plates containing the same medium solidified with 2% agar. The communities were all incubated in dim light at ambient temperature in the field laboratory on Bylot Island until the return to our home laboratory. These cultures were then used to obtain unialgal cultures of the dominant species of cyanobacteria for further characterization and experiments.

Isolation was performed on agar plates with BG-11 medium. The plates were streaked with field material from the different types of environment. To prevent the growth of eukaryotic cells, cycloheximide was added to the medium (50 mg 1) as in Stein (1973). Regular microscopic examinations , of cultures were made with an Utermôhl inverse microscope using Nomarski and epi-fluorescence. All strains were maintained at the mean temperature measured in the field (13°C) and under a 24-h light cycle with cool-white fluorescent light at an intensity of 30 µmol photons $m^{-2}s^{-1}$ which we have found optimal for phycobiliprotein production. Light measurements were made with a Biospherical Instruments QSL-100 quantum scalar irradiance (47π) meter. Each strain was described according to taxonomic group, source, cell size, colour and phycobiliprotein composition.

In vivo characteristics

A sample of each strain was dispersed by agitation in a loose-fitting Teflon tissue grinder. The in vivo absorbance spectrum was then determined with a diode array spectrophotometer (Hewlett Packard model HP-8452A) fitted with an integrating sphere (Labsphere model RSA-HP-84). The diode array measurements from 190 to 820 nm, were obtained in 0.1 s, thereby eliminating the traditional problem associated with cell sedimentation during a spectral scan. The integrating sphere eliminated the effects of scattering and gave scans with well-defined peaks. The in vivo absorbance peaks were measured for Chla (430 and 680 nm), carotenoids (490 nm), phycocyanin (620 nm) and phycoerythrin (565 nm). Carotenoids and phycobiliproteins in vivo absorbance values were expressed per unit of Chla absorbance in order to compare the different species.

Growth versus irradiance

Cultures were transferred to ten compartments in a temperature-controlled chamber at 13°C. The compartments were made of a rectangular box with a Plexiglass floor and white cardboard walls and cover. The compartments were illuminated from below with two cool-white fluorescent lamps and a Powerstar sodium halide Osram HQI-T 250-W bulb to achieve a high irradiance and a balanced spectral composition. The PAR (photosynthetic available radiation) in each compartment was controlled by neutral density filters to levels of 10, 20, 35, 55, 80,100,160, 320, 450 and 700 µmot photons m s'. The Plexiglass sheet and the filters completely filtered out the UV radiation from the light source.

The growth assays were run in 100 ml sterilized liquid BG-11 media in 125-ml Erlenmeyer flasks. For each experiment, the inocula were taken from exponentially growing cultures that had been dispersed homogeneously with a syringe fitted with a 1-mm needle. This dispersion process ensured that identical aliquots of cells were used for inoculation. Every 2 days during the experiments, the cultures were shaken by hand and their position changed in each of the compartments to ensure the same average light conditions for each replicate.

Cell densities were determined from measurements of absorbance at a wavelength of 750 nm with a Spectronic 1001 Plus spectrophotometer. This optical measurement has been shown to correlate well with cell concentration for mat-forming cyanobacteria (Quesada and Vincent 1993), as well as for small unicellular cyanobacteria (Lönneborg et al. *1985).* The specific growth rate (µ) was estimated by measuring the increase of biomass at 2-day intervals, for 12-20 days and then determining the slope of the growth curve by log-linear regression. The growth rate (µ) as a function of growth irradiance (I) data was fitted to a three parameter model originally developed by Platt et al. (1980) for photosynthesis:

$$\mu = \mu_s(1 - e^{-(\alpha I/\mu_s)})(e^{-(\beta I/\mu_s)})$$

where α and β provide a measure of the growth response of the cultures to irradiance in the light-limited and light-inhibited portions of the irradiance gradient and μ_s is the maximum growth rate in the absence of growth photoinhibition. This equation was fitted to the growth rate versus irradiance data by non-linear regression using the method of partial derivatives. The maximum growth rate, $_{/coax,}$ was calculated by the equation:

$$\mu_{max} = \mu_s(\alpha/(\alpha+\beta))(\beta/(\alpha+\beta))^{\beta/\alpha}$$

The irradiance at which growth becomes saturated, $I_{u\text{-}max}$, was estimated graphically as the lowest irradiance at which a achieves umax in the µ versus irradiance plot. The minimum irradiance at which species are able to grow, $I_{u\text{-}min}$, was taken from the extrapolation to zero of the µ versus log (I) plot.

Results

Physical and chemical environment

The waterbodies could be separated into two groups according to their physical location. The majority were situated in thermokarst depressions on the valley floor, with the others in the terminal or lateral moraines of the glacier (Fig. 1). The size of the ponds and lakes sampled varied from 1 m^2 up to 178,000 m^2; however, 81% of them had a surface of less than 1,000 m^2 and 44% were

less than 100 m² (Fig. 2a). Depth varied from 10 cm to a few meters (< 3 m).

Water temperature at this time of year varied from 1.8 to 16.8°C (Fig. lb), with an average temperature of 13°C. Three ponds had a temperature lower than 4°C, reflecting their proximity to the glacier. Water pH averaged 7.6 and ranged from 6.2 to 9.2 (Fig. 2c). Conductivity varied from 1.5 to 1700 µS cm ^{1} and averaged 312 µS cm' (Fig. 2d). Most of the ponds (68%) contained dilute meltwaters; 68% had a conductivity less than 200 µS cm^{-1}.

All of the waters were characterized by low nutrient concentrations (Table 1). The dissolved reactive phosphorus concentration was at, or below, our limits of detection at all sites. Nitrate concentration was often less than 5 µg N 1^{-1}, but at the two glacier sites it exceeded 10 µg N 1^{-1} . Silicate concentrations ranged from 20 to 1 706 µg Si 1^{-1}, with highest levels in two of the rock-based moraine ponds.

Table 1 Silica and nitrate concentrations in freshwater environments on Bylot Island, 23–28 July 1993. Pond (*P*), lake (*L*) and stream (*S*)

Code	Description	SiO_2-Si (µg l^{-1})	NO_3-N (µg l^{-1})
P1	Tundra pond	34.4	7.3
P2	Tundra pond	155.1	1.0
P3	Tundra pond	135.2	1.4
P4	Pond near glacier	19.6	10.1
P5	Pond near glacier	141.4	37.1
S1	Glacial stream	15.7	3.1
L1	Tundra lake	430.1	1.4
P6	Moraine pond	823.5	1.0
P7	Moraine pond	1705.8	16.4
P8	Moraine pond	429.8	1.0

Planktonic communities

Phytoplankton community dominants included picoplankton cells *(Synechococcus spp.* 1-2 µm), colonial cyanobacteria *(Aphanocapsa* sp., *Aphanothece sp.), fil*amentous cyanobacteria *(Anabaena sp., Nostoc commune, Phormidium spp., Oscillatoria spp.),* desmids *(Cosmarium spp., Staurastrum sp.)* and other chlorophytes *(Pediastrum sp., Scenedesmus sp., Dictyosphaerium sp.).* The overall dominants were often *Phormidium spp.* and *Aphanothece* sp.. Intense blooms of *Dictyosphaerium sp.* were observed in a few of the small ponds. The planktonic Chla concentration ranged from 0.1 to 29.8 µg Chla 1^{-1} with a mean of 4.9 µg Chla 1^{-1} (Fig. 3a). The majority of the ponds (68%) were oligotrophic with less than 5 µg Chla l^{-1}.

Benthic community structure

The bottom of 90% of the ponds contained a thick, mucilaginous benthic algal mat with a surface coloration varying from orange to brown. There was a pronounced gradient of pigments inside the mats, changing from orange in the upper layer towards a blue-green stratum at the bottom. Diverse substrates were colonized by this community, including rocks and sand. Submerged moss communities were established in many

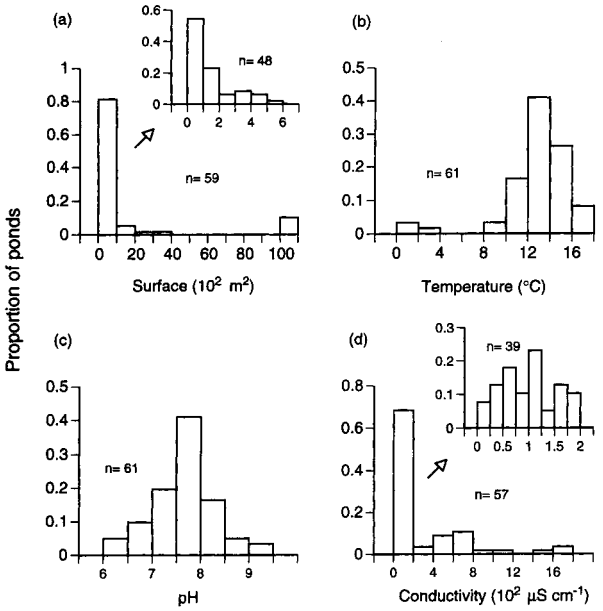

Fig. 2a–d Frequency diagrams of the surface area, temperature, pH and conductivity of the waters sampled on Bylot Island

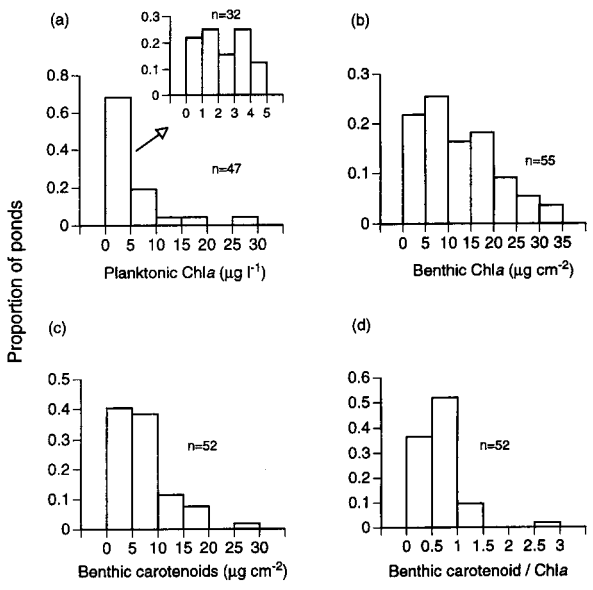

Fig. 3a–d Frequency diagrams of the Chl*a* biomass within the planktonic and periphytic communities, and the carotenoid content of the periphyton in the freshwater ecosystems of Bylot Island

of the ponds and were usually coated by a layer of the orange algal community. The thickness of the mats varied from 1 mm up to 50 mm. Lift-off mats (sensu Wharton et al. 1983) were also found floating at the surface of certain ponds. Most of these had the same structure and colour gradient as the benthic mats. Some of the ponds also contained floating, 1 to 3-mm thick, dark olive-green sheets of *Nostoc commune*. Pieces of dry microbial mats were found exposed around margins of many of the ponds, which appeared to be in the process of drying up.

The algal mats were sampled at five sites, and were found to be dominated by cyanobacteria (77.3%) (Table 2). Filamentous Oscillatoriaceae, such as *Phormidium* spp. (48.6%) and *Oscillatoria spp. (15.4%),* were the most abundant species. There was also a significant number of colonial cells such as *Pleurocapsa sp. (5.1%)* and *Aphanothece* sp. (4.6%).

Table 2 Relative abundance of algal taxa in five periphytic communities sampled on Bylot Island (* < 0.2%)

Taxon	Occurrence (%)					Average
	Site					
	P1	P2	P61	P50	P54	
Cyanobacteria	92.7	98.3	76.6	69	49.6	77.3
Oscillatoria sp1.	1.7	9.1	3.6	2.7	3.7	4.2
Oscillatoria sp2.	0.9	0.4	5.1	5.4		2.4
Oscillatoria sp3.				43.2		8.6
Oscillatoria sp4.				0.8	*	0.2
Oscillatoria sp5.				*	0.6	*
Phormidium sp1.	28.9	5	23	1.1	9.9	13.6
Phormidium sp2.	59.2	52.7	34.7		28.5	35
Nostoc commune	2	0.4	0.7		2.2	1.1
Pleurocapsa sp.		19.1	4.4	1.1	0.9	5.1
Aphanothece sp.		11.6	5.1		3.4	4
Calothrix sp.				1.9		0.4
Hyella sp.				12.8	0.6	2.7
Diatoms	7	1.6	10.3	31	33.2	16.6
Achnanthes minutissima					2.5	0.5
Asterionella formosa	1.2					0.2
Caloneis sp.	*					*
Hannaea arcus				20.4		4.1
Cymbella sp.				0.3	0.6	0.2
Eunotia sp.	0.3	0.8			*	0.2
Fragilaria crotonensis	0.3		*	7.9	8.4	3.3
Fragilaria spp.					8.7	1.7
Gomphonema sp.					0.6	*
Anlacoseira sp.	0.3		*			*
Navicula sp.	4.9	0.4	9.9	0.3	1.2	3.3
Pinnularia sp.	*	0.4	*		9.3	1.9
Synedra ulna				1.6		0.3
Tabellaria flocculosa	*	*	0.4	0.5	1.9	0.6
Chlorophyceae	*	*	12	*	12.7	4.9
Cosmarium sp1.	*	*			0.6	*
Cosmarium sp2.			0.4		*	*
Staurastrum sp.	*	*			*	*
Scenedesmus sp.	*	*			*	*
Zygnema sp.			1.4	*	8.7	2
Chlamydomonas sp.		*	10.2	*	3.4	2.7
Pediastrum sp.					*	*
Dictyosphaerium sp.	*	*			*	*
Chrysophyceae	0.3	*		*	*	*
Dinobryon sp.	0.3					*
Kephyrion sp.		*				*
Cryptophyceae			1.1		4.3	1.1
Chroomonas sp.			1.1		4.3	1.1

Diatoms (16.6%), Chlorophyceae (4.9%) and Chrysophyceae (1.1 %) were also found, but in much lower abundance than cyanobacteria. Amongst the diatoms, *Fragilaria spp. (5.0%), Hannaea arcus (4.1%), Navicula* sp. (3.3%) and *Pinnularia sp.* (1.9%) were the most common species. Members of the Chlorophyceae and Chryptophyceae that were represented were mostly small flagellates such as *Chlamydomomas sp.* (2.7%) and *Chroomonas sp. (1.1%).* The filamentous Chlorophyte, *Zygnema* sp. (2.0%), was present in three of the mats. An additional benthic sample from site 19, in the vicinity of the glacier, was similarly dominated by *Phormidium* spp. but also contained *Calothrix sp., Scytonema sp.* and the diatom *Hannaea arcus* in abundance.

Chlorophyll *a* content in the microbial mats varied from 1.1 μg cm^{-2} in the thin communities to 34.8 μg cm^{-2} in the thickest ones, with an average concentration of 12.3 μg cm^{-2} (Fig. 3b). The same mats had carotenoid concentrations ranging from 0.4 to 26.5 μg cm^{-2} with a mean of 7.1 μg cm^{-2}; the ratio of carotenoid to Chla content averaged 0.6 (Fig. 3c, d).

Culture of species

Five picoplanktonic species (P1-P5) and nine periphytic filamentous species (E1-E9) were brought into unialgal culture (non-axenic but low bacterial contamination). The isolates included representatives from each of the microbial habitats, but most of the strains were from the tundra ponds (Table 3).

The periphytic isolates were all filamentous members of the Oscillatoriaceae *(Phormidium spp.).* Seven of the nine species formed cohesive mats in culture, whereas the other two species grew as dispersed filaments. For all but one isolate (E2-E9), the width of the trichomes varied from 1 to 3 μm and the length of the cells from 2 to 3 μm. These thin-trichome species were identified as *Phormidium autumnale* (Anagnostidis and Komàrek 1988) on the basis of cell size; however, they represented genetically different strains because each isolate had distinct macroscopic characteristics and pigmentation under the same culture conditions (Table 3). The wide-trichome isolate E 1 had a filament diameter of 8 μm and a cell length of 2 μm, and possessed an external sheath and a differentiated terminal cell (calyptra). It was identified as *Phormidium subproboscideum* (Anagnostidis and Komàrek 1988).

Picoplanktonic cells were all strains of the genus *Synechococcus* with a cell diameter of ca. 1 μm. As observed with the periphytic species, the isolates differed in their culture characteristics. Two of the isolates formed aggregates in culture, while the other strains grew as dispersed cells, and there were differences in pigmentation under the same light and nutrient conditions (Table 3).

Pigmentation

Under culture conditions of low irradiance (30 μcool photons m^{-2} s^{-1}), the colour of the isolates was blue green or brown-red, depending on the kind of phycobiliproteins present. The blue-green colour is usually attributed to the presence of phycocyanin (PC) (blue pigment) and the brown-red colour is attributed to the presence of phycoerythrin (PE) (red pigment) in addition to phycocyanin (Table 4). Only two strains of periphytic species (E1 and E5) showed sufficient phycoerythrin production to affect their colour and absorbance spectra.

Table 3 Morphological and pigment characteristics of 14 strains of cyanobacteria isolated into unialgal culture from ponds and streams of Bylot Island. E1 was subsequently identified as *Phormidium subproboscideum*; E2–E9 as *P. autumnale* and P1–P5 are *Synechococcus* spp. (*PB* phycobiliproteins; *PC* phycocyanin; *PE* phycoerythrin)

Code	Source	Cell size (μm)	Characteristics	Colour	PB
Periphytic					
E1	Glacial stream	2 × 8	Mat forming	Black-green	PC + PE
E2	Tundra pond	1 × 3	Mat forming	Olive-green	PC
E3	Moraine pond	2 × 2	Free filaments	Blue-green	PC
E4	Tundra pond	2 × 3	Mat forming	Blue-green	PC
E5	Tundra pond	2 × 3	Free filaments	Brown-red	PC + PE
E6	Tundra pond	2 × 3	Mat forming	Blue-green	PC
E7	Tundra pond	2 × 2	Mat forming	Blue-green	PC
E8	Glacial stream	2 × 3	Mat forming	Blue-green	PC
E9	Tundra pond	2 × 2	Mat forming	Blue-green	PC
Planktonic					
P1	Tundra pond	1	Free cells	Blue-green	PC
P2	Tundra pond	1	Floc	Blue-green	PC
P3	Tundra pond	1	Free cells	Blue-green	PC
P4	Tundra pond	1	Floc	Blue-green	PC
P5	Tundra pond	1	Free cells	Blue-green	PC

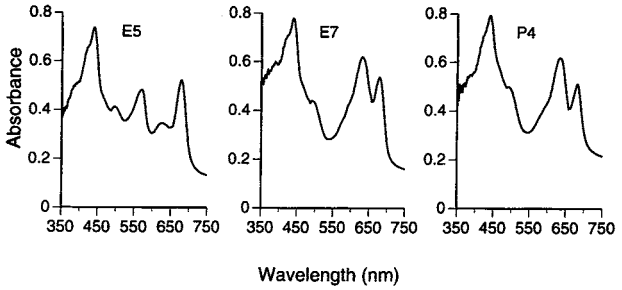

Fig. 4 Absorbance characteristics of three strains of Bylot Island cyanobacteria isolated into unialgal culture. E5, mat-forming species with PE and PC; E7, mat-forming species with PC only; P4, picoplanktonic species with PC only. Absorbance maxima: Chl*a*: 430 and 680 nm; phycocyanin 620 nm; phycoerythrin 565 nm

Three characteristic spectra of in vivo absorbance are shown in Fig. 4. All species possessed distinct in vivo absorption peaks characteristic of specific pigments. The carotenoid to Chla ratio varied from 0.67 to 1.61, and the PC to Chla ratio from 0.55 to 1.56. The PE to Chla ratio for the two species E 1 and E5 varied from 0.89 to 0.90 (Table 4). Comparisons of pigment ratios between the two ecological groups of cyanobacteria showed that the carotenoid/Chla ratio did not differ significantly; however, the PC/Chla ratio was found to be higher in the planktonic species (non-parametric Mann-Whitney test, $P < 0.05$). For the two periphytic PE-producing species, the PE/Chla ratios were similar but the PC/Chla ratios differed by a factor of 2.

Table 4 In vivo absorbance pigment ratios for the periphytic and picoplanktonic strains of cyanobacteria. Statistical comparisons were by the non-parametric Mann-Whitney test (*C.V.* coefficient of variation; *N.S.* not significant)

	Pigment ratios		
Species	Carotenoid/Chl*a*	PC/Chl*a*	PE/Chl*a*
E1	0.902	0.943	0.890
E2	1.608	0.938	
E3	0.668	0.954	
E4	0.844	0.921	
E5	0.720	0.547	0.903
E6	1.099	1.031	
E7	0.745	1.219	
E8	0.915	1.066	
E9	0.769	1.226	
Average	0.919	0.983	0.896
(C.V.)	(31)	(20)	(1)
P1	0.987	1.310	
P2	1.010	1.320	
P3	1.103	1.561	
P4	0.963	1.358	
P5	0.942	1.157	
Average	1.001	1.341	
(C.V.)	(6)	(11)	
Differences	N.S.	*	

* $P < 0.05$

Growth versus irradiance curves

All isolates followed the same general growth-irradiance relationship, which was reasonably approximated (r^2 = 0.43-0.88) by the Platt et al. (1980) photosynthetic model (Fig. 5). Growth rate increased as a saturating exponential function of log irradiance up to a saturation value. Many of the species showed inhibited growth rates at irradiances > 200 µmol photons $m^{-2}s^{-1}$. There was no significant difference in maximum growth rates between the periphytic and picoplanktonic groups (Mann-Whitney non-parametric test, $P > 0.05$), but large differences in model parameters between the species within each group.

Maximum growth rates varied from 0.17 (E2) to 0.61 day^{-1} (P4), equivalent to generation times of 4.1 to 1.1 days (Table 5). The irradiance at which growth first saturated ($I\mu\text{-max}$) varied from 40 (E4) to 200 µcool photons $m^{-2}s^{-1}$ (E5 and P4) and averaged 115-116 µcool photons $m^{-2}\,s^{-1}$ for both ecological groups (Table 5). The minimum irradiance for growth ($I_{\mu\text{-min}}$) was low for all species, ranging from 3.1 to 7.9 µcool photons $m^{-2}\,s^{-1}$

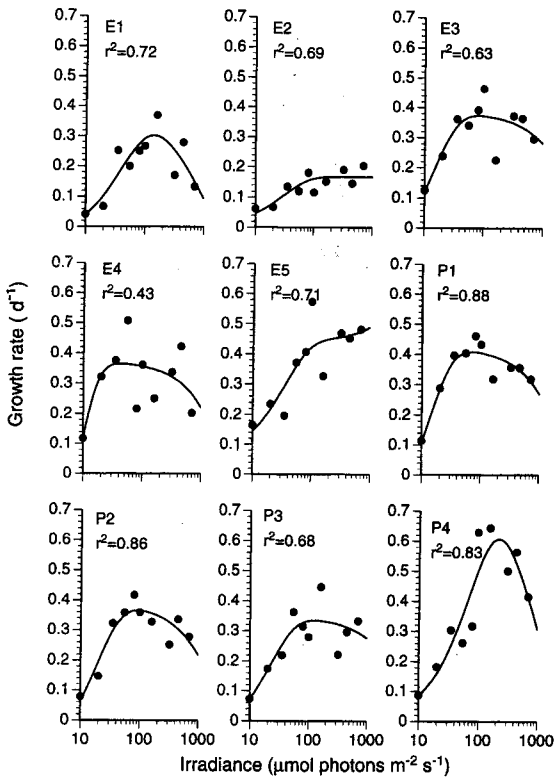

Fig. 5 The relationship between growth rate and irradiance experienced during growth for nine strains of mat-forming (E1–E5) and picoplanktonic (P1–P4) cyanobacteria from Bylot Island. The r^2 value refers to the goodness-of-fit to the Platt et al. (1980) model

Table 5 Growth-irradiance parameters for benthic mat-forming (E1–E5) and picoplanktonic (P1–P4) cyanobacteria in culture, isolated from Bylot Island freshwaters. Irradiance values are in μmol photons m^{-2} s^{-1}

Isolate	μ_{max} (day^{-1})	Generation time (days)	$I\mu_{max}$	$I\mu_{min}$
E1	0.31	2.2	130	4.6
E2	0.17	4.1	130	3.1
E3	0.38	1.8	80	4.7
E4	0.37	1.9	40	7.9
E5	0.50	1.5	200	3.2
Average (CV)	0.34 (32)	2.3 (45)	116 (52)	4.7 (41)
P1	0.41	1.7	60	6.6
P2	0.37	1.9	100	5.3
P3	0.34	2.1	100	3.5
P4	0.61	1.1	200	5.0
Average (CV)	0.43 (28)	1.7 (25)	115 (51)	5.1 (25)

Discussion

The Arctic aquatic ecosystems studied here encompass a broad range of habitats: moderately deep lakes, shallow ponds and glacier-fed streams. Despite this range of conditions, picoplanktonic and periphytic cyanobacteria were common elements of most of the waterbodies sampled. In this respect, Arctic freshwater ecosystems closely resemble those in Antarctica. A comparison of limnological properties of Arctic and Antarctic waters is given in Tables 6 and 7.

Although water temperatures are typically in the range 0-15°C, higher values have been recorded in both polar regions, with the coolest summer temperatures in the streams and large lakes. The pH range measured in this study is similar to that previously reported for the Arctic and Antarctic. Higher pH values have been found in both environments, and this may reflect catchment geochemistry or,, as Matsumoto et al. (1992) found, may be attributed to the continuous photosynthetic activity of algae during the polar summer.

Arctic and Antarctic freshwater environments are often characterized by low nutrient concentrations, although some Antarctic ponds can be highly enriched in phosphate and ammonium. Differences in nutrient content can be explained by the drainage basin characteristics, extent of rock weathering and input of allochthonous material, for example from catchment vegetation. This latter input would be of much greater importance in the Arctic than in the Antarctic. Howard-Williams et al. (1990) suggested that the age and stability of a pond may influence its nutrient characteristics: in older, stable ponds there can be a long-term accumulation of nutrients and biomass.

The biomass concentrations achieved by many of the benthic communities on Bylot Island were in striking contrast to the low nutrient, low Chla water-column environment. However, the nutrient concentrations in the overlying water are unlikely to reflect those in the microenvironment of the mat. In Alaska ponds, Stanley (1976) measured DRP concentrations of 1-3 μg 1^{-1} in the water and 7 μg 1^{-1} in the interstitial water of the benthic mat. In Antarctica, Vincent et al. (1993c) measured 29 ug DRP 1^{-1} and 1 ug N03-N 1^{-1} in the water and 300-1,000 μg DRP 1 and 7-15 μg NO_3-N 1^{-1} in the mat. These observations show that the microbial mats constitute micro-environments with their own distinctive chemical properties.

Periphytic cyanobacteria were widely distributed across a full range of lakes and ponds sampled on Bylot Island. The pigment stocks within the periphyton measured in this study fall within the range of values reported for benthic mats in Antarctica. For example, the benthic carotenoid content was equivalent to that reported by Vincent et al. (1993b), who measured an average concentration of 7.1 μg cm^{-2}, and an average ratio of carotenoids to Chla of 0.7 in Antarctic mats. Our Chla estimates were also similar to those in Antarctica and approached the theoretical limit of 40 μg cm^{-2} at which all light is completely absorbed within the mats (Hawes 1989). A biomass of more than 10 μg cm^{-2} is considered a nuisance growth in the temperate environment (Welch et al. 1988). In Antarctica the high standing crop of periphyton is sometimes explained by the absence of macroinvertebrate grazers and the high daily radiation flux (Vincent and Howard-Williams 1986). These factors may also contribute to the rich development of benthic cyanobacteria that we have observed in the Arctic.

The thickness of the microbial mats on Bylot Island indicates that they are probably the result of several seasons of growth. Perennial mats of cyanobacteria are common throughout Antarctica (Hawes 1993). Experiments with such mats have shown that the freeze-dried overwintering populations are able to reinitiate photosynthesis within 30 min of rewetting (Vincent and Howard-Williams 1986). In Antarctic ponds, one of the most severe environmental effects over winter is the osmotic stress due to the concentration of salts during freeze-up (Schmidt et al. 1991). Similar effects may

Table 6 Physical and chemical characteristics of Arctic and Antarctic lakes (*L*), ponds (*P*) and streams (*S*)

Area	Type	Temperature (°C)	pH	Conductivity ($\mu S\ cm^{-1}$)	Nutrients in water ($\mu g\ l^{-1}$)		References
					DRP	NO_3-N	
Arctic							
Bylot Island, NWT	L, P, S	1.8–16.8	6.2–9.2	1.5–1700	< 5	1–37.1	This study
Char Lake, NWT	L				2		Kalff and Welch 1974
Barrow, Alaska	L, P	4–16			1–3		Stanley 1976
Barrow, Alaska	P	8–15				0–90	Alexander et al. 1980, 1989
Northwest Territories	L, S	11–17	7–7.3		< 3–9	5–80	Moore 1979
Saqvaqjuac, NWT	L				5–10		Welch et al. 1989
Toolik Lake, Alaska	L	6–15				0–46	Alexander et al. 1980, 1989
Toolik Lake, Alaska	L	14	7.3	73	< 3		Kling et al. 1992
Ellesmere Island, NWT	P		7.4–8.6	100–300			Douglas and Smol 1993a
Yukon	L	12–23	5.9–9.3	24–1500		9–208	Pienitz and Smol 1993
NWT	L	7.5–14.5	6.2–8.9	0–100	3.4–12.7	Detection limit	
Ellesmere Island, NWT	L, P		7.4–8.5	79–2000	2.4–32.9	0.8–25	Hamilton et al. 1993
Antarctic							
McMurdo Sound area	S						Vincent and Howard-Williams 1986
McMurdo Sound area	S						Howard-Williams and Vincent 1989
McMurdo Ice Shelf	P			163–2800	1–153	3–95	Howard-Williams et al. 1989
McMurdo Ice Shelf	P			57–4000	0–120	0–25	Howard-Williams et al. 1990
Cape Evans, Ross Island	P	−12–5		2–268	6–3234	< 1–13	Schmidt et al. 1991
Antarctic Peninsula	L	1–4			6–425		Hansson 1992
McMurdo Sound area	L, P, S						Vincent et al. 1993b
Ross Island	P			20–3190	9		Vincent et al. 1993c
Livingston Island	P		7.3–7.8		10–15	120–220	Davey 1993
Signy Island	S						Hawes 1993
Ross Ice Shelf	S	0–9.5	6.9–10	10–5300	1–573	1–600	Vincent and Howard-Williams 1994

Table 7 Biological characteristics of planktonic and periphytic communities in lakes (*L*), ponds (*P*) and streams (*S*) of the Arctic and Antarctic. (*Osc* Oscillatoriaceae; *Dia* diatoms; *Chloro* Chlorophyceae)

Area	Type	Planktonic Chl*a* ($\mu g/l$)	Periphytic Chl*a* ($\mu g/cm^2$)	Dominant periphytic species	References
Arctic					
Bylot Island, NWT	L, P, S	0.1–29.8	1.1–34.8	Osc (64%), Dia (17%), Chloro (5%)	This study
Char Lake, NWT	L	0.2–0.6			Kalff and Welch 1974
Barrow, Alaska	L, P			Chloro + cyano (> 90%)	Stanley 1976
Barrow, Alaska	P	0.6			Alexander et al. 1980, 1989
Northwest Territories	L, S			Diatoms, cyano, chloro	Moore 1979
Saquajuac, NWT	L	1–2.4			Welch et al. 1989
Toolik Lake, Alaska	L	1.4			Alexander et al.1980, 1989
NWT	S			Chloro + cyano (79%)	Sheath and Cole 1992
Antarctic					
McMurdo Sound area	S		9.5–30	Osc	Vincent and Howard-Williams 1986
McMurdo Sound area	S		10–30	Osc	Howard-Williams and Vincent 1989
McMurdo Ice Shelf	P		8–70	Osc (70%), diatoms, chloro	Howard-Williams et al. 1989
Ross Ice Shelf	P			Osc, diatoms	Broady 1989
McMurdo Ice Shelf	P		0–30	Osc, diatoms, chloro	Howard-Williams et al. 1990
Cape Evans, Ross Island	P			Cyano, diatoms	Schmidt et al. 1991
Antarctic Peninsula	L		2–40		Hansson 1992
McMurdo Sound area	S		1–20	Osc, diatoms	Vincent et al. 1993a
McMurdo Sound area	L, P, S		2–40	Osc	Vincent et al. 1993b
Ross Island	P			Osc	Vincent et al. 1993c
Livingston Island	P			Osc	Davey 1993
Signy Island	S		10.9–16.5	Osc	Hawes 1993
Ross Ice Shelf	S	0.1–5	0.4–55	Osc, diatoms	Vincent and Howard-Williams 1994

operate in Bylot Island ponds, and may be a factor contributing towards the selection and dominance of cyanobacteria in the benthic communities of both polar regions (Table 7). The abundant mucilage production by polar mat-forming cyanobacteria may reduce the damaging effects of freezing and thawing (by reducing ice nucleation in the vicinity of the cell) (Vincent 1988) and may also help protect some of the less resistant species within the mat communities, such as diatoms. This mucilage also confers a hydrophobicity to the mats that may aid their adhesion to the benthic substrate and reduce their tendency to be plucked from the bottom by melting ice, as described for sediments by Nichols (1967).

Pigment profiles in the cyanobacterial mats were very similar to Antarctica (cf. Vincent et al., 1993b). Surface layers were composed of low concentrations of Chla and phycobiliproteins whereas the bottom layers were enriched in these compounds. Carotenoids were present throughout the mat but the ratio to Chla decreased with depth. The orange colour of the mat surface was thus due to this ratio effect, rather than a surface enrichment in carotenoid content.

The chlorophyll a levels of phytoplankton on Bylot Island were similar or higher than in the other polar studies (Table 7). The abundance of picoplanktonic species in the ponds sampled is typical of many types of aquatic environment of low nutrient status; however, little seems to be known about the importance of picocyanobacteria in Antarctic lakes. Bloom-forming cyanobacteria such as *Anabaena, Aphanizomenon* and *Microcystis* were largely absent from the Bylot Island freshwaters, as well as the Antarctic environments listed in Table 7.

Our observations reported here underscore the number of different cyanobacteria forms on Bylot Island. Filamentous and colonial periphytic species and small picoplanktonic species are found in all lakes, ponds and streams. Periphytic Oscillatoriaceae demonstrated morphological and physiological differences in shape, size, colour, capacity to form mats and pigment characteristics. In Antarctica, Oscillatoriaceae also demonstrate a wide abundance and a diversity of biological properties (Broady and Kibblewhite 1991). Morphological and morphometric characteristics of trichomes can be used to define field populations; however, additional criteria such as physiological and growth attributes in culture are necessary to separate taxa (Broady and Kibblewhite 1991). Like Komàrek (1970), we found major differences in the physiological characteristics of different strains assigned on the basis of morphological criteria to *Phormidium autumnale.* Both *Phormidium autumnale* and *Phormidium subproboscideum* are known to also occur in Antarctica (Broady and Kibblewhite 1991), but their genetic affinity with Arctic strains remains unknown at this stage.

Phycoerythrin-rich species were under-represented on Bylot Island. This parallels observations in Antarctica (Vincent et al. 1993b), and is in striking contrast to the cyanobacterial communities of the temperate habitats where phycoerythrin production is very common. This suggests that some feature of the polar environment (e.g. continuous light in summer)- selects against species with large, phycoerythrin-containing phycobilisomes.

The picoplanktonic, as well as oscillatorian, isolates were able to grow over a broad range of irradiances including extremely low irradiances (10 µcool photons $m^{-2}s^{-1}$) and bright light conditions (700 µcool photons $_m$-2 s-1). The estimated compensation irradiance for growth is in agreement with other studies of cyanobacteria, which report values of 6 smol photons $m^{-2}s^{-1}$ (Raps et al. 1983), 5 smol photons $m^{-2}s^{-1}$ (Richardson et al. 1983) and 1-2 smol photons $m^{-2}s^{-1}$(Tandeau de Marsac and Houmard 1993). The onset of maximum growth rates at irradiances from 40 to 200 µcool photons $m^{-2}s^{-1}$ for the Arctic Oscillatoriacae is consistent with the I_K values for photosynthesis from 27 to 178 µmot photons $m^{-2}s^{-1}$ for *Phormidium-dominated* mats in Antarctica (Howard-Williams and Vincent 1989; Vincent et al. 1993a). The large between-species variability in these values, as well as in growth rates, provides further evidence of the genetic diversity of polar cyanobacteria, even within groups of morphologically identical taxa *(Synechococcus, Phormidium autumnale).* The maximum growth rates (range of 0.17-0.50 day^{-1} for the Oscillatoriaceae) were comparable with those observed for Antarctic isolates grown under similar culture conditions, e.g. 0.62 day^{-1} for *Phormidium murrayi* and 0.44 day^{-1} for *Oscillatoria priestleyi* (Vincent and Quesada 1994). These growth-irradiance observations also underscore the adaptive range of polar cyanobacteria, with an ability to grow under bright 24-h irradiance in exposed, shallow water habitats, as well as extreme shade conditions under ice and snow or deep within the microbial mat environment.

Cyanobacteria are often considered to be favored by warm temperatures (e.g. Robarts and Zohary 1987) but, as shown here, they may also dominate in extreme cold environments. This study has shown that the limnological properties of Bylot Island and Antarctica are similar and that cyanobacteria occur in equivalent abundance and diversity in both polar environments. The morphological, as well as physiological, diversity of cyanobacteria may contribute towards their ecological success in a broad range of Arctic and Antarctic habitats.

Acknowledgements This research was supported financially by the Natural Sciences and Engineering Research Council of Canada with logistic support from the Polar Continental Shelf Project (this is publication number PCSP/EPCP/25). We thank Dr. Gilles Ga uthier for kindly allowing access to his field camp on Bylot Island, Dr. Josef Elster (University of Toronto) for assistance with identification of the cyanobacteria, and Dr. David Wynn-Williams (British Antarctic Survey) and two anonymous reviewers for helpful comments on the manuscript.

References

Anagnostidis K, Komârek J (1988) Modern approach to the classification system of cyanophytes. 3. Oscillatoriales. Arch Hydrobiol Suppl 80:327-472

Alexander V, Stanley DM, Daley RJ, McRoy CP (1980) Primary producers. In: Hobbie JE (ed) Limnology of tundra ponds Dowden, Hutchinson and Ross, Stroudsburg, Pa, pp 179-250

Alexander V, Whalen SC, Klingensmith KM (1989) Nitrogen cycling in Arctic lakes and ponds. Hydrobiologia 172:165-172

American Public Health Association (1976) Standard methods for the examination of water and waste water. 14th edn. APHA, Washington, DC

Britton G (1985) General carotenoid methods. Methods Enzymol 111:113-149

Broady PA (1989) Broadscale patterns in the distribution of aquatic and terrestrial vegetation at three ice-free regions on Ross Island, Antarctica. Hydrobiologia 172:77-95

Broady PA, Kibblewhite AL (1991) Morphological characterization of Oscillatoriales (Cyanobacteria) from Ross Island and southern Victoria Land, Antarctica. Antarct Sci 3:35-45

Chapin FS, Jeffries RL, Reynolds JF, Shaver GR, Svoboda J (1991) Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego

Croasdale H (1973) Freshwater algae of Ellesmere Island, N.W.T. Nat Mus Can Publ Bot 3:1-131

Davey MC (1993) Carbon and nitrogen dynamics in a small pond in the maritime Antarctic. Hydrobiologia 257:165-175

Douglas MVS, Smol JP (1993a) Freshwater diatoms from high Arctic ponds (Cape Herschel, Ellesmere Island, N.W.T.). Nova Hedwigia Kryptogamenkd 57:511-552

Douglas MVS, Smol JP (1993b) The geographical and physicochemical characteristics of 35 ponds from Cape Herschel, Ellesmere Island. In: Hamilton PB (ed) Proceedings of the fourth Arctic-Antarctic Diatom Symposium (Workshop). Canadian Museum of Nature, Ottawa, Ontario

Fay P (1983) The blue-greens (Cyanophyta-Cyanobacteria). The Institute of Biology - Studies in Biology no. 160. London

Hamilton PB, Edlund SA (1994) Occurrence of *Prasiola fluviatilis* (Chlorophyta) on Ellesmere Island in the Canadian Arctic. J Phycol 30:217-221

Hamilton PB, Lean DRS, Poulin M (1993) The physicochemical characteristics of lakes and ponds from the northern regions of Ellesmere Island. In Hamilton PB (ed) Proceedings of the fourth Arctic-Antarctic Diatom Symposium (Workshop). Canadian Museum of Nature, Ottawa, Ontario

Hansson L-A (1992) Factors regulating periphytic algal biomass. Limnol Oceanogr 37:322-328

Hawes I (1989) Filamentous green algae in freshwater streams on Signy Island, Antarctica. Hydrobiologia 172:1-18

Hawes I (1993) Photosynthesis in thick cyanobacterial films: a comparison of annual and perennial antarctic mat communities. Hydrobiologia 252:203-209

Henry GHR, Svoboda J (1986) Dinitrogen fixation (acetylene reduction) in high arctic sedge meadow communities. Arct Alp Res 18:181-187

Hickman M (1974) The epipelic diatom flora of a small lake on Baffin Island, Northwest Territories, Canada. Arch Protistenkd 116:270-279

Howard-Williams C, Vincent WF (1989) Microbial communities in southern Victoria Land streams (Antarctica). 1. Photosynthesis. Hydrobiologia 172:27-38

Howard-Williams C, Pridmore R, Downes MT, Vincent WF (1989) Microbial biomass, photosynthesis and chlorophyll *a* related pigments in the ponds of the McMurdo Ice Shelf, Antarctica. Antarct Sci 1:125-131

Howard-Williams C, Pridmore RD, Broady PA, Vincent WF (1990) Environmental and biological variability in the McMurdo Ice Shelf ecosystem. In: Kerry KR, Hempel G (eds) Antarctic ecosystems. Ecological change and conservation. Springer, Berlin Heidelberg New York, pp 23-31

Kalff J, Welch HE (1974) Phytoplankton production in Char Lake, a natural polar lake, and in Meretta Lake, a polluted polar lake, Cornwallis Island, Northwest Territories. J Fish Res Board Can 31:621-636

Kalff J, Kling HJ, Holmgren SH, Welch HE (1975) Phytoplankton, phytoplankton growth and biomass cycles in an unpolluted and in a polluted polar lake. Verh Int Verein Limnol 19:487-495

Kling GW, O'Brien WJ, Miller MC, Hershey AE (1992) The biochemistry and zoogeography of lakes and rivers in arctic Alaska. Hydrobiologia 240:1-14

Komârek J (1970) Morphological variability of several *Phormidium* species. Annual Report of the Laboratory of Algology, Trebon, 1969, pp 19-22

Lönneborg A, Lisbet KL, Kalla SR, Gustafsson P, Oquist G (1985) Acclimation processes in the light-harvesting system of the cyanobacterium *Anacystis nidulans* following a light shift from white to red light. Plant Physiol 78:110-114

Lovejoy C, Vincent WF, Frenette J-J, Dodson JJ (1993) Microbial gradients in a turbid estuary: application of a new method for protozoan community analysis. Limnol Oceanogr 38:12951303

Marker AFH, Nusch EA, Rai H, Riemann B (1980) The measurement of photosynthetic pigments in freshwaters and standardization of methods: conclusions and recommendations. Arch Hydrobiol Beih Ergebn Limnol 14:91-106

Matsumoto GI, Nakayas S, Murayama H, Masuda N, Kawana T, Watanuki K, Torii T (1992) Geochemical characteristics of Antarctic lakes and ponds. Proceedings of the National Institute of Polar Research Symposium in Polar Biology 5:125-145

McLean AL (1918) Bacteria of ice and snow in Antarctica. Nature 102:35-39

Moore JW (1979) Distribution and abundance of attached, littoral algae in 21 lakes and streams in the Northwest Territories. Can J Bot 57:568-577

Nichols H (1967) The disturbance of Arctic ice sediments by bottom ice: a hazard for palynology. Arctic 20:213-4

Nogrady T, Smol JP (1989) Rotifers from five arctic ponds (Cape Herschel, Ellesmere Island, N.W.T.). Hydrobiologia 173:231242

Pienitz R, Smol JP (1993) The ecology and physicochemical characteristics of lakes in the subarctic and arctic regions of the Yukon Territory, Fennoscandia (Finland, Norway), the Northwest Territories and northern Québec. In: Hamilton PB (ed) Proceedings of the fourth Arctic-Antarctic Diatom Symposium (Workshop). Canadian Museum of Nature, Ottawa, Ontario

Platt T, Gallegos CL, Harrison WG (1980) Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. J Mar Res 38:687-701

Quesada A, Vincent WF (1993) Adaptation of cyanobacteria to the light regime within Antarctic mats. Verh Int Verein Limnol 25:960-965

Raps S, Wyman K, Siegelman W, Falkowski PG (1983) Adaptation of the cyanobacterium *Microcystis aeruginosa* to light intensity. Plant Physiol 72:829-832

Richardson K, Beardall J, Raven JA (1983) Adaptation of unicellular algae to irradiance: an analysis of strategies. New Phytol 93:157-191

Rippka R, Deruelles J, Waterbury JB, Herdman M, Stanier RY (1979) Generic assignments, strain histories and properties of pure cultures of cyanobacteria. J Gen Microbiol 111:1-61

Robarts RD, Zohary T (1987) Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. NZ J Mar Freshwater Res 21:391-399

Schindler DW, Kalff J, Welch HE, Brunskill GJ, Kling H, Kritsch N (1974) Eutrophication in the High Arctic - Meretta Lake, Cornwallis Island (75°N lat.). J Fish Res Board Can 31:647662

Schmidt S, Moskal W, De Mora SJ, Howard-Williams C, Vincent WF (1991) Limnological properties of Antarctic ponds during winter freezing. Antarct Sci 3:379-388

Sheath RG, Cole KM (1992) Biogeography of stream macroalgae in North America. J Phycol 28:448-460

Stanley DW (1976) Productivity of epipelic algae in tundra ponds and lake near Barrow, Alaska. Ecology 57:1015-1024

Stein JR (1973) Handbook of phycological methods: culture methods and growth measurements. Cambridge University Press, Cambridge

Tandeau De Marsac N, Houmard J (1993) Adaptation of cyanobacteria to environmental stimuli: new steps towards molecular mechanisms. FEMS Micriobiol Rev 104:119-190

Truesdale VW, Smith CJ (1975) The formulation of molybdosilicic acids from mixed solutions of molybdate and silicate. Analyst 100:203-212

Vincent WF (1988) Microbial ecosystems of Antarctica. Cambridge University Press, Cambridge

Vincent WF, Howard-Williams C (1986) Antarctic stream ecosystems: physiological ecology of a blue-green algal epilithon. Freshwater Biol 16:219-223

Vincent WF, Howard-Williams C (1994) Nitrate-rich inland waters of the Ross Ice Shelf region, Antarctica. Antarct Sci 6:339346

Vincent WF, Quesada A (1994) Ultraviolet radiation effects on cyanobacteria: implications for Antarctic microbial ecosystems. Antarct Res Ser 62:111-124

Vincent WF, Howard-Williams C, Broady PA (1993a) Microbial communities and processes in Antarctic flowing waters. In: Friedmann El (ed) Antarctic microbiology. Wiley, New York, pp 543-569

Vincent WF, Downes MT, Castenholz RW, Howard-Williams C (1993b) Community structure and pigment organisation of cyanobacteria-dominated microbial mats in Antarctica. Eur J Phycol 28:213-221

Vincent WF, Castenholz RW, Downes MT, Howard-Williams C (1993c) Antarctic cyanobacteria: light, nutrients, and photosynthesis in their microbial mat environment. J Phycol 29:745755

Welch EG, Jacoby JM, Homer RR, Seeley MR (1988) Nuisance biomass levels of periphytic algae in streams. Hydrobiologia 157:161-168

Welch HE, Legault JA, Kling H (1989) Phytoplankton, nutrients, and primary production in fertilized and natural lakes at Sagvagjuac, N.W.T. Can J Fish Aquat Sci 46:90-107

Wharton RA, Parker BC, Simmons GM (1983) Distribution, species composition and morphological algal mats (stromatolites) in Antarctic dry valley lakes. Phycologia 22:355-365

Whitledge TE, Malloy SC, Patton CJ, Wirick CD (1981) Automated nutrient analyses in seawater. Technical report. Brookhaven National Laboratory, Upton, N.Y.

Wynn-Williams DD (1990) Ecological aspects of Antarctic microbiology. Adv Microbiol Ecol 11:71-146