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Community and pigment structure of Arctic cyanobacterial assemblages: the occurrence and distribution of UV-absorbing compounds

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Abstract

Three groups of cyanobacterial communities were widely distributed in the benthic environment of lakes, ponds and streams on Ellesmere Island and Cornwallis Island in the Canadian High Arctic: (1) sheets or spherical colonies of *Nostoc* (up to 20 mm diameter); (2) biofilms up to 7 mm thick, dominated almost exclusively by *Oscillatoria*; (3) microbial mats up to 8 mm thick containing several taxa, particularly *Scytonema* and *Phormidium*. The abundance of heterocystous genera (communities 1 and 3) implies that N_2 fixation plays an important role in the nitrogen economy of these ecosystems. Most of the communities were rich in pigments absorbing in the UV-blue end of the spectrum, such as scytonemin and mycosporine-like amino acids. Spectroradiometric analyses of sections of the communities showed that short wavelength radiation did not reach the bottom layer where phycobiliprotein-rich cells were located. This lower community experienced low irradiance in the photosynthetically active radiation band (400–700 nm), restricted to the wavelengths of the yellow-red waveband (550–650 nm). The surface screening of high energy wavelengths may confer an adaptive advantage to these communities which grow under continuous light during the polar summer.

Keywords: Arctic; Cyanobacterium; Pigment; Ultraviolet; Polar; Absorbance

1. Introduction

Antarctic studies have shown that mat- and biofilm-forming cyanobacteria are major elements of the biota in south polar lakes, ponds and streams as well as terrestrial habitats [1]. By comparison, much less is known about the distribution of cyanobacteria in Arctic environments. The N_2 fixation capabilities of some terrestrial cyanobacteria have been studied and identified as an important input of N to Arctic soil ecosystems [2] in which nitrogen appears to be a limiting element [3]. The benthic algal flora of Arctic aquatic ecosystems has recently been the subject of increasing study [4,5] and there is now evidence from a small number of sites that cyanobacteria may be as abundant in the north polar zone as in Antarctica [3].

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Reports on Antarctic cyanobacteria have shown that the mats are vertically structured with distinct layers containing different pigments [6,7]. Vincent and Quesada [8] suggested that this pigment distribution conferred resistance against the effects of UV radiation and photo-oxidation in the continuous bright light regime which characterises the polar summer. No information is available from the north polar region to determine whether this is a general feature of high latitude cyanobacteria.

Ultraviolet radiation in the polar regions is lower than across the rest of the Earth's surface, but incident radiation in the UVB waveband (280–320 nm) has substantially increased in the Antarctic [9] because of stratospheric ozone depletion. The beginning of a similar trend has now been observed in the northern hemisphere [10]. UV radiation is known to have a range of strong inhibitory effects on the growth and physiology of microorganisms including cyanobacteria [11]. The presence of UV-screening pigments such as scytonemin and mycosporine-like amino acids (MAA) present in cyanobacteria [12] can provide an effective defence against UV radiation.

In the present study we evaluated the occurrence and distribution of cyanobacterial communities in High Arctic freshwater ecosystems, and their physiological adaptation in terms of pigment characteristics to this extreme environment. Our specific objectives were to (i) examine in detail the species composition and photosynthetic pigment distribution through the cyanobacterial mats; (ii) analyse the occurrence of UV-absorbing pigments; (iii) determine the in situ spectral irradiance within different strata of the cyanobacterial communities and (iv) compare our results with similar studies undertaken in Antarctic freshwater ecosystems.

2. Materials and methods

Sampling and measurements were undertaken at three locations in the Canadian Arctic: (a) The Lake Hazen area (Ellesmere Island; 81.5°N, 71.2°W) including Skeleton Lake and nearby water bodies; (b) Two Basin Lake near Eureka Station, southern Ellesmere Island (80°N, 84.5°W); and (c) North Lake on Cornwallis Island (74°N, 95°W). The fieldwork was conducted in the late summer (August) of 1994. Each cyanobacterial community was assigned a code (Table 1), H1–H6 and Omat were obtained in the Lake Hazen area, OSCTBL and NOSTBL in the Eureka area, and OSCNL on Cornwallis Island. Water temperature and conductivity were measured with a submersible probe (Yellow Spring Instruments Ltd.), and pH with a Corning® probe. At each sampling location, water characteristics were measured in situ between 10.00 and 13.00 h.

2.1. Species description and identification

Species composition of the cyanobacterial communities was firstly examined in the field with a portable microscope. Samples were stored frozen and later thawed for further examination with a Zeiss inverted microscope (Axiovert 10) under bright field, epifluorescence and Nomarski illumination.

2.2. In vivo absorbance measurements

Spectral irradiance was measured at 280–800 nm in 2-nm intervals using an Optronics 752 spectroradiometer equipped with a quartz fibre optic cable attached to a 15 cm diameter collecting sphere. The penetration of irradiance was measured after setting to record sky radiation with the same calibration. The mats were sectioned in the field with a broad, flat razor and then discrete water-saturated layers were placed over the detector, covering it completely.

2.3. Pigment extraction and analysis

From each cyanobacterial community two to four cores were taken for pigment extraction. Values quoted are means of these replicates. Standard deviation was less than 15% of the means. Square cores (10×10 mm) were sampled for pigment description, and round cores of 14 mm diameter for layer separation were obtained from representative sections of each cyanobacterial community, stored frozen in the dark and transferred within 4 days to −20°C. The cores were maintained at −20°C for 2 weeks until extraction and analysis. Chlorophyll *a* (Chl *a*), carotenoids (Car) and scytonemin (Scyt) were extracted by grinding the cores in 90% acetone with a Teflon

tissue grinder. Samples were left at 4°C in the dark for 2–3 h and the extracts were then shaken and centrifuged. Absorption spectra of the supernatant were obtained using a diode array spectrophotometer (Hewlett Packard HP-8452A). Repeated extractions (usually four) were made of the same pellet until no more pigment was detected. Results shown here are from the addition of values from all the extractions for each sample.

UV-absorbing substances with properties similar to MAA were extracted in 20% aqueous methanol at 45°C for 1 h [12] and the extracts were then centrifuged and scanned in the diode array spectrophotometer at 200–800 nm. Absorbance values were determined at 326 nm. The extraction procedure was repeated until no more absorbance in the UV band was detected, and the values from each extraction were then summed. The application of this technique, in combination with HPLC, to Antarctic cyanobacterial mats showed that the 326-nm absorption peak corresponded to MAA [13], but this was not confirmed in the present study. Phycobiliproteins were extracted using repeated glycerol treatments as in [14].

The pigment peaks were converted to concentrations using equations from the literature for Chl *a* [15], Car [16], Scyt [17] and phycobiliproteins [18]. Apparent MAA concentrations were measured as the optical density (OD) at 326 nm, since this fraction may contain several compounds. The absorbance values were normalised to Chl *a*, but not to dry weight because in microbial mats the latter may include a large fraction of inorganic material such as silt particles and sand grains.

3. Results

3.1. Study sites

Cyanobacterial communities were found in benthic habitats, ranging from shallow environments exposed to full sunshine to deep shade conditions at the bottom of a lake. Most of the water bodies were alkaline (Table 1), with conductivities in the range of 137–780 μS cm^{-1}. Ponds H1, H3, H5 and H6 are small and shallow. Two Basin Lake and North Lake are the largest and deepest lakes in this study. H2 and Crack were semi-aquatic environments; the former was a water-saturated bog, while the latter was a dim light environment with no liquid water at the time of sampling, but ice-covered at the bottom; the community grew on the walls of the crack.

3.2. Community structure

The communities at each site differed in terms of taxonomic composition and physical structure. Three broad categories could be distinguished: (i) non-structured (usually almost monospecific) communities containing *Nostoc* spp. (NOSTBL and H2 community); (ii) microbial films dominated almost exclusively by *Oscillatoria* spp. with thick (around 6 μm diameter) filaments (OSCTBL and OSCNL), and (iii) complex microbial mat communities typically dominated by heterocystous filaments of *Scytonema* spp. (H4 or H5), and by thin (less than 2 μm) *Phormidium* spp. (H3 and H6). The matrix of the H1 mat was a mixture of both organisms. In communities ii and iii other cyanobacterial genera, in particular *Anabaena*,

Table 1
Description of the High Arctic water bodies and their cyanobacterial communities

Site	Size (m^2)	Depth (m)	Conductivity (μS cm^{-1})	pH	Temperature (°C)	Surface colour	Thickness (mm)	Community code
H1 pond	7.8×10^3	≤1	780	8.63	3.9	orange	6–8	H1
H2 pond	semi-aquatic		430	8.07	4.9	brown	variable	H2
H3 pond	7.8×10^3	≤1	370	8.43	4.2	white	4	H3
Skeleton lake	3.1×10^4	4	180	8.58	7.2	pink	3–5	H4
Skeleton lake	3.1×10^4	4	180	8.58	7.2	orange	3–5	Omat
H5 pond	7.8×10^3	≤1	140	8.43	5.7	pink	4	H5
H6 pond	7.8×10^3	≤1	137	8.36	6.1	orange-brown	6	H6
Crack	semi-aquatic		–	–	–	blue-green	2	OSCTBL
North lake	0.7×10^6	12	–	–	–	sandy	7	OSCNL
Two Basin lake	1.2×10^5	9	390	8.01	10.8	variable	variable	NOSTBL

Nodularia, *Calothrix*, *Schizothrix* and *Synechococcus*, were present as subdominants. Other algal groups (mostly diatoms and chlorophytes) were also present in communities ii and iii but represented a small proportion of total biomass.

The cyanobacterial mat communities studied formed a compact 2–8 mm thick layer (Table 1) that could be easily separated from the sediment surface. In many cases the benthic mats showed an intense blue-green basal layer beneath a surface layer of variable colour, for example light blue-green or pink. Microscopic observations of the mat material showed that these differentially pigmented surface and bottom layers contained the same species. However, the two layers differed in their physiological status, as indicated by fluorescence microscopy: the surface layers showed dim autofluorescence under green excitation light, while the bottom layer were always intensely autofluorescent. The *Nostoc* community NOSTBL formed spheres that were 2–15 mm in diameter and covered by a pigmented superficial layer ranging from blue-green to red in colour. The H2 community was formed by separate colonies of variable size and thickness.

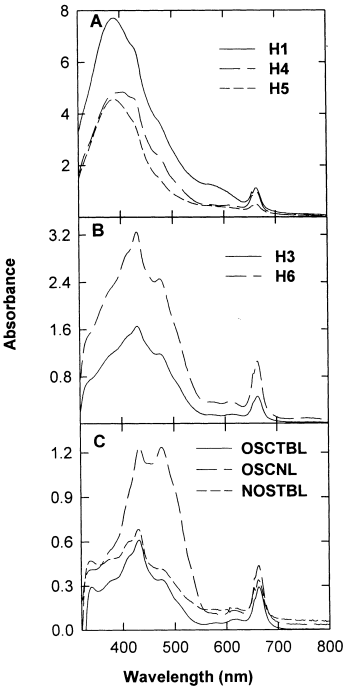

Fig. 1. Absorbance scans of acetone extractions from different cyanobacterial communities. H1, H4, and H5 were communities dominated by *Scytonema* sp. H3 and H6 mats were dominated by Oscillatoriacean species. OSCTBL, OSCNL and NOSTBL were monospecific assemblages.

3.3. Pigment content in whole mats

Scans of the acetone extracts from cyanobacterial mats are shown in Fig. 1. Communities H1, H4 and H5 had similar spectra, with a wide absorbing band from 300 to 500 nm (Fig. 1A). On the other hand, the communities from H3, H6, OSCTBL and NOSTBL (Fig. 1B,C) showed a more distinct separation between peaks, with less relative absorbance in the carotenoid waveband (450–500 nm). *Oscillatoria* from North Lake (OSCNL) showed an unusual pattern, with pronounced minimum absorbance between the 500 and 430 nm peaks. Chl *a* levels ranged from 17 μg cm^{-2} to almost 45 μg cm^{-2}, and carotenoid concentrations varied over a similar range (Table 2). Scytonemin-like sheath pigment was more variable in concentration (from 7.2 to 92 μg cm^{-2}). The Car/Chl *a* ratios were mostly in the range 0.7–

Table 2
Pigment characteristics of the whole cyanobacterial mats or colonies

Code	Chl *a*	Car	Car/Chl *a*	Scyt	Scyt/Chl *a*	Scyt/Car
H1	44.4	44.7	1.04	92.6	2.15	2.07
H3	18.3	14.2	0.77	14.8	0.80	1.04
H4	40.4	28.4	0.70	57.6	1.42	2.02
H5	19.7	18.2	0.92	54.8	2.78	3.00
H6	41.8	29.5	0.70	28.5	0.67	0.96
OSCTBL	–	–	0.38	–	0.45	1.17
OSCNL	17.2	14.8	0.86	7.2	0.41	0.49
NOSTBL	–	–	0.36	–	0.36	1.03

Data are expressed as μm cm^{-2} or μg $μg^{-1}$ (ratios).

0.9, but low values occurred in OSCTBL and NOSTBL, and a high value (1.04) occurred in the H1 community. Scytonemin to Chl *a* and to carotenoid ratios were highest in the H1, H4 and H5 communities.

3.4. Optical properties of the communities

Spectral irradiance after the absorbance of incident PAR by different strata of Omat is shown in Fig. 2. The surface layer (1–2 mm thick) of this benthic cyanobacterial community absorbed radiation mainly in the ultraviolet and blue end of the spectrum (300–500 nm), reducing the radiation in the UVB region (300–320 nm) to 8% of incident, and the UVA radiation (320–400 nm) to 10% of incident. The infrared band of the spectrum (>700 nm) readily passed through the surface layer (40–50% of the incident irradiance). The surface layer had two distinct transmittance minima, corresponding to Chl *a* (680 nm) and to *c*-phycocyanin (620 nm). A minor absorbance peak was detected at 580 nm and was likely related to phycoerythrin absorbance. The bottom (2–3 mm thick) layer of the oscillatorian mat had absorbance properties that differed completely from the overlying surface stratum. This lower layer transmitted maximally in the UV and blue end of the spectrum, with minimum transmission in the waveband 600–680 nm, corresponding to the phycobiliprotein and Chl *a* absorbance band. Maximum transmittance of the surface layer was 45% (in the infrared band) while the bottom layer maximum transmittance was 2% (in the UV region).

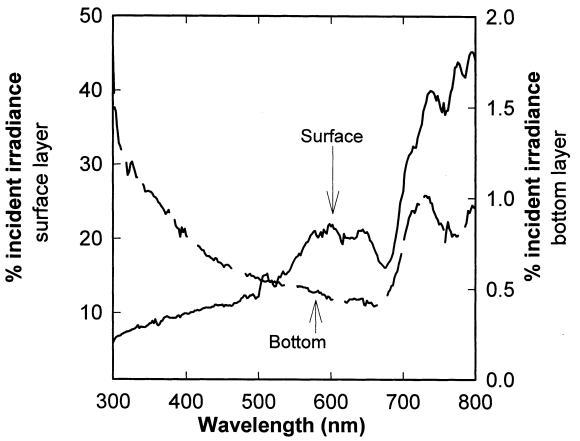

Fig. 2. The spectral attenuation of downwelling irradiance within the cyanobacterial mat Omat. The data for each wavelength were converted to percentage of surface incident radiation. Solid and dotted lines represent the percent transmission through the 1–2-mm surface and 2–3-mm bottom layers respectively.

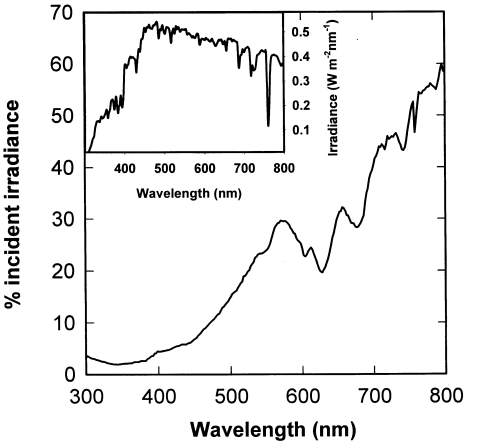

Fig. 3. The spectral attenuation of downwelling irradiance within a *Nostoc commune* biofilm. Data transformation as in Fig. 2. Inset: Incident irradiance at Lake Hazen area recorded before measuring the spectral attenuation through the biofilm.

The optical features of mucilaginous colonies (1–2 mm thick) of *Nostoc commune* are shown in Fig. 3. The irradiance transmission was 60% in the infrared region, but the value dropped to 5% in the UV waveband. Two pigment-related transmittance troughs were apparent, one at 680 nm (Chl *a*) and the other at 620 nm (*c*-phycocyanin), with no evidence of phycoerythrin.

3.5. Pigment distribution within the mats

To examine the pigment zonation within the benthic mats, extracts from the surface and bottom layers of two mats were analysed by spectrophotometry. Two layers were easily separated, the surface (usually brown or pink) and the bottom (blue-green). Lipophilic pigments, phycobiliproteins and MAA were extracted from each layer. Scans of each extraction for mats H1 and H4 are shown in Fig. 4. The top layer was 2–3 mm thick in mat H1 and 1 mm thick in H4 while the bottom layers were 2 mm (H1) and 2–3 mm (H4) in thickness. Acetone extractions (Fig. 4A,D) indicated lower Chl *a* concentrations in the surface strata, with 2.4 (H1) and 4.5 (H4) times

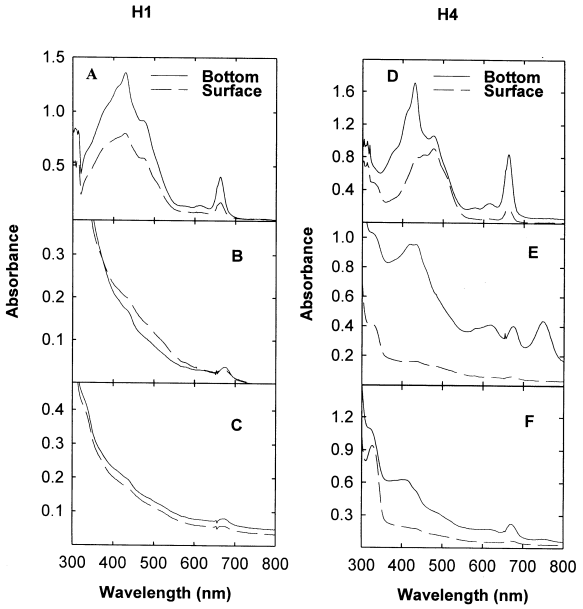

Fig. 4. Absorbance spectra of pigment extraction from split mats H1 and H4. Solid and dotted lines represent the absorbance of bottom and surface layers respectively. A and D are the acetone extractions. B and E represent the glycerol (phycobiliprotein) extractions. C and F are for the warm methanol (MAA) extraction.

higher concentrations in the bottom strata (Table 3), although it should be noticed that the bottom layer of mat H4 was thicker than the top layer. The carotenoid concentrations in the bottom layer were either as high (H4) or twofold higher than the surface concentrations (H1). The resultant Car/Chl *a* ratio was much higher in the surface relative to bottom layers in both communities: in mat H1 the ratio Car/Chl *a* was 50% higher at the surface than at the bottom, but in mat H4 the ratio was more than fivefold higher. The two mats differed in their phycocyanin (PC) profiles, H1 had similar values in the surface and bottom layers while in H4 the bottom layer had a sevenfold higher PC content. Similarly, H1 had a lower PC/Chl *a* in its bottom stratum relative to the surface, while in H4 the inverse pattern was apparent (Table 3). Three main peaks were detected, the phycobiliprotein absorption band (570–640 nm), the Chl *a* (680 nm), and another unidentified peak at 750 nm (Fig. 4E). The scans of the methanolic extractions from the H1 community showed a lack of MAA absorption peaks in either the surface or the bottom stratum (Fig. 4C). In contrast, the top and bottom sections of H4 showed a strong absorbance at 326 nm, which likely corresponds to the MAA absorbance range. The ratio MAA/Chl *a* was four times higher in the surface layer than at the bottom in this mat community (Table 3).

4. Discussion

Cyanobacterial assemblages were the dominant communities in the range of High Arctic pond and lake ecosystems examined in this study. The diversity of species and large biomass stocks indicate the high competitive success of this group of oxyphototrophs in the Arctic freshwater environment. Their high

Table 3
Pigment content (μg cm^{-2}) and ratio to Chl *a* in the upper and lower layers of two mat communities

Pigment	Mat H1			Mat H4		
	Top	Bottom	Bottom/top	Top	Bottom	Bottom/top
Total						
Chl *a*	4.3	10.3	2.39	4.8	21.6	4.53
Carot	4.4	7.1	1.60	8.3	7.0	0.85
Phyco	0.4	0.4	0.93	0.8	5.9	7.14
MAA	0.4	0.4	1.06	0.9	1.1	1.14
Ratios						
Car/Chl *a*	1.04	0.69	0.67	1.73	0.32	0.19
Phy/Chl *a*	0.10	0.04	0.40	0.17	0.27	1.58
MA/Chl *a*	0.09	0.04	0.45	0.19	0.05	0.25

MAAs are in relative units, absorbance at 326 per cm^2.

abundance is similar to that reported from another Arctic environment [3], and to the lakes, ponds and streams of Antarctica [6]. Their high standing stock in the polar regions has been explained in terms of a variety of factors, including low grazing pressure, maintenance of overwintering populations [1] and adaptation to the cold climate which characterises this region. Recently, however, Tang et al. [19] demonstrated that most high latitude mat-forming cyanobacteria are not true psychrophiles but rather are psychrotrophs. Thus, although these species are tolerant of low temperatures, they are not adapted towards optimal growth under these conditions. Other characteristics are, therefore, likely to explain the selective advantage in the polar regions.

The species composition of the communities investigated indicated that in many cases nitrogen-fixing cyanobacteria were present (*Nostoc*, *Anabaena*, *Nodularia*, *Calothrix*, *Scytonema*) and sometimes became dominant, for example by *Scytonema* spp. which was the mat matrix in three out of the five mat communities studied. This genus was also found by Vezina and Vincent [3] in the ponds in Bylot Island but curiously only at one location and with marginal abundance. The dominance of *Scytonema* in the mat matrix may represent an important competitive advantage for the entire mat consortium because it is rich in scytonemin, which is considered a photoprotective pigment absorbing in the UV band, and because N_2 fixation capability minimises any deficiency of combined N, a nutrient that is typically limiting in oligotrophic polar freshwaters [3]. Moreover, the heterocyst frequency in a *Nostoc commune* colony was typical for this species under active N_2-fixing conditions (5.4%). This indicates that N_2 fixation may represent an important N input in the Arctic aquatic ecosystems, as Lennihan et al. [20] have demonstrated in terrestrial systems of the High Arctic. Two mat assemblages were dominated by Oscillatoriaceae, and two more communities were formed almost exclusively by organisms belonging to this cyanobacterial family, as found in another Arctic location [3] and in Antarctica [21].

The pigment concentration range found in our study was similar to or above that found in other polar cyanobacterial mats in the Arctic [3] and in the Antarctic [7]. Our higher values may reflect the multiple pigment extractions conducted in this study with each sample. Chl *a* concentration in three communities was around the theoretical maximum concentration (40 μg cm^{-2}) for complete absorption of ambient PAR by the mats [22].

The variable distribution of sheath pigment concentration suggests different strategies of resistance to bright PAR and/or UV radiation. In the surface layer of *Scytonema*-based mats (H4 and H5), a high proportion of actively motile cyanobacterial filaments was observed. In contrast, the Oscillatoriacean mats (H3 and H6) had low scytonemin concentrations and the surface layer showed very low fluorescence, indicating poorly pigmented cells that may themselves have acted as the shading filter for the brightly fluorescent cells of the filaments lower in the profile.

The Car/Chl *a* ratio in this study separates the communities from two different habitats in terms of irradiance. OSCTBL and NOSTBL grew in extremely dim environments, a narrow crack in the soil surface and the bottom of a deep lake respectively, and presented low values of Car/Chl *a*. In contrast, the other communities were from bright light environments, and showed high Car/Chl *a* values, on average 0.83. These data are consistent with the protecting role of carotenoids against photooxidation in cyanobacteria as Quesada and Vincent [14] suggested for Antarctic cyanobacterial mats. Vezina and Vincent [3] published similar ranges and mean values for the Car/Chl *a* ratio in Arctic communities (Bylot Island). In the Antarctic communities [7] the ratio range is wider and the mean value (0.64) lower than in the Arctic, although different measurement techniques were used.

The surface layers of the mats were highly effective in filtering out the UV region of the spectrum. This absorption of high energy wavelengths is attributable to sheath pigments such as scytonemin [17] and/or to MAA that are found in some but not all species of cyanobacteria [12,13]. This high efficiency in absorbing UV radiation by the surface layer may represent an important role in the polar environments, where solar radiation is continuous in summer and the cumulative UV dose is eventually very high. The photoprotectant pigments absorbed more than 90% of the incident UV radiation, thereby minimising the damaging effects of UV on living cells [1]. The low concentration of UV-screening pigments in the bot-

tom layer of the Omat community is likely to reflect the low flux of solar UV reaching this layer.

Pigment distribution in the upper and bottom layers in the two mats, H1 and H4, showed contrasting strategies of light adaptation. The low carotenoid concentration, as well as the high concentration of phycobiliproteins per unit Chl *a* in the bottom layer of H4, may indicate that less radiation reached deep layers in this community despite being thinner than H1. This distinct pattern may be due to the taxonomic differences of both mats (H4 was rich in *Scytonema* and H1 was a mixture of *Phormidium* and *Scytonema*) or to a different stage in mat development, being H4 older (more sheath material in the surface) than H1. The pigment distribution within cyanobacterial mats seems ideal for optimal utilisation of the incident irradiance, since at the surface most of the high energy (blue and UV) radiation is absorbed, and a dim red-yellow light climate reaches the bottom layer where most of the physiologically active cells are located [6]. This spectral irradiance regime is highly appropriate for cyanobacterial photosynthesis because phycobiliproteins harvest photons with high efficiency in the red-yellow waveband.

In conclusion, our observations are consistent with the view that cyanobacteria are among the dominant biota in aquatic and semi-aquatic ecosystems of the High Arctic [1]. Arctic cyanobacteria form a variety of macroscopic communities: stratified mats, mucilaginous colonies and monospecific biofilms. The spectroradiometric measurements within the communities showed that they are highly structured in terms of their light-capturing and light-screening characteristics. The surface layer of the mats is optimised for filtering out high energy blue and UV wavelengths, while the bottom layer is optimised for harvesting longer wavelength PAR. This vertical sequence of biological filter may be especially important in the polar regions where organisms experience continuous solar radiation and a large cumulative UV dose in summer.

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References

[1] Vincent, W.F. (1999) Cyanobacterial dominance in the polar regions. In: The Ecology of Cyanobacteria (Whitton, B.A. and Potts, M., Eds.). Kluwer Academic, Dordrecht.
[2] Henry, G.H.R. and Svoboda, J. (1986) Dinitrogen fixation (acetylene reduction) in high arctic sedge meadow communities. Arct. Alp. Res. 18, 181–187.
[3] Vezina, S. and Vincent, W.F. (1997) Arctic cyanobacteria and limnological properties of their environment: Bylot Island, Northwest Territories, Canada (73°N, 80°W). Polar Biol. 17, 523–534.
[4] Hamilton, P.B. and Edlund, S.A. (1994) Occurrence of *Prasiola fluviatilis* (Chlorophyta) on Ellesmere Island in the Canadian Arctic. J. Phycol. 30, 217–221.
[5] Sheath, R.G., Vis, M.L., Hambrook, J.A. and Cole, K.M. (1995) Tundra stream macro-algae of North America: composition, distribution and physiological adaptations. In: Biogeography of Freshwater Algae (Kristiansen, J., Ed.), Kluwer Academic, Dordrecht.
[6] Vincent, W.F., Castenholz, R.C., Downes, M.T. and Howard-Williams, C. (1993) Antarctic cyanobacteria: light, nutrients and photosynthesis in the microbial mat environment. J. Phycol. 29, 745–755.
[7] Vincent, W.F., Downes, M.T., Castenholz, R.W. and Howard-Wiliams, C. (1993) Community structure and pigment organisation of cyanobacteria-dominated microbial mats in Antarctica. Eur. J. Phycol. 28, 213–221.
[8] Vincent, W.F. and Quesada, A. (1994) Ultraviolet radiation effects on cyanobacteria, implications for Antarctic microbial ecosystems. In: Ultraviolet Radiation in Antarctica: Measurement and Biological Effects (Weiler, C.S. and Penhale P.A., Eds.), Antarctic Research Series 62. American Geophysical Union, Washington, DC.
[9] Weiler, C.S. and Penhale, P.A. (Eds.) (1994) Ultraviolet radiation and biological research in Antarctica. In: Ultraviolet Radiation in Antarctica: Measurement and Biological Effects (Weiler, C.S. and Penhale, P.A., Eds.), Antarctic Research Series 62. American Geophysical Union, Washington, DC.
[10] Kerr, J.B. and McElroy, C.T. (1993) Evidence of large upwards trends of ultraviolet-B radiation linked to ozone depletion. Science 262, 1032–1034.
[11] Quesada, A., Mouget, J.L. and Vincent, W.F. (1995) Growth of Antarctic cyanobacteria under ultraviolet radiation: UVA counteracts UVB inhibition. J. Phycol. 31, 242–248.
[12] García-Pichel, F. and Castenholz, R.W. (1993) Occurrence of UV-absorbing, mycosporine-like compounds among cyano-

bacterial isolates and an estimate of their screening capacity. Appl. Environ. Microbiol. 59, 163–169.
[13] Quesada A., Goff, L. and Karentz, D. (1998) Effects of natural UV radiation on Antarctic cyanobacterial mats. Proc. NIPR Symp. Polar Biol. 11, 98–111.
[14] Quesada, A. and Vincent, W.F. (1993) Adaptation of cyanobacteria to the light regime within Antarctic microbial mats. Verh. Int. Verein. Limnol. 25, 960–965.
[15] Marker, A.F.H., Nusch, E.A., Rai, H. and 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.
[16] Britton, G. (1985) General carotenoids methods. Methods Enzymol. 111, 113–158.
[17] García-Pichel, F., Sherry, N.D. and Castenholz, R.W. (1992) Evidence for an ultra-violet sunscreen role of the extracellular pigment scytonemin in the terrestrial cyanobacterium *Chlorogloeopsis* sp. Photochem. Photobiol. 56, 17–23.
[18] Bennet, A. and Bogorad, L. (1973) Complementary chromatic adaptation in a filamentous blue-green alga. J. Cell. Biol. 58, 419–435.
[19] Tang, E.P.Y, Tremblay, R. and Vincent, W.F. (1997) Cyanobacterial dominance of polar freshwater ecosystems: are high-latitude mat-formers adapted to low temperature? J. Phycol. 33, 171–181.
[20] Lennihan, R., Chapin, D.M. and Dickson, L.G. (1994) Nitrogen fixation and photosynthesis in high arctic forms of *Nostoc commune*. Can. J. Bot. 72, 940–945.
[21] Howard-Williams, C., Pridmore, R., Downes, M.T. and Vincent W.F. (1989) Microbial biomass, photosynthesis and chlorophyll *a* related pigments in the ponds of the McMurdo Ice Shelf, Antarctica. Antarct. Sci. 1, 124–131.
[22] Hawes, I. (1989) Filamentous green algae in freshwater streams on Signy Island, Antarctica. Hydrobiologia 172, 1–18.