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Ecosystems on ice: the microbial ecology of Markham Ice Shelf in the high Arctic☆

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Abstract

Microbial communities occur throughout the cryosphere in a diverse range of ice-dominated habitats including snow, sea ice, glaciers, permafrost, and ice clouds. In each of these environments, organisms must be capable of surviving freeze–thaw cycles, persistent low temperatures for growth, extremes of solar radiation, and prolonged dormancy. These constraints may have been especially important during global cooling events in the past, including the Precambrian glaciations. One analogue of these early Earth conditions is the thick, landfast sea ice that occurs today at certain locations in the Arctic and Antarctic. These ice shelves contain liquid water for a brief period each summer, and support luxuriant microbial mat communities. Our recent studies of these mats on the Markham Ice Shelf (Canadian high Arctic) by high performance liquid chromatography (HPLC) showed that they contain high concentrations of chlorophylls *a* and *b*, and several carotenoids notably lutein, echinenone and β-carotene. The largest peaks in the HPLC chromatograms were two UV-screening compounds known to be produced by cyanobacteria, scytonemin, and its decomposition product scytonemin-red. Microscopic analyses of the mats showed that they were dominated by the chlorophyte genera cf. *Chlorosarcinopsis*, *Pleurastrum*, *Palmellopsis*, and *Bracteococcus*, and cyanobacteria of the genera *Nostoc*, *Phormidium*, *Leptolyngbya*, and *Gloeocapsa*. From point transects and localized sampling we estimated a total standing stock on this ice shelf of up to 11,200 tonnes of organic matter. These observations underscore the ability of microbial communities to flourish despite the severe constraints imposed by the cryo-ecosystem environment.

Keywords: Algae; Arctic; Cyanobacteria; Cryo-ecosystems; Extremophiles; Ice; Lutein; Microbiology; Pigments; Polar; Scytonemin; Snowball Earth

The cryosphere, defined as the ensemble of all ice-containing environments on planet Earth, is now recognized to be a living system with a diversity of microscopic life-forms of great interest to cryobiologists. Snow is the most conspicuous part of this system, and provides a habitat for microbial communities in high latitude as well as

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temperate and alpine regions, typically dominated by green algae [6] or bacteria [1]. So-called cryoconite communities of cyanobacteria and protists occur in melt-holes on glaciers in the Arctic and Antarctica as well as in alpine environments elsewhere, and support micro-invertebrates such as nematodes, rotifers, and tardigrades [14]. Sea ice forms over more than 25 million km^2 of the ocean surface each year and provides a dynamic, highly structured environment for microbial communities and their associated food webs [23,24]. Several other types of extreme low temperature habitats have now been described including lake-ice [18], streams beneath glaciers [21], the junction between ice crystals in the Antarctic ice cap [16], permafrost soils [19], supercooled water in ice clouds [17] and ice shelves [7,24]. These observations underscore the broad success of micro-organisms in surviving freeze-up and near-freezing growth conditions.

The presence of ice biota in such a variety of low-temperature habitats offers opportunities for studying the adaptive responses to extreme cold and freeze–thaw conditions in the modern-day environment. These studies also have implications for understanding survival, growth, and evolutionary processes on early Earth. There is mounting support for the view that the Precambrian biosphere experienced extreme low temperature conditions at several intervals during the Paleo- and Neoproterozoic, and perhaps even during the earliest steps in the emergence and evolution of life [28]. The timing, duration, and extent of cooling during the Precambrian are subjects of considerable discussion and debate, and views range from localized glacial activity to widespread or even complete freeze-up of the ocean surface. The latter 'snowball Earth' hypothesis [5] is consistent with a broad range of geological, glaciological, geochemical, and modeling evidence, although there are also some observations that do not seem to be in accord with complete planetary coverage by thick ice.

Thick sea ice that occurs today as ice shelves in the polar regions is of particular relevance to discussions about Precambrian glaciation. These environments such as the McMurdo Ice Shelf in Antarctica [7,8,24] provide habitats for microbial mat communities. The communities are dominated by cold-tolerant (but not psychrophilic) prokaryotes [22] that in turn provide local refugia for the growth and development of more complex organisms including eukaryotic microalgae and micro-invertebrates. These consortia offer insights into how diverse lifeforms may have persisted and evolved during global episodes of extreme cold [28].

Up until recently, ice shelf ecosystems were thought to be restricted to Antarctica. However, our surveys at the northern limit of North America in 1998 revealed that the largest ice shelf in this region, the Ward Hunt Ice Shelf, contains microbial communities including 'ice-mats' that grow in meltwater lakes over the surface of the ice [27]. Since that time we have found these communities to be more widespread on ice shelves along the Ellesmere coastline (Mueller et al. unpublished data). In this paper we briefly review the published work to date on Arctic Ice Shelf cryo-ecosystems. We then present new observations from our recent expeditions to the richest of these microbial habitats, the Markham Ice Shelf.

Arctic ice shelves

Up until the early 20th century, the northern coastline of Ellesmere Island was fringed by thick land-fast ice floating on the sea. ^{14}C-dating of driftwood and other biogenic materials trapped behind the ice shows that this extensive ice shelf began to form about 4500 years before the present during a period of Holocene cooling, and it has been in place for at least 3000 years. Based on observations during Peary's expedition [15], aerial photographs in the 1950s and satellite data we estimate that this thick ice (20–100 m [9]) had a total aerial extent of about 9000 km^2 at the beginning of the century and contracted by 90% by 1999, probably as a result of climate warming [10,26]. Remnants of this earlier 'Ellesmere Ice Shelf' are now found in embayments along the coastline (Fig. 1), including five main ice shelves of which the largest is the Ward Hunt Ice Shelf [9]. The latter is currently undergoing further fragmentation and loss [13].

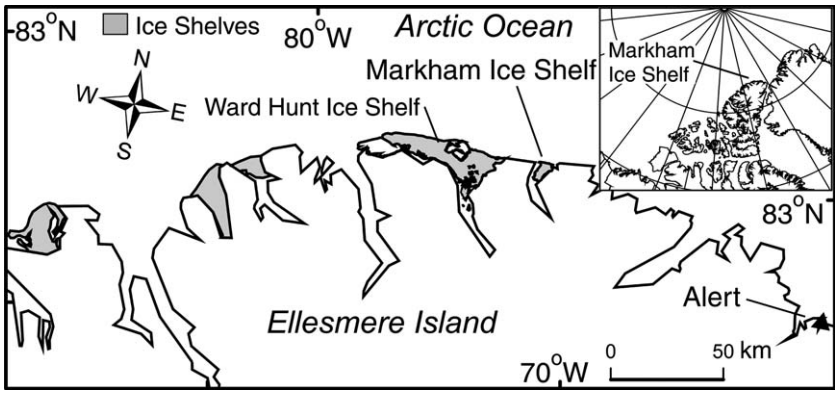

Fig. 1. The location of Markham Ice Shelf and the other ice shelves of northern Ellesmere Island, Nunavut, in the Canadian high Arctic.

All of the ice shelves are distinguished by an undulating surface topography in which elongate lakes and streams occupy troughs that are oriented parallel to each other and to the prevailing wind [9]. As on some Antarctic ice shelves [2], large quantities of marine-sediments have been brought up to the surface of the ice by basal freezing and surface ablation, and redistributed by stream flow and wind activity across the ice shelf.

These sediments at the base of the meltwater lakes on the Ward Hunt Ice Shelf and in melt-holes on the ice-ridges contain highly pigmented microbial mats [25]. The microbial consortia, or 'ice-mats' [27] consist of viruses, bacteria, filamentous cyanobacteria, protists including diatoms, flagellates, and ciliates, and micro-invertebrates including nematodes, rotifers, and turbellaria (flatworms). These perennial communities persist mostly frozen throughout almost all the year, punctuated by a brief period of thaw each summer. They are analogous to microbial mat communities found on the McMurdo Ice Shelf in Antarctica, however, their species composition and mat architecture differ greatly from these south polar ecosystems.

Markham Ice Shelf

Subsequent to the initial discovery of the Ward Hunt Ice Shelf cryo-ecosystem we have begun to explore the other ice shelves along the Ellesmere Island coastline. All contain microbial mats of the type found at Ward Hunt, however, the richest communities in terms of biomass concentration per unit area are on the Markham Ice Shelf (Fig. 1; Mueller et al. unpublished data). Over the 2001–2003 field seasons we have visited and sampled this region, and here we report our observations from this productive ecosystem on ice.

Climatology

The nearest meteorological station to Markham Ice Shelf is at Alert, 150 km further eastwards along the northern Ellesmere coast. The climate normal (1971–2000) for this station (Environment Canada, unpublished data) indicates an annual mean air temperature of −18 °C. February, the coldest month, has an average daily minimum of −37 °C and a daily mean temperature of −33.4 °C. The July average daily mean and maximum are 3.3 and 6.0 °C, respectively. On average, 77.5 days each year have maximum air temperatures above 0 °C, and there are 195.2 thawing degree-days per year.

Surface properties

The Markham Ice Shelf is centered at latitude 83°03′N, longitude 71°27′W, and partially occupies the entrance of Markham Fiord (Figs. 1 and 2). Its area at the end of 2002 was 39.5 km^2 (estimated from RADARSAT imagery) covering 35% of the

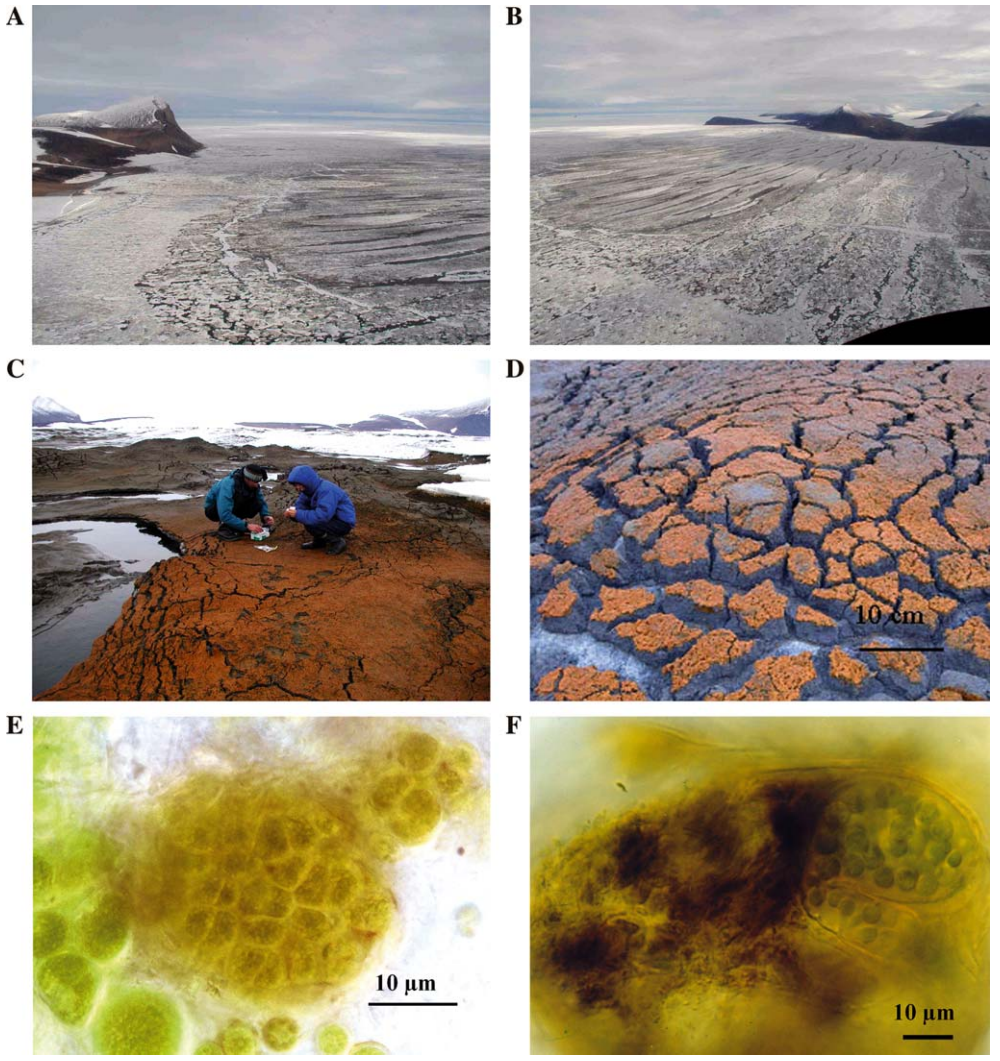

Fig. 2. Markham Ice Shelf and its microbial communities. (A, B) Overview of the ice shelf looking northwest and northeast respectively, August 2003; (C, D) the exposed highly pigmented mat communities on the ice shelf; (E) X1000 micrograph of the surface orange-red layer of the microbial mat showing green algae (cf. *Palmellopsis* sp. and *Bracteococcus* sp.); (F) X1000 micrograph of the microbial mat under-layer showing the colonial cyanobacterium *Gloeocapsa* sp. and the dark pigmentation due to scytonemin and scytonemin-red.

fiord. The surface ice on the northeastern sector of the ice shelf is atmospherically derived (firn ice) and extends over 6.5 km^2. This sector is relatively clean of sediment. Elsewhere, the marine ice has been exposed leaving a sediment-laden surface of 'basement ice.' A point transect analysis near the middle of the basement ice section showed that 31% of the surface is covered with sediment (the presence or absence of sediment was determined every 10 cm over a 180 m north–south trending transect). At each 10 m interval, sediment present within 1 m of the transect was collected and its surface area was noted (36–400 cm^2). Sediment concentrations varied between 0.1 and 27.1 kg dry weight m^{-2}, averaging 6.6 kg m^{-2} ($SD = 9.4$, $n = 23$). Extrapolated to 31% of the surface area of

the basement ice, this gives an estimate of 67.5 Gg of sediment. Determinations of biomass by loss-on-ignition showed that this mat-containing sediment was 9–25% organic matter. Using an average value of 16.6%, this would indicate that the ice shelf ecosystem supported a total standing stock of 11.2 Gg (11,200 tonnes) of organic material. This amount should be interpreted as an upper bound, since the area chosen for the transect may have contained a disproportionately high amount of sediment and a broader synoptic survey is required to refine this first-order estimate.

Meltwater properties

The mat-containing sediments of the Markham Ice Shelf occur in raised mounds of ice and also at the base of melt water lakes that occupy the parallel troughs that are characteristic of all of the Canadian high Arctic ice shelves. At the time of sampling, these waters had a mean pH value of 7.02 (range 6.30–7.86, $n = 6$). In the marine ice area the surface waters were brackish with conductivities in the range 2.7–4.1 mS cm^{-1}, while a value of 0.006 mS cm^{-1} was obtained in a melt pond fed by firn ice. The meltwaters varied in their profile characteristics with some showing vertical stratification while others were well-mixed (Fig. 3). Water temperatures were typically near 0 °C, but increased to in excess of 3 °C in the more saline layers overlying some of the mat communities.

Meltwater was sampled from the surface of the water column by submerging a rinsed collection bottle, and from the bottom of the water column by sampling with a hand pump. The microbial mats were collected, placed in triple-rinsed polyethylene bags, and gently pressed to extract the interstitial water that was then transferred to sample bottles. All water samples were filtered in the field to remove the particulates and subsequently analyzed by the National Laboratory of Environmental Testing in Burlington, Canada. Major ions were determined by atomic absorption (Ca^{2+}, K^+, Mg^{2+}, and Na^+), ion chromatography (Cl^-, SO_4^{2-}) or heteropoly blue colorimetry (SiO_2). Meltwater nutrient concentrations were determined by UV digestion and infrared detection (dissolved organic and inorganic carbon, respectively), by ion chromatography (nitrate) or by automated colorimetry (total nitrogen and ammonium-indophenol, nitrate/nitrite-cadmium reduction, dissolved reactive phosphorus- ammonium molybdate-stannous chloride).

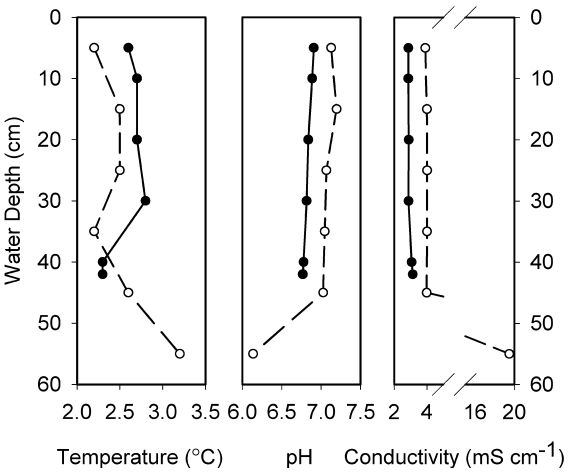

Fig. 3. Profiles of temperature, pH, and conductivity in two contrasting meltwater ponds on the Markham Ice Shelf.

The major ion composition resembled dilute seawater with dominance by sodium and chloride, and high concentrations of sulphate (Table 1). Inorganic carbon concentrations were low in the water, but there were order-of-magnitude higher values in the interstitial waters of the mat communities (Table 2). Dissolved reactive phosphorus concentrations were relatively high suggesting that P-limitation of the microbial mat communities would be unlikely. Dissolved organic carbon

Table 1
Major ion concentrations (in mg L^{-1}) and ratios for a Markham Ice Shelf meltwater pond, sampled August 2002

Ion or ratio	Surface water	Bottom water
Cl^-	1000	1040
SO_4^{2-}	177	169
SiO_2	0.1	0.08
Ca^{2+}	27.2	27.4
K^+	23.9	23.9
Mg^{2+}	72.1	72.6
Na^+	612	624
Mg^{2+}/Ca^{2+}	2.7	2.6
Mg^{2+}/Na^+	0.1	0.1
$Na^+/(Ca^{2+} + Na^+)$	1.0	1.0

Table 2
Nutrient concentrations in a Markham Ice Shelf meltwater pond, sampled August 2002

Nutrient	Surface water	Bottom water	Microbial mat pore water
Dissolved organic carbon	200	100	1714
Dissolved inorganic carbon	2000	2200	2857
Total nitrogen	101	177	429
Ammonium-nitrogen	36	114	120
Nitrite-nitrogen	<1	<1	2.9
Nitrate-nitrogen	<5	<5	14.3
Dissolved organic nitrogen	65	63	309
Dissolved reactive phosphorus	2.6	2.9	3.7

All values are in $\mu g\,L^{-1}$.

concentrations were high in the water column, and 30–40% higher in the mat pore waters, indicating the substantial release of dissolved materials from the microbiota. Consistent with this conclusion, dissolved organic nitrogen was five times higher in the interstitial mats relative to the overlying water column, and the presence of high concentrations of ammonium in all samples (Table 2) indicated active microbial decomposition.

Mat communities

The sediment-containing regions of ice shelf were typically overlain by a thin (100–500 μm) cohesive surface layer of orange pigmented algae (Figs. 2C and D). Microscopic examination of this material showed that it was composed by a small number of taxa, mainly terrestrial and subaerial palmelloid chlorophyte genera (cf. *Chlorosarcinopsis*, *Pleurastrum*, cf. *Palmellopsis*, and cf. *Chlorokybus*) and solitary cells of *Bracteococcus*. Some of the cells were bright green and while others were masked with an orange-yellow pigment (Fig. 2E). These eukaryotic algae were held within a matrix containing cyanobacteria with yellow-brown sheaths (*Nostoc* sp. and *Gloeocapsa* sp.), filaments of *Phormidium* sp. and *Leptolyngbya* sp., and diatoms (*Navicula* spp.). This surface layer was underlain by a cm-thick zone of flocculent material, composed of dark, olive-green coloured flakes of mat. These dense, black aggregates (Fig. 2F) contained chlorophytes, diatoms, *Gloeocapsa* sp. and *Leptolyngbya* sp. (some partially decomposed) and heterotrophic bacteria. This lower layer was directly in contact with the underlying deep-blue ice. In an analysis of a sectioned sample by Utermöhl inverted microscopy, the algal abundance was 4.58×10^5 and 2.51×10^5 cells cm^{-2} in the surface and bottom layers, respectively, with 62–73% of the counts for each taxonomic group (chlorophytes, cyanobacteria, and diatoms) in the surface layer. Cyanobacteria were the overall dominants in terms of cell counts (88% of all algal cells in the surface layer and 89% in the lower layer), however the cells of the cyanobacterial dominants were small relative to the less numerous eukaryotic algae.

Bulk pigment analyses

The surface waters on the Markham Ice Shelf contained low, oligotrophic levels of chlorophyll *a* (mean = 0.18, range = 0.02–0.68 $\mu g\,L^{-1}$, $n = 6$; estimated by filtration onto GF/F glass fibre filters, ethanol extraction, and fluorometry before and after acidification) indicating a sparse phytoplankton community and limited resuspension of benthic communities. Phaeophytin always exceeded chlorophyll concentrations, averaging 1.5 $\mu g\,L^{-1}$ for these water column samples. The vast majority of the algal pigment in this system was located in the microbial mats. For all sites within and outside the meltwater ponds, the mean biomass value for the mats was 147 mg Chl *a* m^{-2} ($n = 22$). However, there was huge range in these estimates (5.4–448 mg Chl *a* m^{-2}) reflecting the high degree of patchiness in this system. Carotenoid levels (as determined by spectrophotometric measurements of absorbance at 480 nm of acetone extracts) ranged from 18 to 6460 $mg\,m^{-2}$, with an

average of 1307 mg m^{-2} ($n = 22$). These values are uncorrected for the presence of the UV-screening compound scytonemin, which interferes with carotenoid determination due to its absorbance of blue wavelengths [3], and the values could be overestimated by up to 25%.

HPLC pigment analyses

Samples of mats from Markham Ice Shelf were separated into the surface and bottom layers using a blade, and then extracted by sonicating for 30 s, two times (17 W) in 4 ml of 100% acetone and incubating overnight in the dark at −20 °C under argon gas. These extracts were then separated by centrifugation (10 min, 4000 rpm), filtered through 0.2 μm Acrodisc filters and stored under argon gas at 4 °C in darkness until the HPLC analysis within 1 h of extraction. Immediately before each injection, extracts were diluted with filtered (0.2 μm) MilliQ water to 80% acetone to improve the sharpness of early eluting peaks. The pigments were analysed by injecting 50 μl of sample into a Varian Prostar HPLC system. The peaks were detected by diode-array spectroscopy (350–750 nm) set to a slit width of 1 nm. Absorbance chromatograms

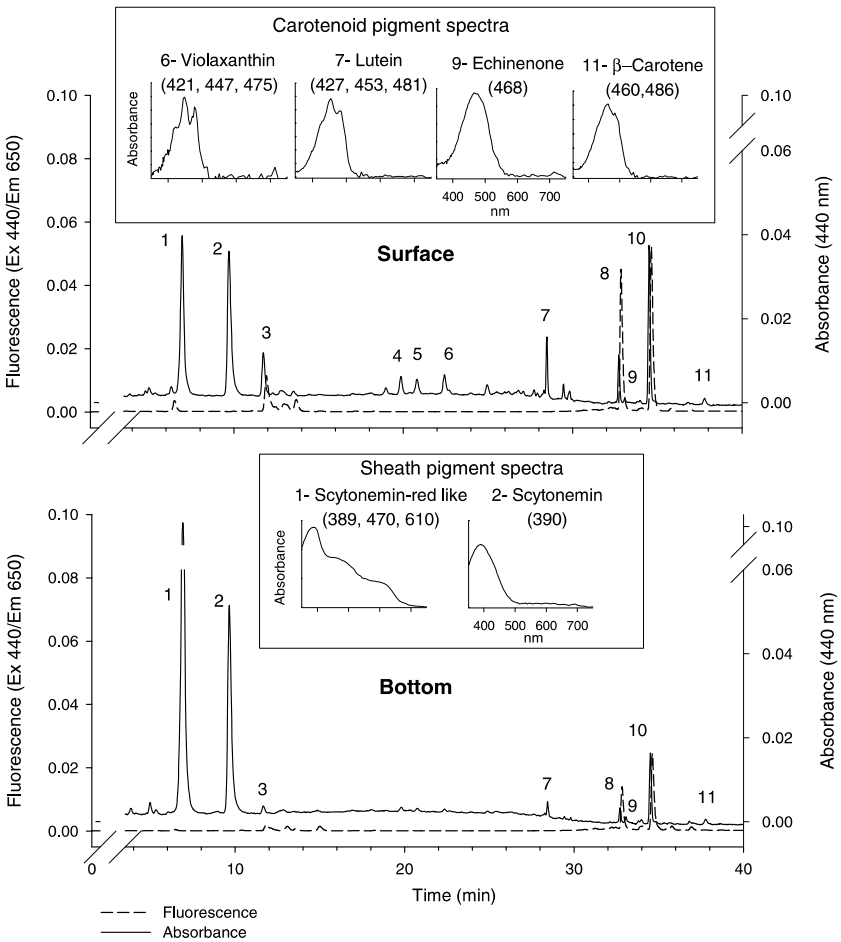

Fig. 4. HPLC chromatograms of the surface and bottom layer of a microbial mat sample from the Markham Ice Shelf, August 2003. The pigments are: 1, scytonemin-red like; 2, scytonemin; 3, chlorophyllide *a*-like; 4, fucoxanthin; 5, unknown carotenoid; 6, violaxanthin; 7, lutein; 8, chlorophyll *b*; 9, echinenone; 10, chlorophyll *a*; and 11, β-carotene. The inset shows the spectra for the main peaks as determined by the HPLC photodiode array detector.

were extracted at 430 (for scytonemin), 440 (for chlorophylls), and 450 nm (for carotenoids). Chlorophylls were also detected by fluorescence (excitation: 440 nm, emission: 650 nm). Standards for identification and quantification of pigments were purchased (chlorophylls *a* and *b*, β-carotene, canthaxanthin, echinenone, fucoxanthin, lutein, violaxanthin, and zeaxanthin), while a secondary standard of scytonemin (purity >95%) was made from samples of *Nostoc commune* according to Garcia-Pichel and Castenholz [3]. The specific extinction coefficient used for scytonemin and scytonemin-red was 112.6 $L\,g^{-1}\,cm^{-1}$ [4]. The HPLC solvent protocol followed the procedure of Zapata et al. [29] using gradients of two solvent mixtures: a methanol, acetonitrile, and aqueous pyridine (50:25:25 v:v:v) solution, and a methanol, acetonitrile, and acetone (20:60:20 v:v:v) solution. The flow rate was 1 $mL\,min^{-1}$.

The HPLC results (Fig. 4, Table 3) show that both layers contained high concentrations of the cyanobacterial UV-screening, sheath-pigment scytonemin, with 50% higher levels in the bottom layer. A compound that closely resembles scytonemin-red, a known degradation product of scytonemin [3,4] also occurred in high concentrations in both layers. It is likely that this degradation pigment, favoured by the reducing environment, represents long-term accumulation and slow rates of decomposition within the mats. Scytonemin and its degradation products are chemically very stable and fossil pigments recovered from lake sediments have been interpreted as indicators of UV exposure in the past [11].

The surface layer contained higher values of both chlorophylls *a* and *b*. The dominant carotenoids throughout the mat were lutein, echinenone, and β-carotene, whereas violaxanthin and the diatom pigment fucoxanthin were only detected in the surface layer. High concentrations of carotenoids are likely to play a key protective role under the combined extremes of cold temperatures and

Table 3
Pigment concentrations and ratios in the surface and bottom layers of the mat community of Markham Ice Shelf, sampled August 2003

Pigment	Pigment concentrations (μg cm^{-2})		Pigment ratios Surface/Bottom
	Surface layer	Bottom layer	
Chlorophylls			
Chlorophyll *a*	32.95	17.19	1.92
Chlorophyll *b*	8.17	2.74	2.98
Chlorophyllide	3.42	0.73	4.70
Scytonemins			
Scytonemin	69.72	99.94	0.70
Scytonemin-red	60.94	169.78	0.36
Carotenoids			
Fucoxanthin	2.40	nd	—
Violaxanthin	2.62	nd	—
Zeaxanthin	2.15	nd	—
Lutein	10.54	2.79	3.78
Canthaxanthin	1.51	0.28	5.28
Echinenone	0.51	0.63	0.80
β-carotene	0.40	0.65	0.62
Total carotenoids	20.12	4.35	4.63
Pigment ratios			
Car/Chl*a*	0.61	0.25	2.41
Scy/Chl*a*	2.12	5.81	0.36
Scy/Car	3.46	22.98	0.15
Scy-red/Scy	0.87	1.70	0.51

Car, total carotenoids; Chl*a*, chlorophyll *a*; Scy, scytonemin; Scy-red, scytonemin-red; nd, not detected.

high solar (including UV) irradiances in which photochemical damage can be substantial [20]. The carotenoid/chlorophyll *a* ratio was more than twice as high in the surface layer than in the bottom, consistent with the protective role of carotenoids against photooxidative stress. In contrast, the scytonemin/chlorophyll *a* ratio was three times higher in the bottom layer reflecting the long term accumulation processes and the relative chemical stability of scytonemin.

Conclusions

The Arctic Ice Shelf cryo-ecosystem described here illustrates the potential for abundant microbial populations despite the severe conditions imposed by this extreme polar environment. The mat communities dominate the overall productivity of the system and have gradually accumulated to very high standing stocks of organic carbon. These communities are perennial, with the persistence of a large over-wintering biomass that is then available to initiate photosynthesis and growth during the brief periods of melt conditions. Strategies that allow these communities to flourish include a tolerance of freeze–thaw cycles, prolonged dormancy, growth at continuously low temperatures and the ability to survive extreme high solar irradiance as well as winter darkness. Our HPLC analyses show that these communities are especially rich in protective pigments, including the UV-screening compound scytonemin. These microbial strategies are also likely to have played an important role in the survival of life during major glaciation events of the Precambrian, suggesting that some adaptive low-temperature features of modern-day biota could have deep phylogenetic origins. Global circulation models all converge on the prediction that future warming trends will be amplified at high latitudes [12], and recent measurements indicate that climatic change is already having pronounced impacts on the Arctic coastal environment [13]. The remarkable cryo-ecosystems of the high Arctic, of great interest to cryobiologists, will be particularly vulnerable to this accelerated warming.

Acknowledgments

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