



Arctic microbial ecosystems and impacts of extreme warming during the International Polar Year

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Abstract

As a contribution to the International Polar Year program MERGE (Microbiological and Ecological Responses to Global Environmental change in polar regions), studies were conducted on the terrestrial and aquatic microbial ecosystems of northern Canada (details at: <http://www.cen.ulaval.ca/merge/>). The habitats included permafrost soils, saline coldwater springs, supraglacial lakes on ice shelves, epishelf lakes in fjords, deep meromictic lakes, and shallow lakes, ponds and streams. Microbiological samples from each habitat were analysed by HPLC pigment assays, light and fluorescence microscopy, and DNA sequencing. The results show a remarkably diverse microflora of viruses, Archaea (including ammonium oxidisers and methanotrophs), Bacteria (including filamentous sulfur-oxidisers in a saline spring and benthic mats of Cyanobacteria in many waterbodies), and protists (including microbial eukaryotes in snowbanks and ciliates in ice-dammed lakes). In summer 2008, we recorded extreme warming at Ward Hunt Island and vicinity, the northern limit of the Canadian high Arctic, with air temperatures up to 20.5 °C. This was accompanied by pronounced changes in microbial habitats: deepening of the permafrost active layer; loss of perennial lake ice and sea ice; loss of ice-dammed freshwater lakes; and 23% loss of total ice shelf area, including complete break-up and loss of the Markham Ice Shelf cryo-ecosystem. These observations underscore the vulnerability of Arctic microbial ecosystems to ongoing climate change.

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1. Introduction

High latitude ecosystems are typically thought of as extreme environments containing a limited diversity of plants and animals. There is increasing evidence,

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however, that such a view is not correct at the micro-biological level, and that the polar regions contain diverse microbes and microbial habitats (Thomas et al., 2008; Vincent and Laybourn-Parry, 2008). The International Polar Year (IPY) and related research programs provided an unprecedented opportunity to explore these microbial ecosystems and to address hypotheses concerning their structure and function.

In this article we briefly summarize some of the activities and results from Canadian contributions to the IPY program MERGE (Microbiological and Ecological Responses to Global Environmental change in polar regions) that focused on microbial habitats, microbial biodiversity and climate impacts in Arctic Canada. During the 2008 IPY field season, we observed multiple effects of unusually warm temperatures at the far northern coastline of the Canadian High Arctic, and these are summarized here. This article also provides a bibliography of MERGE-Canada publications to date from all of the Arctic research sites (updated at: <http://www.cen.ulaval.ca/merge/>). Microbial DNA sequences have been deposited in GenBank (see individual publications for

accession numbers); descriptions of other data sets from these polar ecosystems, including climate and other environmental data, are archived in the IPY Polar Data Catalogue at <http://www.polardata.ca>.

2. Habitat diversity

MERGE-Canada examined a diverse range of habitats in subarctic and Arctic Canada (Figs. 1 and 2) to characterize the physical and chemical characteristics of environments that contain microbial communities. Many of these habitats have equivalents in the south polar region, and one of our primary objectives has been to obtain microbiological data from the Arctic to compare with Antarctica, for example to evaluate hypotheses concerning the global dispersion and biogeography of microbiota. The sites were selected based on prior research activities that provided background environmental information and indicated the potential for more detailed geophysical, ecological and microbiological studies: terrestrial and aquatic environments on Axel Heiberg Island; thermokarst lakes (thaw lakes) on Bylot Island and in northern Québec;

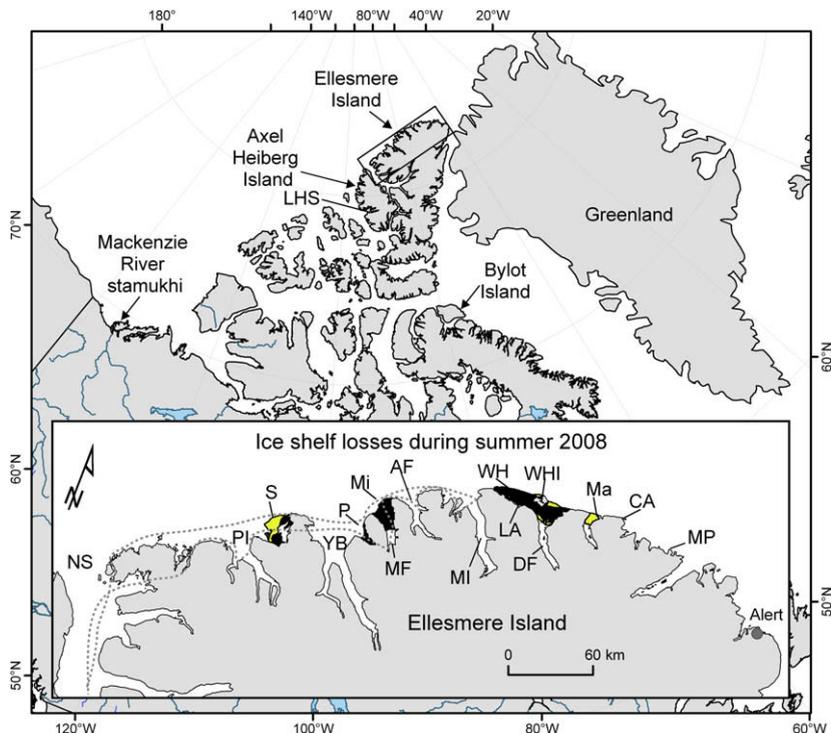


Fig. 1. Location of MERGE research sites in the Canadian High Arctic. The inset map shows the route of MERGE scientists and Canadian Rangers along the northern coast of Ellesmere Island (dashed line), and the ice shelf ice that was lost during summer 2008 (yellow; remaining ice is in black). LHS: Lost Hammer Spring; NS: Nansen Sound; PI: Phillips Inlet; S: Serson Ice Shelf; YB: Yelverton Bay; P: Petersen Ice Shelf; Mi: Milne Ice Shelf; MF: Milne Fiord; AF: Ayles Fiord; MI: M'Clintock Inlet; LA: Lake A; WH: Ward Hunt Ice Shelf; WHI: Ward Hunt Island; DF: Disraeli Fiord; Ma: Markham Ice Shelf; CA: Cape Aldrich; MP: Moss Point.

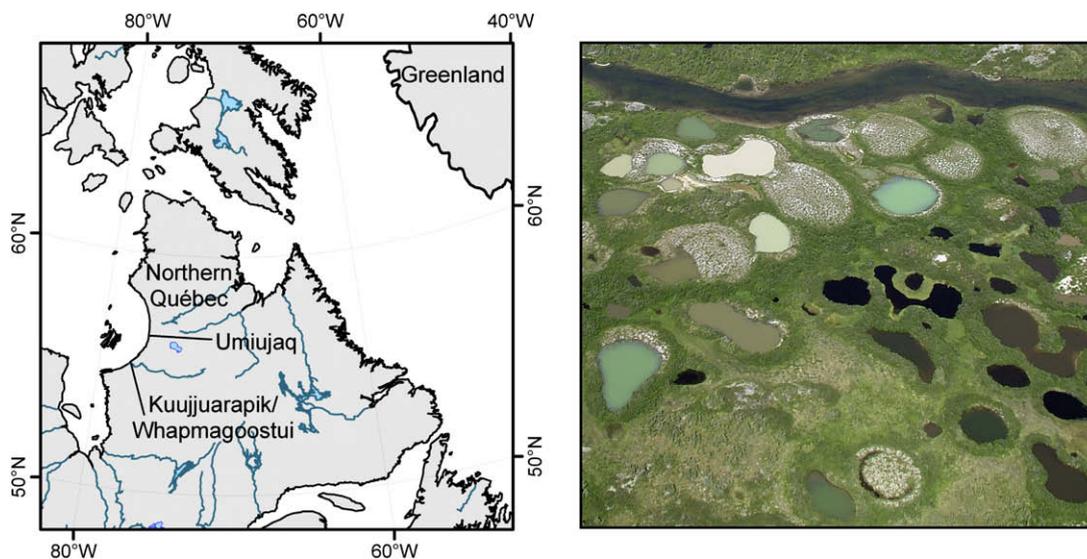


Fig. 2. MERGE thermokarst lakes in northern Québec. Left panel: location of study sites. Right panel: multicoloured thermokarst lakes at Umiujaq; each lake is 10–30 m in diameter (photo: I. Laurion).

ice-dependent aquatic ecosystems along the northern Ellesmere Island coastline; and the Mackenzie River and coastal Arctic Ocean in western Canada (Figs. 1 and 2).

Our research on Axel Heiberg Island in the High Arctic focused on the permanently frozen soils (permafrost) and unique spring systems of this region (Pollard et al., 2009). One of the principal sites was saline Lost Hammer Spring, located within a salt dome about 2 m in height and 4 m in diameter (Fig. 3), with a precipitated salt discharge runoff. During the winter months, the salt dome fills to about 3/4 full with spring water discharge and obvious gas bubbling. It empties during the short Arctic summer months leaving a base containing dark sediments with overlying pore-water, with gas venting as bubbles through the sediment and pore-water (Niederberger et al., 2009a). The spring is a subzero (-5°C), hypersaline (24% salinity), reducing ($\sim 165\text{ mV}$), microaerophilic, oligotrophic environment that is rich in sulfates (100 g/kg) and dissolved H_2S /sulfides (25 ppm).

Thaw lakes and ponds occur across the tundra as a result of differential melting and erosion of the permafrost, and these are a major aquatic ecosystem type throughout the Arctic. The primary study sites for analysis of these waters during MERGE were the contraction crack polygon systems on Bylot Island (Fig. 3) and thermokarst ponds near Kuujjuarapik and Umiujaq in subarctic Québec, in the forest tundra region (Fig. 2; Breton et al., 2009; Laurion et al., 2009).

Many types of aquatic ecosystems occur in the vicinity of Ward Hunt Island and along the northern coastline of Ellesmere Island, in high Arctic Nunavut, Canada, and these have been sites during MERGE for habitat characterisation and microbiological analysis. Extensive ice shelves occur along the coastline and are composed of thick ($>10\text{ m}$) landfast ice floating on the sea, analogous to ice shelf systems in Antarctica, particularly the McMurdo Ice Shelf (Copland and Mueller, in press). Abundant lakes and ponds melt out over the ice shelves each summer and many of these contain bottom sediments and benthic microbial mats. The ice shelves act as a dam at the northern end of embayments and fiords, and these retain inflowing meltwaters that form a freshwater layer overlying the sea water beneath. These so-called epishelf lakes are found in several parts of Antarctica, but are now a rare ecosystem type in the Arctic (Veillette et al., 2008).

Many lakes and ponds occur on land in the northern Ellesmere region, including Ward Hunt Lake, the northernmost lake in the Canadian Arctic. The shallow western side of this lake melts out in summer, while the eastern side has a $>3.5\text{ m}$ -thick layer of ice that is retained throughout summer (Antoniades et al., 2007a). The northern Ellesmere Island coastline is also a site of deep meromictic lakes that contain saline bottom waters, originally derived from the sea by the isostatic uplift of the coastline, overlaid by freshwater. These highly stratified waterbodies (denoted lakes A, B, C1 and C2) have strong salinity gradients and unusual temperature profiles, with mid water column thermal

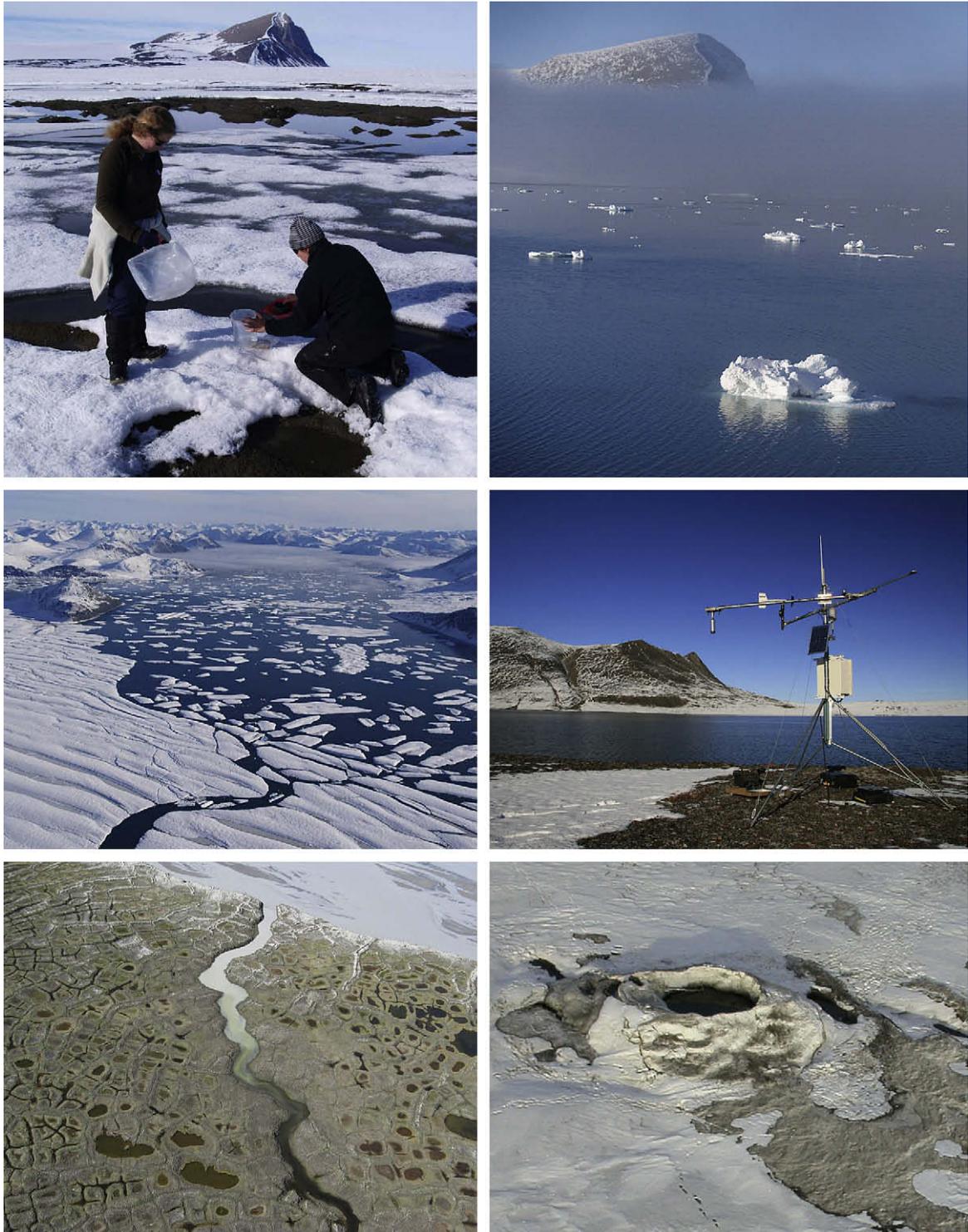


Fig. 3. Microbial habitats in the High Arctic. Markham Ice Shelf in 2007 (top left), and after its breakout in 2008 (top right). Extensive calving at the southern end of Ward Hunt Ice Shelf, 19 August 2008 (middle left), and meromictic Lake A on 20 August 2008 after its loss of perennial ice cover (middle right). Thaw ponds on Bylot Island in July 2008, showing extensive drying up and loss of aquatic habitat (bottom left), and a salt dome containing a saline spring on Axel Heiberg Island (bottom right). Photos: W.F. Vincent, I. Laurion, L. Whyte.

maxima that are the result of solar heating (Vincent et al., 2008). The sediments of these lakes are proving to contain valuable records of past climates (Tomkins et al., 2009, and references therein).

In April 2008, MERGE-Canada contributed to “Northern Ellesmere Ice Shelves, Ecosystems and Climate Impacts” a science project that investigated the current state of ice shelves and their associated microbial ecosystems (Mueller et al., 2008). Logistics and field assistance was provided by the Canadian Rangers, reservists from northern communities, who are tasked with patrolling remote regions by the Canadian Army. Water column profiling and collections of DNA and biomass samples were made from normally inaccessible fjords and epishelf lakes at the top of Ellesmere Island (see Fig. 1 inset for the expedition route; further details at: <http://www.cen.ulaval.ca/merge/>).

An additional set of microbial habitats was studied in the Mackenzie River and vicinity, in the western Canadian Arctic (Fig. 1). These were sampled immediately prior to IPY within the programs Canadian Arctic Shelf Exchange Study (CASES) and Arctic River Delta Experiment (ARDEX), which are described in Vincent and Pedrós-Alió (2008). Microbiological analysis of samples from these sites continued throughout IPY within the MERGE program, and included samples from the Mackenzie River, an ice-dammed coastal lagoon (stamukhi lake) and coastal marine waters (Galand et al., 2008a,b; Garneau et al., 2008, 2009; Payet and Suttle, 2008).

3. Microbial diversity

The MERGE program in northern Canada has encompassed a broad sweep of microbiological methods including culture studies, observations by light and fluorescence microscopy, HPLC pigment analysis, clone library analysis of environmental DNA and metagenomic analysis by 454 pyrosequencing. Individual laboratories have focused on specific groups of microbiota, notably viruses, Archaea, Bacteria, Cyanobacteria and protists.

For the virus studies, planktonic communities were concentrated by filtration from sites in the Beaufort Sea and from seven contrasting ecosystems in the Ward Hunt Island region. Viral concentrations in the coastal Beaufort Sea ranged from 10^5 to 10^7 per ml, with minimum concentrations in winter (Payet and Suttle, 2008). Cyanobacterial mats were sampled from 19 different sites, including ice shelves and freshwater lakes. Bacterial and viral abundances were determined

for all samples, and nucleic acids were extracted for analysis (details in Clasen et al., 2008). These nucleic acid extractions were screened by PCR using primers that are specific for three groups of cyanophage: g20, psbA and MCP5.

Archaeal studies were initially focused in the Mackenzie River region, which revealed a high diversity and striking differences between freshwater, stamukhi lagoon and coastal marine communities (Galand et al., 2008a,b). Studies on the Ellesmere Island meromictic lakes discovered major differences in archaeal community structure down through their water columns, and the presence of the archaeal *amoA* gene in the oxycline of the lakes, implying highly localized populations of nitrifying Archaea (Pouliot et al., 2009).

The Mackenzie River contained high concentrations of Bacteria, and most of the population appeared to be associated with sediment particles in this highly turbid system (Vallières et al., 2008). There were large gradients in bacterial community structure in the transition from river water to the brackish stamukhi lagoon to coastal marine waters (Galand et al., 2008b). Diverse bacterial communities were also recorded in microbial mats of the Markham Ice Shelf and Ward Hunt Ice Shelf. All heterotrophic isolates and >95% of bacterial 16S rRNA gene clone library sequences from both ice shelves grouped within the phyla *Bacteroidetes*, *Proteobacteria*, and *Actinobacteria*, and experimental evidence was obtained that bacterial heterotrophic activity could continue down to -10 °C (Bottos et al., 2008). Photosynthetic sulphur bacteria were identified as the dominant phototrophic communities in the water column of high Arctic meromictic lakes, and their pigment signatures offer a novel proxy for determining periods of reduced ice cover and climate change in the past (Antoniades et al., 2009).

Microscopic and DNA analyses have shown the presence of many taxa of Cyanobacteria in the ice shelf microbial mats, and pigment analysis indicated that this group dominates the total phototrophic biomass of the mat communities (A. Jungblut et al., unpublished), consistent with studies elsewhere in the polar regions (Vincent, 2007; Zakhia et al., 2008; Vincent, 2009). Initial work on the meromictic lakes of northern Ellesmere Island showed that there were abundant populations of picocyanobacteria in their upper water columns, with some evidence of phylogenetic differences between lakes and depths (Van Hove et al., 2008). Picocyanobacteria also occurred in high concentration in the Mackenzie River, but populations dropped off rapidly in the coastal marine waters (Vallières et al., 2008).

The thaw lake analyses combined direct microscopy with molecular approaches, and gave special attention to the greenhouse gas production in these ubiquitous high latitude waters (Laurion et al., 2009). Protist research at these and other MERGE sites is still in an early stage of collection and analysis, but our initial analyses of high Arctic snow samples suggest the cosmopolitan distribution of many taxa, including microbial eukaryotes (T. Harding et al., unpublished), and the presence of mixotrophic protists in high Arctic lakes (S. Charvet et al., unpublished). HPLC analysis of samples from the Mackenzie River showed strong freshwater–saltwater gradients in protist community structure (Retamal et al., 2008). The stamukhi lake system appeared to have a distinctive protist composition, with low flagellate diversity but a high abundance and diversity of ciliates (Galand et al., 2008b). Strong vertical gradients were observed in the pigment composition of phytoplankton communities in the Milne Fiord epishelf lake, and clone library analyses of these communities combined with microscopy indicated that ciliates were also a major component of this ice-dammed ecosystem (J. Veillette et al., unpublished). Pigment and microscopic analysis revealed the presence of eukaryotic phototrophs in the microbial mats on the ice shelves (A. Jungblut et al., unpublished), and metagenomic analysis (massive DNA pyrosequencing) confirmed the presence of a wide range of eukaryotic genes (T. Varin et al., unpublished).

A detailed series of microbiological analyses of permafrost soils has now been completed (Nadeau et al., 2008; Niederberger et al., 2009b; Steven et al., 2007a,b, 2008a,b,c). A stable isotope probing technique was developed to identify the active methanotrophic bacteria and their activity in supra-permafrost and active layer soils (Martineau et al., 2008). Our microbial investigations of the saline spring sediments determined that a small but viable microbial population exists within the extreme environmental constraints of these unique halophilic cryohabitats (Perreault et al., 2008). Most intriguingly, our culture-independent analyses indicated that Lost Hammer Spring contains unique *Archaea* related to methanogens that perform anaerobic methane oxidation; i.e., that utilize methane as an energy source and sulphate as the electron acceptor. We also investigated the microbiology of filamentous biofilms that develop in the snow-covered runoff channels during the winter months. These highly unusual filaments consist of novel chemolithoautotrophic sulfur-oxidizing Bacteria in the genus *Thiomicrospira*, which appears to flourish via chemolithoautotrophic, phototrophic-independent

metabolism during the extreme high Arctic winter (Niederberger et al., 2009a). Interestingly, the dominant phylotype recorded in DNA clone libraries from a hypersaline spring in the south polar region (Blood Falls, McMurdo Dry Valleys) had a 99% sequence similarity to *Thiomicrospira arctica* (Mikucki and Priscu, 2007).

A phylogenetic gene microarray (PGMA) containing *Cpn60* or *16S rRNA* gene targets representing most genera of Bacteria (design based on ribosomal database backbone phylogenetic tree), is being developed to assess and compare the microbial biodiversity present in DNA isolated from a range of previously characterized high Arctic habitats: permafrost (moderate diversity); cold saline springs (moderate to low diversity) and ice shelf microbial mats (high diversity). The development of such a “polar” PGMA will improve the comprehensive study of microbial diversity and ecology in polar ecosystems, while increasing our understanding of important processes such as biogeochemical cycles and bioremediation in the Arctic (Greer, 2009; Greer et al., 2009).

4. Environmental change

During the summer of 2008 we recorded many pronounced changes in microbial habitats at the northern Canadian coastline, including loss of perennial sea ice, loss of ice-dammed freshwater lakes and unusual open water conditions in lakes and the coastal ocean. Mean daily air temperatures at our Ward Hunt Island 10-m automated climate station (part of the CEN Arctic Observation Network) were mostly above 0 °C throughout June–August and more frequently above 10 °C than in the preceding 2 years (Fig. 4), with an unusual daily maximum of 19.8 °C at 13:00 h on 2 August 2008. For the same date, our 3-m automated climate station adjacent to Lake A on northern Ellesmere Island (Fig. 3) recorded a maximum of 20.5 °C. Given the short records at both sites, we are unable to fully assess whether these mean and maximum daily temperatures are unprecedented. The nearest official (Environment Canada) climate station to these sites is Alert (82°31'N, 62°16'W; Fig. 1), on Ellesmere Island, 175 km to the east of Ward Hunt Island. For the period 1950–2005 of available data from Alert (http://www.climate.weatheroffice.ec.gc.ca/climate_normals), the record maximum daily temperature was 20 °C (on 8 July 1956). Summer temperatures at Alert correlate closely with those at our Ward Hunt Island station but are warmer, with an average offset of 1.3 °C (Antonides et al., 2007b). This comparison implies that the

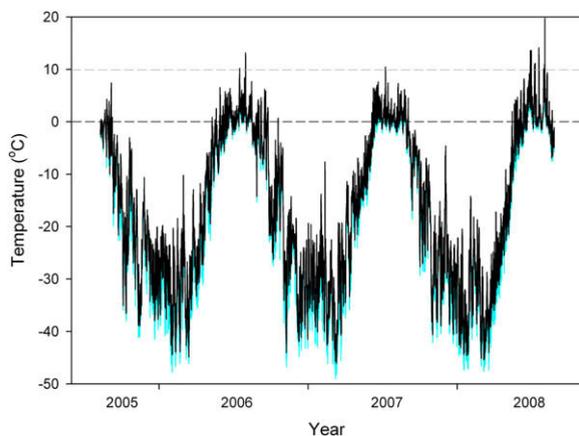


Fig. 4. Maximum (black) and minimum (blue) daily air temperatures at the Ward Hunt Island climate station, from 2005 to 2008. The HMP45C212 temperature and humidity probe (Campbell Scientific Canada Corp.) was housed in a RM Young 12-Plate Gill radiation shield located at 10 m height, read every 60 s, and the maximum and minimum values were recorded every hour with a Campbell CR10X data logger.

air temperatures at Ward Hunt Island and Lake A in summer 2008 were at or above extreme maximum values for the northern Ellesmere Island region over the last half century.

Warming effects were also recorded in the permafrost soil on Ward Hunt Island (Fig. 5). The soil profile achieved higher temperatures in late July/early August

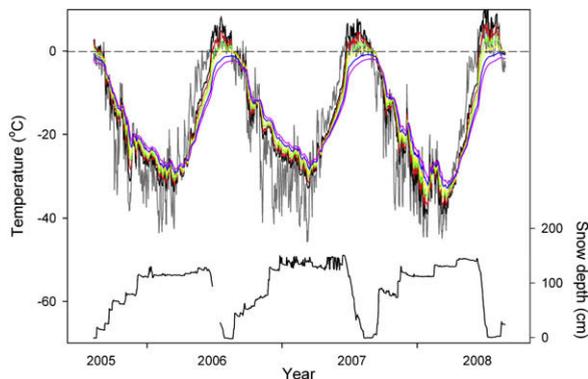


Fig. 5. Air and soil profile temperatures and snowpack depth at the Ward Hunt Island climate station, from 2005 to 2008. Grey, air temperature at 10 m height; black, soil just under the surface; red, soil at 20 cm; green, soil at 40 cm; yellow, soil at 60 cm; blue, soil at 90 cm; pink, soil at 120 cm depth. Lower black curve: depth of snowpack adjacent to the climate station, measured with a Sonic SR50 snow depth sensor. Air temperature was measured as in Fig. 4. For the soil profile, each thermistor (YSI 44033, attached to the data logger via a Belden 88761 cable; precision of 0.1 °C) was inserted into a 5 mm diameter, 500 mm deep horizontal hole produced at right angles to the vertical access hole that was then refilled and compacted with soil. The data are daily averages of readings taken every 60 s.

than in the preceding 2 years, with a maximum surface (1–2 cm depth) temperature of 12.3 °C at 15:00 h on 2 August 2008. In 2006 and 2007, summer soil temperatures remained below freezing at depths ≥ 60 cm, but in 2008 the 0 °C isotherm was near 90 cm, implying a deepening of the active layer. Winter soil temperatures in 2007/8 dropped 5 °C below those in the preceding two winters during two episodes of cold air temperatures. The continuous snow cover record (Fig. 5) indicates a reduced thickness of insulating snow during the periods of winter soil minima in 2008 relative to earlier years. There was a faster rate of loss of snow pack in summer 2008 relative to the previous 2 years: for the early summer period 1 May to 27 June (end of the broken record in 2006) there was a 21% decline in snow in 2006 (from 119 to 94 cm), 7% decline in 2007 (from 134 to 124 cm) and 54% decline in 2008 (from 144 to 66 cm). We also observed much greater production of meltwater and stream flow at all sites along the northern coast in summer 2008.

The northern Ellesmere Island ice shelves experienced dramatic and irreversible disintegration in the 2008 summer, with an overall loss of 23% of their total area within 3 weeks (Mueller et al., 2008; further details at: <http://www.cen.ulaval.ca/merge/>). These ice shelves are composed of the thickest and oldest marine ice in the Arctic basin topped with ice formed from snow and rain. In contrast to the relatively thick and expansive ice shelves of Antarctica, these northern ice shelves are not typically fed by glaciers. The Serson Ice Shelf (Fig. 1 inset), which does receive some input from glaciers, lost 60% of its area (122 km²; approximately 5 billion tons of ancient ice overlain with a patchy distribution of microbial mats). The Serson Ice Shelf break-up may have impacted its ice-dammed epishelf lake, which could have completely drained during this event. We observed complete loss of the Markham Ice Shelf (50 km²), the richest microbial cryo-ecosystem along the northern coast in terms of standing stocks and biodiversity (Vincent et al., 2004; Bottos et al., 2008). This ice shelf broke away from Markham Fiord in early August, leaving the fiord ice-free, perhaps for the first time in thousands of years (Fig. 3).

Striking changes were observed in the vicinity of Ward Hunt Island during July–August 2008 (Fig. 6). Ward Hunt Lake lost 25% of its ice cover and the thick (>3 m) perennial ice became detached from the eastern shoreline, for the first time on record. Quttinirpaaq Lagoon, the usual drinking water for our camp, rose in conductivity from 270 $\mu\text{S cm}^{-1}$ in summer 2007 to >10,000 $\mu\text{S cm}^{-1}$ as a result of the breaching

of its ice dam at the eastern end, and was no longer a potable water source. Large expanses of open sea occurred along the northern edge of the Ward Hunt Ice Shelf, which showed large fractures south of the island and extensive fissuring throughout much of the ice shelf. It continued to calve at its northern (seaward) edge and to the south into Disraeli Fiord (Fig. 2). This ice shelf, the largest in the Arctic, is likely to experience severe attrition and even complete loss over the next few years.

The areal extent of Arctic summer sea ice (also a habitat for diverse microbiota; see Thomas et al., 2008) dropped precipitously to a record minimum in 2007 (Stroeve et al., 2008), and approached similar minimum levels in 2008. The latter may have set a record minimum in ice volume, as thick multiyear floes diminished through melting and export were replaced with first year sea ice (details at: <http://nsidc.org>). These effects have been attributed to a combination of natural and anthropogenic forcing that may result in the almost complete loss of summer sea ice within the next few decades (Wang and Overland, 2009). At the northern coast of Ellesmere Island wide expanses of open water along the shore facilitated the calving of ice shelves and the loss of multiyear landfast sea ice in bays and fiords. While open water can occur in this dynamic region at any time of year it is typically restricted in time and space. In summer 2008, open water stretched up to several km off the coast for 5 weeks.

Additionally during 2008, multiyear landfast sea ice was lost from Phillips Inlet (to the west of Serson Ice Shelf), around Bromley Island (near M'Clintock Inlet)



Fig. 6. View looking NNW across Ward Hunt Island, 19 August 2008, showing multiple effects of the extreme summer warming, with large cracks up to 20 m wide and many fissures permeating the ice shelf. The island is approximately 5 km wide along its east–west axis.

and from Cape Aldrich to Moss Point. These are areas of semi-permanent ice, which would have eventually grown into ice shelves, if the climate had returned to colder conditions. There was complete break-up of inner fiord ice in Disraeli Fiord (south of the Ward Hunt Ice Shelf) and in Markham Fiord by the first week in August. Unprecedented break-up of this inner ice of the fiords has been observed over the last decade, beginning in 2003 for Disraeli Fiord (after the loss of its epishelf lake; Mueller et al., 2003) and 2007 for Markham Fiord.

Ice-covered lake ecosystems at the northernmost Ellesmere Island are also in a transition from perennially to seasonally ice-covered. Five of these lakes (including Lake A, Fig. 3) lost all their ice covers in the summer of 2008 following the warm temperatures in July and the beginning of August (Figs. 4 and 5). When this occurred in 2000, the upper water column of meromictic Lake A mixed. These mixing events can now potentially occur with greater regularity owing to more prolonged periods of open water on these lakes, which were normally ice-covered even in summer (Mueller et al., 2009). Changes to microbial communities in these formerly stable environments have not yet been determined but sampling for microbial DNA and pigments was carried out in Lakes A and C2. There was evidence of ecological change at the macrofauna level, with the colonisation of Lake A by a pair of Red throated loons (*Gavia stellata*) immediately after ice loss; this would have added a new higher trophic level to the Lake A ecosystem, with potential impacts by predation on the resident Arctic Char population. A variety of other effects of the warm 2007 and 2008 seasons have also been noted, including the drying up of many thaw ponds further south, for example on Bylot Island (Fig. 3).

Overall, these observations of extreme warming, melting, ice loss and evaporation in the Canadian High Arctic underscore the vulnerability of polar microbial ecosystems to climate change. The unusual climate and ice conditions during IPY 2007/8 resulted in major perturbation of these far northern environments, and the complete extinction of some ecosystems.

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