SHORT COMMUNICATION

Ice Shelf Microbial Ecosystems in the High Arctic and Implications for Life on Snowball Earth

W.F. Vincent (✉), J.A.E. Gibson, R. Pienitz, V. Villeneuve
Centre d'Études Nordiques, Université Laval, Sainte-Foy QC G1K 7P4, Canada
e-mail: warwick.vincent@bio.ulaval.ca, Tel.: +1-418-6565644, Fax: +1-418-6562043

P.A. Broady
Department of Plant and Microbial Sciences, University of Canterbury, Christchurch, New Zealand

P.B. Hamilton
Canadian Museum of Nature, Ottawa, ON K1P 6P4, Canada

C. Howard-Williams
National Institute of Water and Atmospheric Research, Christchurch, New Zealand

Abstract The Ward Hunt Ice Shelf (83°N, 74°W) is the largest remaining section of thick (>10 m) land-fast sea ice along the northern coastline of Elles-mere Island, Canada. Extensive meltwater lakes and streams occur on the surface of the ice and are colonized by photosynthetic microbial mat communities. This High Arctic cryo-ecosystem is similar in several of its physical, biological and geochemical features to the McMurdo Ice Shelf in Antarctica. The ice-mats in both polar regions are dominated by fil-amentous cyanobacteria but also contain diatoms, chlorophytes, flagellates, ciliates, nematodes, tardi-grades and rotifers. The luxuriant Ward Hunt consortia also contain high concentrations (10^7–10^8 cm^{-2}) of viruses and heterotrophic bacte-ria. During periods of extensive ice cover, such as glaciations during the Proterozoic, cryotolerant mats of the type now found in these polar ice shelf eco-systems would have provided refugia for the survi-val, growth and evolution of a variety of organisms, including multicellular eukaryotes.

Palaeomagnetic and other geological evidence of glaciation at low latitudes during the Proterozoic has been interpreted in terms of major shifts in the earth's obliquity and a reversal of climate zonation relative to today (Williams 1998), or alternatively by global-scale glaciations during which the entire world ocean was frozen by runaway ice-albedo events (Hoffman 1999; Hoffman et al. 1998). The latter 'snowball Earth hypothesis' is supported by modeling results (Jenkins and Smith 1999), but has been criticized on the basis that most or all surface life would have been extinguished by freeze-up events of this magnitude (Williams 1998). Our ob-servations from the Arctic reported here, and our earlier studies in the Antarctic, show the existence of extensive microbial mat communities growing in meltpools, on the surface of ice shelves (>10-m thick, multi-year sea ice connected to the coast), a habitat that would have been more widespread dur-ing episodes of extreme cold. In contrast to the mod-ern-day sea ice biota, which is dominated by diatoms (Vincent 1988), the ice shelf communities in both polar regions are dominated by oscillatorian cyano-bacteria, a group that is widely distributed in the Ar-chaean and Proterozoic fossil records (Schopf 1993, 1994). These filamentous micro-organisms secrete mucilaginous organic compounds and bind together sediment particles, resulting in cohesive mats and films that would offer protected microhabitats for less tolerant biota during periods of extensive glacia-tion.

Our research was conducted on the Ward Hunt Ice Shelf (WHIS) on the northern coast of Ellesmere Is-land in the Canadian High Arctic, and followed from our similar studies on the McMurdo Ice Shelf (MIS) in the Ross Sea sector of Antarctica. At the time of our Arctic sampling expedition (July 1998), the surface morphology of WHIS was similar to that shown in Fig. 1. The upper ice surface was charac-terized by a parallel system of wave-like troughs and

Fig. 1. Aerial view of the Ward Hunt Ice Shelf showing the parallel, elongate meltwater lakes. Since the date of this photograph (18 August 1950) the ice shelf has ablated back to the ice rise seen to the north (*left*) of the central Island (Ward Hunt island). (Copyright 1950 by Her Majesty the Queen in Right of Canada, reproduced by permission of Natural Resources Canada from the National Air Photo Library, Roll Number T404L-04)

Table 1. Comparison of the Ward Hunt Ice Shelf and McMurdo Ice Shelf. The enrichment factors (see text) are the ranges for all data from the present study for WHIS or calculated from published MIS data (from de Mora et al. 1994)

Ice shelf or meltwater properties	Ward Hunt Ice Shelf	McMurdo Ice Shelf
Latitude, longitude	83°N, 74°W	78°S, 166°E
Dimensions (km)	10×60	30×50
Area (km^2)	485	1200
Ice thickness (m)	30–80	10–50
Meltwaters	Lake P9	Fresh Pond
Depth (cm)	40	50
Conductivity ($\mu S/cm$)		
Surface	25	212
Bottom	2300	1140
Temperature (°C)		
Surface	1.0	2.2
Bottom	0.5	4.6
pH		
Surface	4.2	9.8
Bottom	7.1	–
K^+ enrichment	0.6–1.2	0.9–9.2
SO_4^{2-} enrichment	1.0–67	0.8–151

ridges, with an amplitude of 2–6 m and a distance between ridge crests of c. 250 m. The troughs contained elongate meltwater lakes and streams, typically 5–15 m wide, 0.3–3 m deep and 5–30 km long. The ice shelf was reduced in extent relative to that shown in Fig. 1, consistent with the major changes in this environment that have taken place over the course of the twentieth century (Jeffries 1992). The current area of WHIS, based on our digital analysis of a RADARSAT image at the time of our sampling, is 485 km^2 (excluding the ice rises and new multi-year ice) which is less than half the estimate based on observations within the same quadrat during the 1906 Peary expedition. Commander Peary reported that the northern coast of Ellesmere Island had a continuous fringe of undulating ice with lakes and streams similar to those observed today on WHIS (Peary 1907), and observations from his expedition indicate that there was a total ice shelf extent of 8900 km^2 in the early 1900s. Smaller fragments of this earlier ice shelf fringe occur at several sites along the northern Ellesmere Island coastline (e.g., McClintock, Milne and Ayles Ice Shelves) and these are likely to have similar ecosystem properties to WHIS.

Our reference site in the south polar region, the MIS ablation zone, is similar in ice thickness to WHIS (Table 1); however, it has a more varied topography (Howard-Williams et al. 1990; Vincent 1988). About 30% of the MIS surface is characterized by an undulating ice terrain covered by a layer of moraine and marine sediments, with the hollows occupied by ponds ranging in size up to 30,000 m^2. The remaining 70% is composed of irregular pinnacle ice in which the ponds are typically small and shallow with a thin and irregular distribution of sediments. MIS has also undergone substantial calving over the course of the twentieth century (Frezzotti 1997).

The WHIS lakes and streams were underlain by smooth ice with irregularly spaced, circular 'cryoconite holes' (sediment-containing depressions in the ice), up to 40 cm wide and 30 cm deep, and concentrated along the margins of the lakes (Figs. 2, 3). Similar holes in the ice also occurred as discrete meltwater-filled pools (1–70 cm in diameter) at slightly higher elevations on the ice ridges; these might eventually be incorporated into the lakes by subsequent melting processes. Our sampling of the lake holes showed that they had a similar temperature but much higher salinity (as measured by electrical conductivity) and pH than the overlying water (Fig. 2, Table 1). We have observed similar gradients in conductivity in the MIS ponds (Table 1). The surface WHIS meltwaters had an extremely low pH (down to 3.8) that may be the result of acid deposition from the polluted Arctic atmosphere (Wadleigh 1996) in combination with the weak buffering capacity of the waters. In contrast, the MIS ponds are invariably alkaline, with pH values up to 10.6. The major ion ratios of the ice shelf waters from both polar regions indicate that their salts are large-
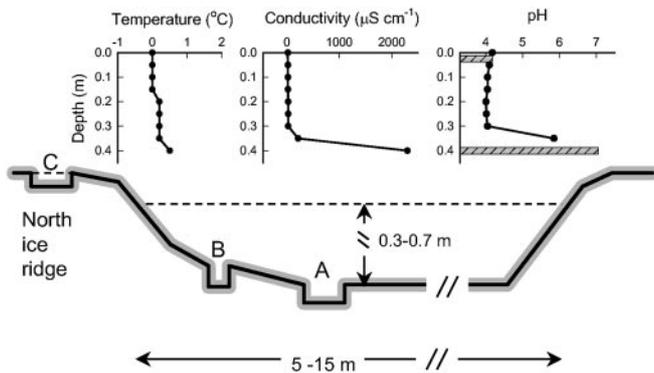
Fig. 2. Cross-sectional diagram of one of the elongate meltwater lakes on the Ward Hunt Ice Shelf (Lake P9) and profiles through the water column, 27 July 1998. *Dashed lines* water levels. Circular or oval depressions in the ice (cryoconite holes) contained benthic microbial mats, and were either at the bottom of the lake (*A*, *B*) or on the adjacent ice ridge (*C*). The profiles extend to the bottom of *hole B* which was 10 cm deep and overlain by the 30 cm water column of the lake. The pH measurements were made at the lake surface and in the mat at the bottom of the hole (*bars*) and by a more complete profile (*line*, *dots*)

ly derived from the sea. The enrichment factor for K^+ ($[K^+]/[Cl^-]$ relative to the same ratio for seawater) is typically around 1.0, while that for sulphate is much higher in some of the ponds on both ice shelves (Table 1) consistent with the re-dissolution of mirabilite ($Na_2SO_4 \cdot 10H_2O$) that has precipitated out during freeze-concentration of the sea water (de Mora et al. 1994). The marine origins of both ice shelves is further supported by the presence of benthic marine organisms which have been incorporated into the bottom of the ice and ultimately released at the surface. For example, we have observed the remains of sponges, mollusks and benthic crustaceans on the surface of WHIS and MIS. Isotopic analysis of WHIS ice has shown that freshwater inputs from nearby Disraeli Fjord also contribute to the ice shelf, in particular on its eastern side (Jeffries 1992).

Photosynthetic microbial mats are a feature of the meltwater environments of both ice shelves. The cryoconite holes within and outside the WHIS lakes contained a 2–10 mm layer of sediment that was loosely bound together by filamentous cyanobacteria of the order Oscillatoriales (Figs. 2, 3) and sometimes highly pigmented by a thin surface layer of cyanobacteria and chlorophytes containing orange carotenoids (Fig. 3). Orange pigmented oscillatorian cyanobacteria are also common in the MIS meltwater habitats, although at some sites N_2-fixing cyanobacteria (Nostocales) are codominants, perhaps reflecting the higher phosphorus availability and low N:P ratios in MIS environments (Howard-Williams

et al. 1990). Chlorophyll *a* concentrations in the WHIS holes ranged from 0.4–15.3 µg cm^{-2}, with a mean ratio of 2.1 ± 1.0 µg carotenoid per microgram of Chl *a* ($n = 30$). These ranges overlap with our MIS pigment values (Howard-Williams et al. 1990); however, the mats cover a much greater percentage of the bottom of each pond (up to 100%) on MIS, and the total standing stock of pigments in this cryo-ecosystem is likely to be orders of magnitude higher than on WHIS where the mats are restricted to the discrete cryoconite holes. The carotenoid-rich characteristics of the mats on both ice shelves, in combination with the known UV-screening properties of Arctic and Antarctic mat communities (Quesada et al. 1999), indicate a high level of protection from the effects of short wavelength radiation. The mucopolysaccharide matrix is also likely to protect the biota living within the mat against freeze-thaw cycles and desiccation (Vincent 1988).

The microbial mats of both ice shelves harbored many other organisms including bacteria, eukaryotic algae, ciliates, flagellates, nematodes, rotifers, platy-helminthes (WHIS only) and tardigrades. We made a series of agar plate enrichment cultures from WHIS ice-mat samples, and these yielded a high diversity of chlorophyte genera, tentatively identified as *Palmellopsis*, *Chlorosarcinopsis*, *Pleurastrum*, *Chlamydomonas*, *Chlamydocapsa*, *Chlorella*, *Bracteacoccus*, *Chlorococcum* and *Klebsormidium*. Light and scanning electron microscopy of our samples and cultures showed that the WHIS ice-mats also provided the habitat for an assemblage of small, benthic and aerophilic diatoms (Fig. 3) dominated by *Chamaepinnularia begeri* (Krasske) Lange-Bertalot (syn. *Navicula begeri* Krasske). Analysis of a WHIS ice-mat sample prepared for diatom enumeration by polarized light microscopy gave the following relative abundance of species: *C. begeri* (90%), *Nitzschia homburgiensis* Lange-Bertalot (5%), *Nitzschia palea* (Kützing) W. Smith (2.3%), *Navicula phylleptosoma* Lange-Bertalot (1%), *C. krookii* (Grunow) Lange-Bertalot, *C. gandrupii* (Petersen) Lange-Bertalot and Krammer, *Pinnularia borealis* Ehrenberg, *Luticola palaearctica* (Hustedt) Mann, *Achnanthes petersenii* Hustedt and *Nitzschia* cf. *pusilla* Grunow (all <1%). Chrysophyte cysts were also present. MIS mats similarly contained coccoid chlorophytes and a diatom assemblage dominated by the genera *Navicula*, *Nitzschia*, *Pinnularia* and *Achnanthes* (Howard-Williams et al. 1990). For further microbiological analysis, mat samples from three WHIS lakes were dispersed and stained with the combination of fluorochromes SYBR Green I and II (C. Lovejoy, unpublished). Subsequent examination of this stained material by epifluorescence
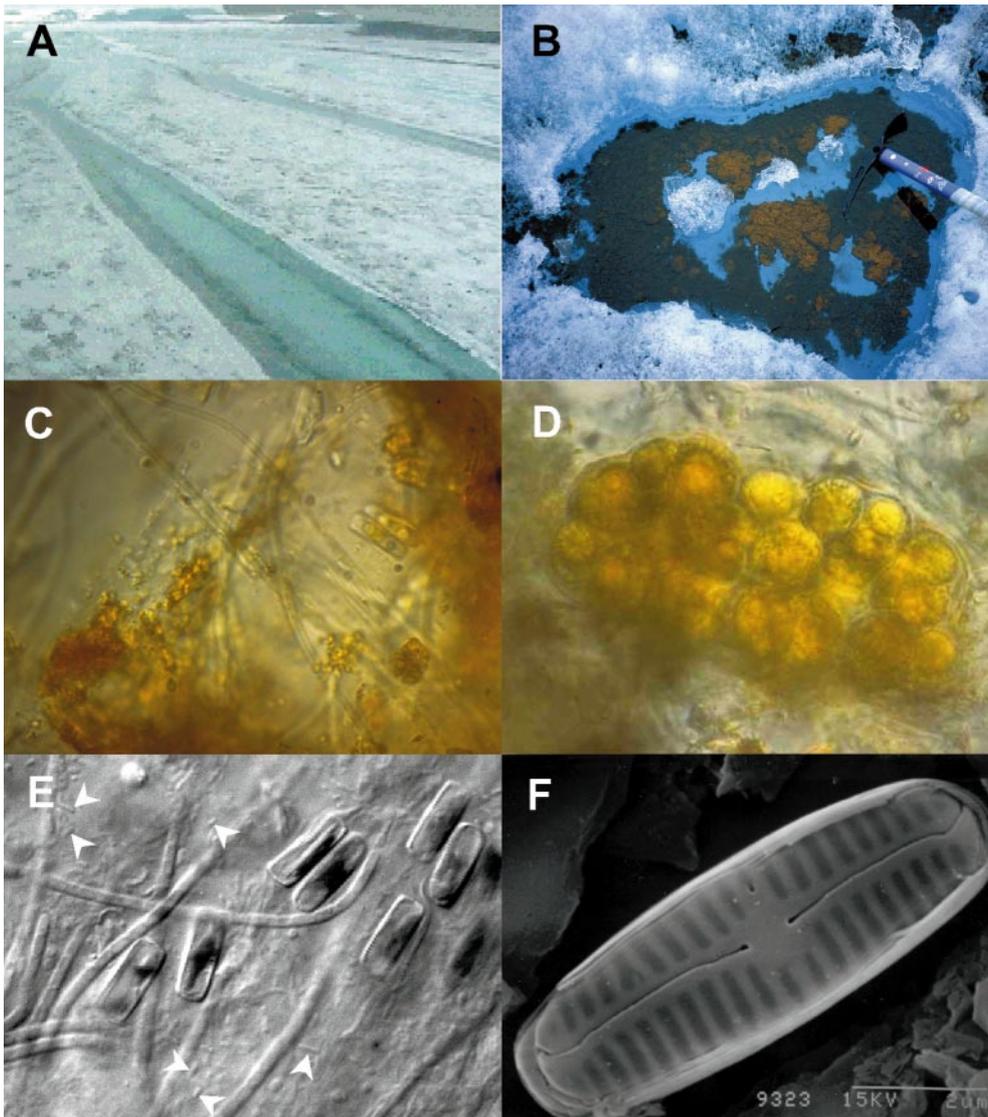
Fig. 3A–F. The Ward Hunt Ice Shelf ecosystem and biota. A) Elongate meltwater lake on the surface of the ice (29 July 1998). B) Orange ice-mat in a cryoconite pool near the edge of a meltwater lake. C) Light micrograph of the mat (the filaments are c. 1 μm diameter). D) cf. *Palmellopsis* (each cell is c. 8 μm diameter), one of nine chlorophyte taxa recorded in the mats. E) Nomarski interference micrograph of a live sample of the ice-mat showing oscillatorian cyanobacteria embedded within a mucilaginous matrix, plastid-containing diatoms and heterotrophic bacteria (some identified by *arrowheads*). F) Scanning electron micrograph of *Chamaepinnularia begeri*, the dominant diatom species within the ice-mat consortium

microscopy (Noble and Fuhrman 1998) showed the presence of viruses and heterotrophic bacteria, with a range for the three mats of $2.3–16.5 \times 10^7$ viruses and $0.7–7.5 \times 10^7$ bacteria per square centimetre of mat.

Highly concentrated microbial consortia (i.e. populations from diverse microbial groups in physical contact with each other) of the type that we have found in these extreme polar environments would favour strong chemical and biological interactions between species, including the potential development of symbiotic associations through evolutionary time. Endosymbiosis is believed to account for the origin and development of eukaryotic cells, although the discussions to date have mostly considered this evolutionary process within the context of higher temperature microbial mat communities (Margulis and Sagan 1997). Given the biotic richness of the ice-mat consortia described here and the prospect of extensive glaciation in the ancient earth environment, we suggest that ice shelves and other ice-bound habitats (e.g. cryoconite holes in glaciers and ice sheets) have provided opportunities for microbial evolution, including radiation of the eukaryotic cell type at the onset of the Neoproterozoic about 1 million years before the present (Knoll 1994). As with MIS and WHIS today, these ancient cryo-ecosystems are likely to have remained deep-frozen through all but a few days to weeks of the year when the late summer radiation balance allowed for meltwater production and a brief resumption of metabolic activity in the mat communities. Oscillatorian cyanobacteria are widely distributed in the Proterozoic fossil record, with many of the forms having

sheath diameters less than 5 μm (Schopf 1994), as found in our ice-mat samples (Fig. 3). The biological productivity of such palaeo-ecosystems may also have been substantial. We have measured photosynthetic rates in the MIS mats in the range 200–1200 mg C/m^2 per day (Vincent et al. 1993), which is of the same magnitude as the highly productive algal blooms in the marginal ice zone of modern-day polar oceans (Vincent 1988).

Ice microbial communities dominated by oscillatorian cyanobacteria are known from several other types of habitat (Friedmann 1993; Priscu et al. 1998; Vincent 1988), albeit with low biomass relative to the luxuriant ice shelf mats observed on MIS and WHIS. Polar oscillatorians have broad thermal tolerances (Tang et al. 1997), probably reflecting their warm temperature origins and alternate habitats, and the thermally unstable nature of ablating glacial environments. The gradual disintegration of WHIS during the twentieth century emphasizes the evanescent nature of the ice shelf environment and the need for the resident microbiota to colonize alternate habitats during warmer periods. Conversely, during periods of extensive ice cover, such as the Proterozoic glaciations, these cryotolerant mats would have provided refugia for the survival, growth and evolution of a variety of organisms, including multicellular eukaryotes.

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