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Environmental Gradients, Fragmented Habitats, and Microbiota of a Northern Ice Shelf Cryoecosystem, Ellesmere Island, Canada

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Abstract

Over the course of the last century, the 9000-km^2 "Ellesmere Ice Shelf" (82–83°N, 64–90°W) fragmented into six main ice shelves now totaling 1043 km^2. This ensemble of thick ice environments lies along the northern coast of Ellesmere Island in the Canadian High Arctic and provides a cryohabitat for microbial communities that occur in association with eolian and glacially entrained sediments on the ice surface. We undertook a comparative analysis of physical, chemical, and biological characteristics of five of the remnant ice shelves including geographic information system (GIS) mapping of ice types. Each of these remnants is a thick ($>$20 m) mass of ice with substantial sediment overburden that promotes the formation of oligotrophic meltwaters in the summer. Microbiota occurred in all sampled sediment, forming a continuum of abundance from sparse to loosely cohesive and pigmented microbial mats. Using digital images from over-flight transects we determined that 8% of the combined ice-shelf area was suitable microbial mat habitat, and contained an estimated 34 Gg of organic matter stocks for the entire system. A gradient of increasing chlorophyll *a*, organic content, and conductivity was found from west to east. This is likely related to the surface ice type (meteoric versus marine) and to the relative availability of sediment. Our results indicate that differences in phototrophic community structure (microalgae and cyanobacterial morphotypes) were associated with different ice and microbial mat types. In addition, the relative abundance of dominant taxa was significantly associated with environmental gradients of conductivity, soluble reactive phosphorus, and nitrate and ammonium concentrations. There were distinct differences between each ice shelf with regards to ice type and sediment availability but no differences in taxonomic richness or diversity, indicating little effect of habitat fragmentation on these community attributes. However, the ensemble of ice shelves that compose this unique cryoecosystem remains vulnerable to habitat attrition and complete loss with ongoing climate warming.

Introduction

Ice shelves, thick masses of coastal ice floating on the ocean, are found in both the North and South polar regions and have been traditionally viewed as abiotic components of the cryosphere. However, numerous articles have shown that a rich diversity of microbial life exists in seasonal meltwaters on the surface of certain Antarctic ice shelves (Vincent, 1988; Howard-Williams et al., 1990; Suren, 1990; Hawes et al., 1993; Mountfort et al., 1997). More recently, the importance of similar microbial communities on the Ward Hunt Ice Shelf (lat. 83°N, long. 74°W) in High Arctic Canada was recognized (Vincent et al., 2000).

The Ward Hunt Ice Shelf is the largest remaining ice shelf in the Northern Hemisphere and is accompanied by five other substantial ice shelves along the northern coast of Ellesmere Island in the Canadian Arctic: Markham, Ayles, Milne, Petersen, and Serson (formerly known as Alfred Ernest Ice Shelf) ice shelves (Fig. 1). In addition to the main ice shelves, there are a few minor ice shelves (a few square kilometers in area) and scattered shelf ice fragments locked in multiyear landfast sea ice. These ice shelves are remnants of the "Ellesmere Ice Shelf" that spanned a ~400 km stretch of the northwestern coast of Ellesmere Island at the beginning of the last century (Koenig et al., 1952). Much of the fragmentation of this large ice shelf occurred prior to the 1950s; however, since then several calving and break-up events have taken place, further fragmenting this feature into smaller pieces (Hattersley-Smith, 1963; Jeffries and Serson, 1983; Jeffries, 1986a; Mueller et al., 2003).

The existence of ice shelves in the Northern Hemisphere is limited to the aforementioned Canadian Arctic examples, several in the Russian Arctic (Dowdeswell et al., 1994; Williams and Dowdeswell, 2001), and some potential candidates in northern Greenland (Higgins, 1989). This is in marked contrast with Antarctica that has 40% of its coastline fringed with ice shelves, some as large as half a million square kilometers (Jeffries, 1992b). There, they are typically formed by floating glacier tongues that aggregate into broad expanses of ice up to hundreds of meters in thickness. In contrast, Arctic ice shelves are mostly formed by *in situ* ice accumulation of marine "basement" ice and meteoric (atmospherically derived) "iced firn," and in some cases, this is added to by glacial ice.

The surface of Arctic ice shelves is marked by an east-west trending ridge and trough topography with an amplitude of 2 to 7.5 m and a wavelength of 87 to 450 m (Jeffries et al., 1990). This

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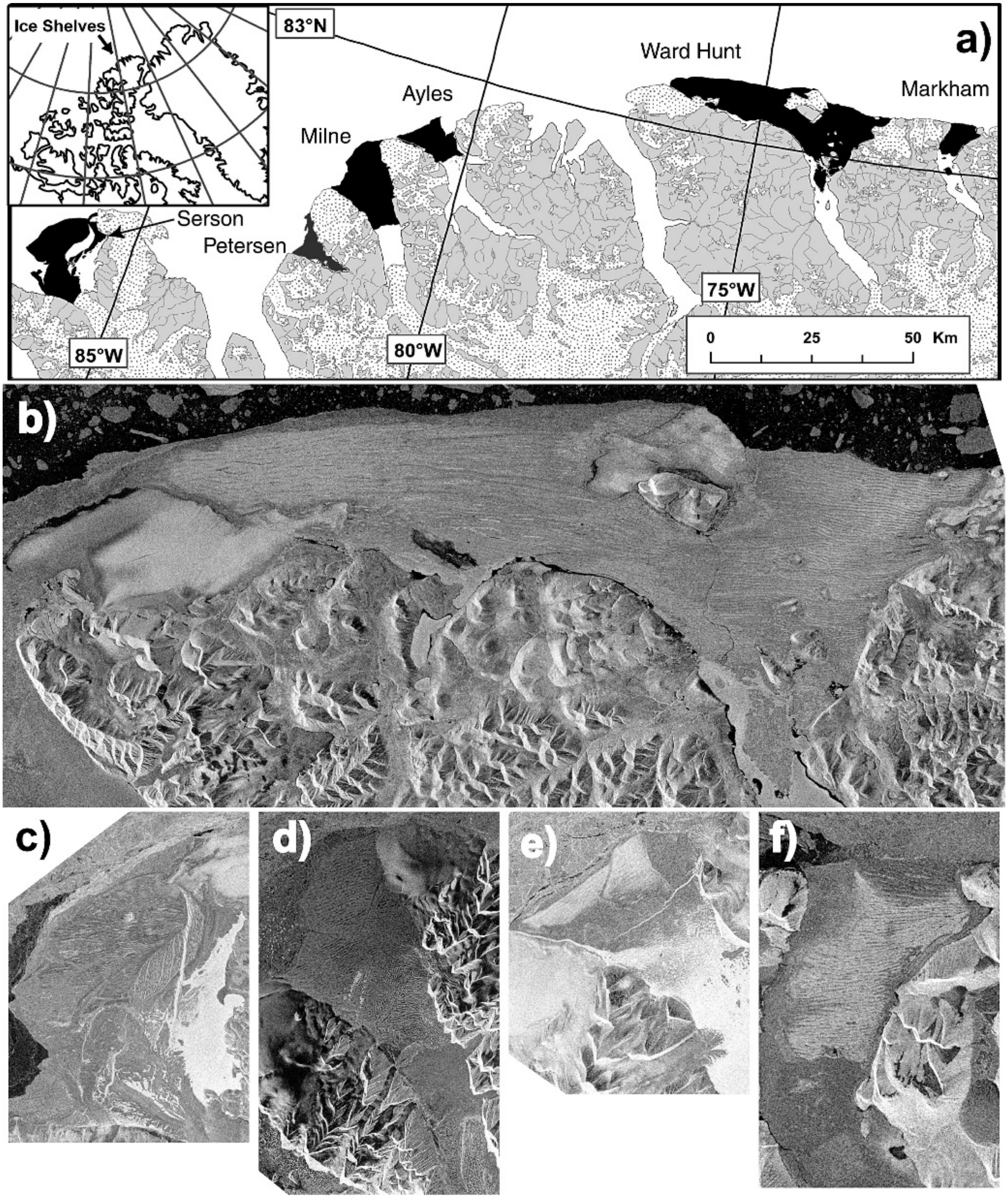

FIGURE 1. Map and RADARSAT images of ice shelves in the Canadian High Arctic that were the subject of this study. (a) The location of ice shelves along the coast of Ellesmere Island. Petersen Ice Shelf (dark gray) was not visited, but was included in areal extent calculations. This map was modified from NTS 120F&G, 340E&H, 340F and 560E 1:250 000, Natural Resources Canada (© Her Majesty the Queen of Canada). (b) Ward Hunt Ice Shelf, RADARSAT image number r1_35477_208, August 21, 2002. (c) Serson Ice Shelf, image number r1_22728_211, March 12, 2000. (d) Milne Ice Shelf, image number r1_29859_214, July 25, 2001. (e) Ayles Ice Shelf, image number r1_37462_215, January 7, 2003. (f) Markham Ice Shelf. image number r1_35261_215, August 6, 2002. All RADARSAT images (© Canadian Space Agency) were radiometrically calibrated and georeferenced. Note that the scale for each image is different (refer to Fig. 1a).

regular undulating surface becomes more chaotic closer to coastlines (Hattersley-Smith, 1957) and the relative importance of wind versus tidal and other potential controls on Arctic ice shelf morphology has not yet been conclusively determined (Holdsworth, 1987). In this northern region, air temperatures can approach or exceed 0°C beginning in late June and continuing until late August (Alert, Nunavut; Meteorological Service of Canada, Climate Normals 1971–2000). During this period, meltwater flowing into the troughs accumulates in long (up to 15 km), thin (10 to 200 m) and shallow (up to 3 m) lakes. Liquid water is then seasonally available for biological processes, and this period constitutes the main growth season for resident microbiota.

In addition to snow, ice, and water, sediment is a conspicuous constituent on the ice shelf surface. It can be delivered in three ways or by a combination of these modes: across the ice surface via eolian distribution (Crary, 1958), pushed with the ice as glacial moraine debris (Lemmen et al., 1988), or through the ice via basal accretion and subsequent surface ablation (Crary, 1960). Microbial consortia are associated with sediment at the bottom of meltwater lakes and are arranged in a loosely cohesive microbial mat (organosedimentary matrix). Microbial mats may be found in discrete melt holes up to 50 cm in diameter (termed cryoconite holes on glaciers; see Mueller et al., 2001) or they may be found in more extensive and interconnected patches of sediment. In some areas, sediment and microbial mats may be located on the ice but not overlain by water. Overwinter measurements made on the Ward Hunt Ice Shelf (2001–2002) suggest that these mats become covered with snow and/or ice and remain below 0°C for 300 days of the year reaching minimum temperatures of −17°C (Mueller and Vincent, 2006). Oscillatorian cyanobacteria dominate the microbial assemblage but diatoms, green algae, other protists, heterotrophic bacteria, and viruses are also present. In addition, microinvertebrates such as rotifers, tardigrades, and turbellarian worms have been identified within the microbial mats (Vincent et al., 2000). This contrasts with microbial mats on the McMurdo Ice Shelf, which lack turbellarians, and are generally highly cohesive and layered (Howard-Williams et al., 1990; Vincent et al., 2000).

The cryohabitats of Arctic ice shelves have been little characterized and all work to date has focused on the Ward Hunt and Markham ice shelves. This includes a study of the environmental conditions at the microbial scale (Mueller and Vincent, 2006), pigment analysis of microbial mats (Vincent et al., 2004; Mueller et al., 2005) and an assessment of the microbial mat ecophysiology (Mueller et al., 2005). No analysis has been undertaken to assess the microbial ecology of the entire "Ellesmere Ice Shelf" cryoecosystem. It is therefore not known how much habitat exists across all these ice shelves, what the limnological properties of the meltwater lakes are, and the extent of spatial variability of the microbial communities. In the present study, we redress this by way of detailed transects, remote sensing and sampling of microbial mats and surface waters from five of the largest "Ellesmere ice shelves." Our objectives were to quantify habitat availability (at two spatial scales), limnological conditions and taxon relative abundance over the entire cryoecosystem. We used these data to estimate the current standing stocks of microbial mats on the "Ellesmere Ice Shelf" remnants and to address the hypothesis that the microbial mat relative abundance and biomass is associated with environmental gradients (i.e., features of the environment that vary spatially). Our observations allowed us to delineate three categories of microbial mat as well as two ice types and to evaluate the hypothesis that differences exist in the relative abundance and environmental conditions among these nominal groups. Finally, we considered the ecological ramifications of the ongoing habitat fragmentation of the "Ellesmere Ice Shelf" and the implications of cryohabitat loss and isolation between glacial epochs.

Methods

SAMPLING

Fieldwork was undertaken in late July and early August of 2001 and 2002. In 2001, five major ice shelves were visited by helicopter. We did not visit Petersen Ice Shelf or the minor ice shelves and shelf ice fragments locked in multiyear landfast sea ice. Sampling of surface waters and microbial mats (if present) took place on each ice shelf (Fig. 2). Samples were distributed as evenly as possible (given logistical constraints such as aircraft range and weather) down the centerline of each ice shelf (inshore/offshore). The eastern and western portions of the Ward Hunt Ice Shelf were also sampled, owing to this ice shelf's overall size and breadth. The Ward Hunt Ice Shelf was also accessible on foot, allowing supplementary sampling near Ward Hunt Island (Fig. 2a). In addition to the samples from each ice shelf, an auxiliary sample was taken on the Ward Hunt Ice Rise (a grounded portion of shelf ice) and another was taken in an area of multiyear landfast sea ice (MLSI; this ice type can be considered as a nascent ice shelf) to the west of the Ward Hunt Ice Shelf (Fig. 2a). *In situ* measurements of surface water pH, conductivity, and temperature were taken using portable instruments (Hydrolab Quanta, Hach Environmental, Loveland, CO in 2001 and pH/Con 10 Series, Oakton Instruments, Vernon Hills, IL in 2002) and GPS positions were recorded. Surface waters were sampled in 2-L HDPE bottles (rinsed three times with sample water) and kept cool and dark prior to subsampling and preservation at our field laboratory. Microbial mat type was noted at the time of sampling and classified into four categories: "orange," "matlet," "sediment," and "none," if no macroscopic mat or sediments were visible. This mat classification system was designed as a rapid, visual census only (Fig. 3). Microbial mat samples were scooped into clean plastic containers, kept cool and dark until they were processed (subsampled and preserved for transport to Quebec) in the field laboratory.

TAXON RELATIVE ABUNDANCE

Subsamples of microbial mat were preserved with a gluteraldehyde/formaldehyde solution (Lovejoy et al., 1993) and refrigerated prior to analysis in Quebec. These samples were vortexed, diluted with water, dispersed by repeatedly passing them through a syringe and subsequently examined on an inverted microscope (Zeiss Axiovert 10) at 1000 times magnification (Villeneuve et al., 2001). Taxa were identified or assigned to a morphotype and their relative abundance was determined by counting at least 500 fields or, more commonly, enumerating no less than 200 natural units (individuals or colonies, depending on habit) per sample. Phototrophs were found to be the dominant group in terms of productivity and biomass in previous analyses (Mueller et al., 2005) and we therefore focused on cyanobacteria, green algae, diatoms, and other protists. We recorded microinvertebrates whenever encountered but we did not include heterotrophic bacteria, archaea, or viruses in our analyses. Diatoms were enumerated only if cell contents were visible. Due to the morphological variability of oscillatorian cyanobacteria, three morphotypes were used to classify filaments that were not identified to genus level. The morphotype Osc. 1 was defined as filaments up to 2 μm wide with a clear sheath and no discernable cross walls, Osc. 2 was as above but with cross walls clearly visible, and Osc. 3 was similar to Osc. 1 but with a diffuse, often ragged

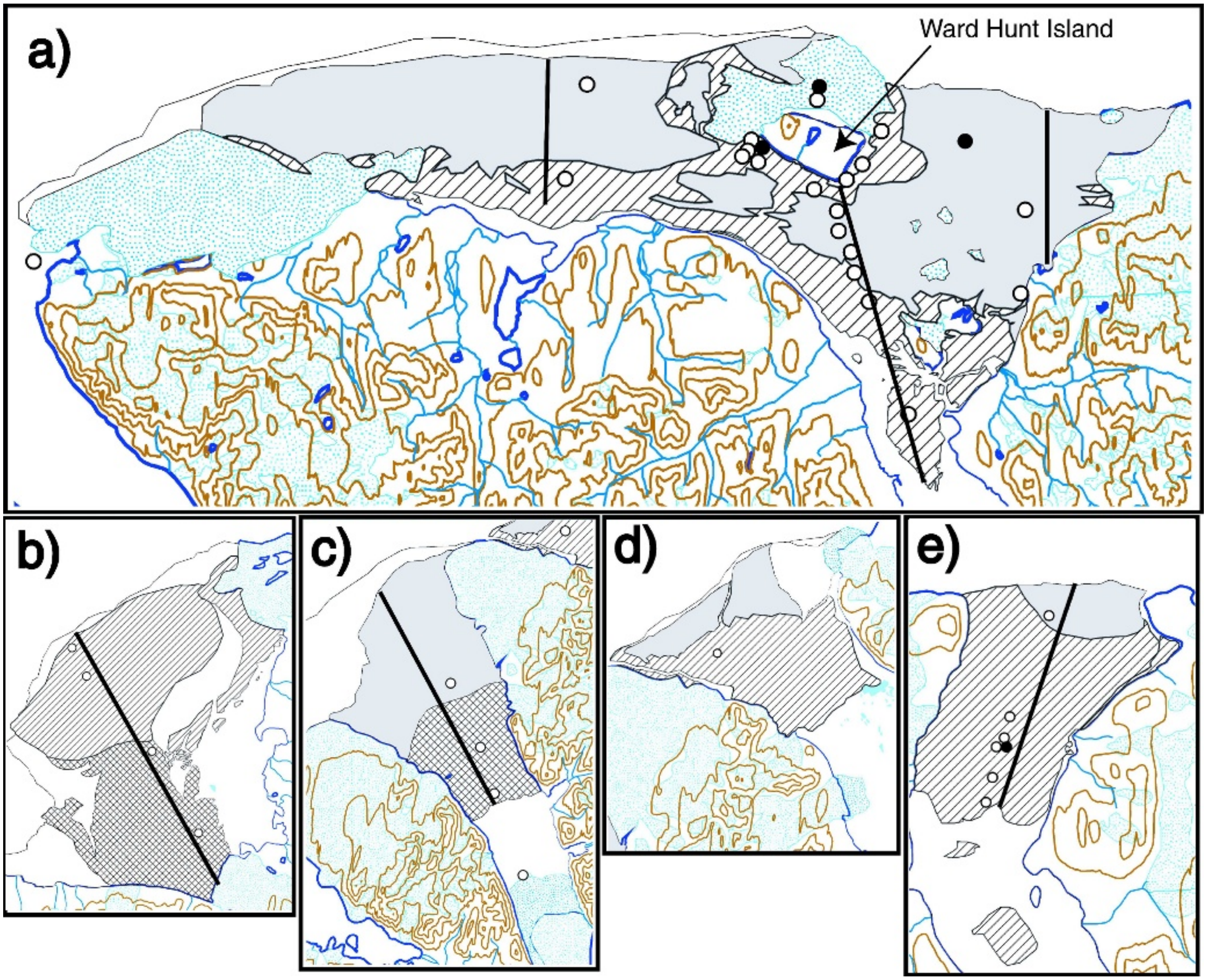

FIGURE 2. Ice types, sample sites, and transect locations used in this study. Stipple indicates ice rises and glaciers, a simple hatch indicates exposed basement ice, solid grey indicates iced firn and cross hatch indicates floating glacier portions of ice shelves. Multiyear landfast sea ice (MLSI) is outlined to the seaward side of several ice shelves. Bold, straight lines are the over-flight transects. Sample sites on the ice are denoted by open circles. Solid circles indicate the approximate location of point transects on the ice. (a) Ward Hunt Ice Shelf, showing western, middle and eastern transects; also note sample on MLSI to the west of the ice shelf and one sample on the Ward Hunt Ice Rise, north of Ward Hunt Island. (b) Serson Ice Shelf. (c) Milne Ice Shelf. (d) Ayles Ice Shelf. (e) Markham Ice Shelf. These maps were modified from NTS 120F&G, 340E&H, 340F and 560E 1:250 000, Natural Resources Canada (© Her Majesty the Queen of Canada) and available RADARSAT images. Refer to Figure 1a for scale.

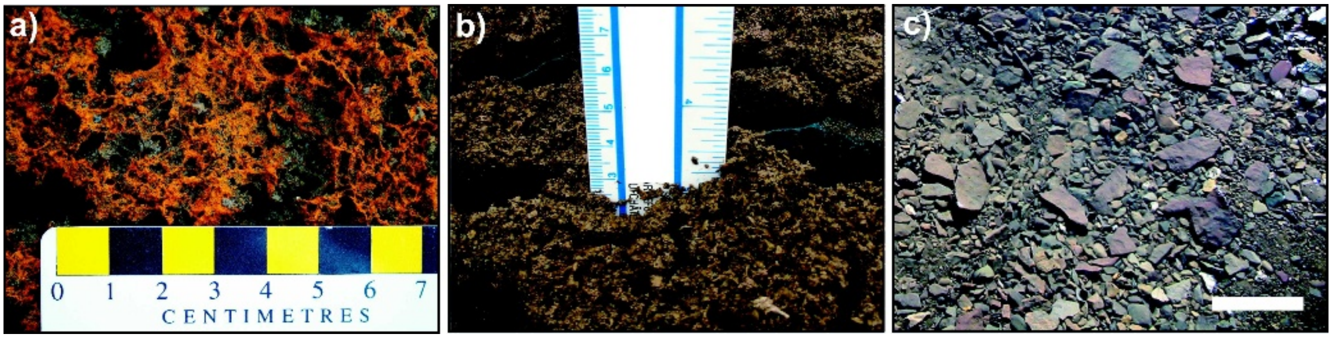

FIGURE 3. Microbial mat types found on the ice shelves along the northern coast of Ellesmere Island. (a) "Orange" mat: luxuriant, thick (>0.5 cm) loosely cohesive mats with a thin surface layer of orange pigmentation. (b) "Matlet": 1- to 2-mm–wide flakes lying loosely on the ice up to a thickness of 3 cm (the ruler extends to the bottom of the mat). (c) "Sediment" mat: no visible biological aggregates in a fine to coarse sediment. The white scale bar in Figure 3c is approximately 10 cm wide.

looking, sheath. For these filaments, the presence of phycobiliproteins was verified under green excitation epifluorescence microscopy and, in the same study, an HPLC analysis did not detect any bateriochlorophyll, which confirmed that these filaments were cyanobacteria and not green nonsulfur bacteria (Mueller et al., 2005). Given the uncertain taxonomy of oscillatorians, molecular analysis would be required to define these taxa at a more precise level (Castenholz, 1992). Our analysis therefore provides a first order estimate of phototrophic diversity and does not encompass the full biodiversity of the microbial mats, which could be revealed in future using molecular techniques.

MICROBIAL MAT AND WATER ANALYSES

Microbial mats were subsampled for pigment determination and were stored frozen and in the dark for transport. In the laboratory, samples were thawed in 90% acetone:water (v/v) and sonicated (Microson XL2000, Misonix, Farmingdale, NY) at approximately 10 W for two 30-s bursts with a pause of 30 s between sonication steps or samples were homogenized using a tissue grinder (Camafro R2R1, Wiarton, ON) for 1 min (there was no significant difference between these methods: paired *t*-test, $t = 0.867$, $P = 0.415$, $n = 8$). Pigment extraction took place in the dark for 1 h at 4°C and terminated with centrifugation at 4000 rpm for 5 min at 4°C. The supernatant was removed and chlorophyll *a* concentrations were determined at 663 nm and 750 nm, before and after acidification, while total carotenoid content was determined at 480 nm in a Cary 300 Bio UV-Visible spectrophotometer (Varian, Mulgrave, Australia) (Strickland and Parsons, 1972; Britton, 1985). This procedure was carried out three times to ensure complete extraction, and total chlorophyll *a* and total carotenoid content was determined by summing each extraction (Villeneuve et al., 2001). Total carotenoids were postcorrected for scytonemin (Garcia-Pichel and Castenholz, 1991) based on spectrophotometric analysis of similar samples. These analyses showed that the absence of such a correction would result in an overestimate of carotenoid content by 57% (SE = 4%, $n = 70$). Meltpond water (420 ml) was subsampled and filtered onto GF/F equivalent filters (AMD Manufacturing, Mississauga, ON) and preserved frozen in aluminum foil for transport. These plankton chlorophyll *a* samples were subsequently extracted with boiling ethanol extraction and measured using a model 450 Sequoia-Turner fluorometer (Turner Corporation, Mountain View, CA) (Nusch, 1980).

Microbial mat organic content was determined in subsamples collected from a known surface area and frozen for transport. In the laboratory, the sediments were weighed and then dried to constant weight at 95°C. The mass of organic and inorganic fractions were determined by loss on ignition at 500°C for 7 h.

Nutrients (NH_4^+, NO_3^-, NO_2^-, soluble reactive phosphorus [SRP], dissolved organic and inorganic carbon [DOC and DIC], and total nitrogen and phosphorus) were determined from filtered (cellulose acetate, 0.2 μm) surface water subsamples by the National Laboratory for Environmental Testing (NLET), Environment Canada, Burlington, Ontario. Methods were UV digestion and infrared detection (dissolved organic and inorganic carbon, respectively), ion chromatography (nitrate), and automated colorimetry (total nitrogen and ammonium by the indophenol method; nitrate/nitrite by cadmium reduction; soluble reactive phosphorus by the ammonium molybdate/stannous chloride method). Sample water (420 ml) was filtered through GF/C equivalent filters (AMD Manufacturing) to remove particulate carbon and nitrogen, which were determined by elemental analysis at NLET. Particulate phosphorus was calculated by subtraction of unfiltered and filtered total phosphorus determinations (NLET: stannous chloride colorimetry). Major ion concentrations at some sample sites were also determined by NLET using ion chromatography (Cl^-, SO_4^{2-}), atomic absorption (Na^+, K^+, Mg^{2+}, Ca^{2+},) or heteropoly blue colorimetry (SiO_2). Bicarbonate concentration was determined from pH and DIC concentration (Wetzel and Likens, 2000). If measurements were below the limits of detection, "not detected" as substituted by half the detection limit for statistical tests (detection limits were: 5 μg NH_4^+–N L^{-1} for NH_4^+, 5 μg NO_3^-–N L^{-1} for NO_3^-, 1 μg NO_2^-–N L^{-1} for NO_2^-, 50 μg L^{-1} for Ca^{2+}, 200 μg L^{-1} for SO_4^{2-}, 20 μg L^{-1} for SiO_2).

SATELLITE REMOTE SENSING

The spatial extent of each ice shelf was determined using radiometrically-corrected RADARSAT-1 synthetic aperture radar (SAR) images that were projected to a common geographical system (UTM zone 18N) in ArcMap 8.0 (ESRI, Inc., Redlands, CA). Ice type identification was based on our field observations, air photographs, and SAR images, following Lemmen et al. (1988) and Jeffries (1986a, 1986b, 1992a, 2002). In this paper, we define shelf ice as floating ice having a freeboard of 2 m or more (Jeffries, 1992b). In contrast, MLSI is relatively thick and stable sea ice with a freeboard of less than 2 m. Meteoric ice includes glacial ice and iced firn. Iced firn is a term specific to the "Ellesmere ice shelves" that refers to the product of a rapid transformation of snow to ice by meltwater percolation and refreezing (Marshall, 1955). It accumulates in place but is not subject to flow as occurs on glaciers. Marine ice includes basement ice (sea or brackish ice, which accreted on the underside of the ice shelf; Lyons et al., 1971) and MLSI. A nonfloating ice feature related to ice shelves is called an ice rise, which is formed by the grounding of an ice shelf on subjacent land (Lyons et al., 1972).

Polygons were traced over SAR imagery raster layers using vector National Topographic System (NTS) 1:250,000 scale maps (Natural Resources Canada: 120F, 120G, 340E, 340F, 340H) to confirm shoreline position. Ice shelves were digitized from the following image numbers and reflect the spatial extent at the latest image (Serson Ice Shelf: r1_24186_211, June 22, 2000; r1_22728_211, March 12, 2000; Petersen Ice Shelf; r1_23185_213, April 13, 2000, Milne Ice Shelf: r1_29859_214, July 25, 2001; Ayles Ice Shelf: r1_37462_215, January 07, 2003; r1_34062_209, May 14, 2002; Ward Hunt Ice Shelf: r1_35605_210, August 30, 2002; r1_35477_208, August 21, 2002; Markham Ice Shelf: r1_35261_215, August 6, 2002). All of these images were obtained in standard beam mode with the exception of one fine beam image (r1_35605_210). The image used to delineate Petersen Ice Shelf was a low resolution product and was not suitable for ice type discrimination. Surface ice type (marine vs. meteoric) was determined for the Ward Hunt Ice Shelf by performing the following operation on the radar backscatter amplitude from a Radarsat image at peak melt (A: r1_35261_215, August 6, 2002) and from an image recorded in winter (B: r1_37462_215, January 7, 2003) on a pixel by pixel basis in ENVI 3.2 (Research Systems Incorporated, Boulder, CO):

$$(A - B)/2 + 128 \tag{1}$$

The resultant image was digitized as above keeping ice types in contiguous zones. Meteoric ice, which has a relatively small radar backscatter during the melt season and a relatively large radar backscatter in the winter, had a digital number of less than 128 in this classification scheme. Marine ice areas were denoted by lighter areas (digital numbers of 129 to 255) due to a high radar backscatter in August and a low backscatter in January.

OVER-FLIGHT TRANSECTS

In 2001, six helicopter transects were flown at a constant speed, bearing and altitude across the ice shelves and perpendicular to the Ellesmere Island shoreline (Fig. 2; Ward Hunt West, Ward Hunt Middle, Ward Hunt East, Serson, Milne, and Markham). The transects were flown along the centerline of each ice shelf with extra transects halfway between the center and shorelines for the Ward Hunt Ice Shelf due to its greater size and breadth. The Ayles and Petersen ice shelves were not surveyed in this manner due to logistical constraints. Images were extracted from a digital video sequence (every 40th frame, or 1 image every ~1.3 s, which ensured that images did not overlap). The images were de-interlaced and the cover of each class (sediment, water, and snow/ice) was estimated to the nearest tenth or, if present at less than 0.5 tenths cover, was recorded as a trace amount and was represented by 0.25 tenths in subsequent calculations.

The mean percentage area occupied by sediment was scaled-up to the size of the ice shelves to estimate the potential extent of microbial habitat over all the ice shelves. An estimate of the mass of chlorophyll *a*, organic matter and sediment on each ice shelves was made by combining potential habitat extent and mean determinations of these quantities (±SE).

POINT TRANSECTS

Point transect analyses over different areas on Ward Hunt and Markham ice shelves were undertaken to provide a detailed examination of potential habitat at a smaller scale in marine and meteoric ice areas (Fig. 2). The substrate was characterized at 10-cm intervals by visually recording the presence or absence of snow and sediment. These transects were between 120 and 360 m long and ran perpendicular to ridges and troughs. At the Ward Hunt Ice Shelf marine ice area, the main point transect was flanked by two auxiliary transects running parallel to and positioned at approximately 50 m from the main transect.

STATISTICS

Several approaches were used to compare ice shelves, ice types, and mat types. Univariate analyses were undertaken for several variables using one-way ANOVAs or *t*-tests and non-parametric ANOVAs or *t*-tests when warranted (non-normal distributions and/or unequal variances). For multivariate analysis, variables with more than several data points missing were removed and the remaining missing data points (25 out of 684 data points) were replaced by the mean for that particular variable (Legendre and Legendre, 1998). Non-normally distributed environmental and pigment data were normalized using a Box-Cox transformation (conductivity, DIC, total nitrogen, total phosphorus, soluble reactive phosphorus $\lambda = 0$, chlorophyll *a*, and carotenoids $\lambda = 0.25$, NH_4^+ $\lambda = -0.25$). Some variables were not transformable and therefore remained unaltered (temperature, DOC, NO_3^-, and NO_2^-). Taxon relative abundance data were not transformed. A detrended correspondence analysis (DCA) was undertaken using the abundance data and the dispersion was found to be <2, which indicated that a linear ordination technique should be employed (ter Braak and Smilauer, 1998). Therefore, redundancy analysis (RDA) was used to investigate the association between environmental and taxon relative abundance data. An overall solution was calculated using all 28 samples that were enumerated microscopically and 13 environmental variables. This was followed by a manual forward selection of variables that yielded a more parsimonious model.

To examine differences between ice shelves, ice types and microbial mat types, a one-way analysis of similarities (ANOSIM, Primer 8.5) was used (Clarke and Warwick, 1994). Similarity matrices were constructed using Bray-Curtis distances for taxon relative abundance data and normalized Euclidean distances for environmental and pigment data (the latter matrix contained several samples that did not have equivalents in the taxon abundance matrix). The ANOSIM is a multivariate procedure that tests for differences between groups determined *a priori* (ice shelf, ice type, mat type). The average ranked similarity value of pairs of replicates (*R* statistic) is calculated and the probability of obtaining a higher *R* with a given dataset is based on 999 randomly selected permutations of the dataset.

Results

ICE SHELF COMPARISONS

The six largest remnant ice shelves in the Canadian High Arctic totaled 1043 km^2 at the time of observation, and 8% of this surface provided a sediment cryohabitat for microbiota. The area of each ice shelf and their constituent ice types are given in Table 1. All the ice shelves except Milne were found to have substantial areas of marine ice exposures. Transect data showed that Ward Hunt and Markham ice shelves contained the greatest amounts of potential microbial mat habitat (10% and 44%, respectively) and this translated to high estimates for total chlorophyll *a* and organic matter relative to the other ice shelves (Table 1). This trend was also reflected in the estimates of sediment load for each ice shelf.

The five ice shelves had similar values for many of their limnological properties (Table 2) and differed greatly in others (Fig. 4). The western ice shelves had less chlorophyll *a*, carotenoids, and organic matter per unit area than the Ward Hunt and Markham ice shelves (Fig. 4b; ANOVA results: H = 12.6, $P = 0.005$; H = 15.8, $P = 0.001$; F = 5.9, $P = 0.003$; respectively). This pattern was mirrored by conductivity, but there were no significant differences in sediment load (H = 5.8, $P = 0.22$) and pH (F = 1.4, $P = 0.25$) among the ice shelves (Fig. 4a). Nutrient concentrations were significantly different among the five ice shelves with the exception of total nitrogen (H = 6.3, $P = 0.18$) and ammonium (H = 3.9, $P = 0.42$) concentrations. DIC concentrations (H = 10.1, $P = 0.039$) were highest in Markham Ice Shelf sites (Table 2), while DOC (F = 3.99, $P = 0.016$) concentrations were highest in both Markham and Ward Hunt ice shelves. Nitrate (H = 11.4, $P = 0.023$) and nitrite (H = 16.3, $P = 0.003$) concentrations were highest in Serson Ice Shelf samples and these variables were lowest in the easternmost ice shelves. Total phosphorus (H = 9.5, $P = 0.05$) and soluble reactive phosphorus (H = 11.0, $P = 0.027$) concentrations were highest on Ward Hunt Ice Shelf (Table 2) and did not vary systematically across the ice shelves. For samples taken from marine ice, ionic composition indicated evaporative concentration (high Mg^{2+}/Ca^{2+}) consistent with a seawater source of major ions. Most samples taken from meteoric ice were enriched with magnesium relative to sodium, a proxy of rock interaction (Vincent and Howard-Williams, 1994), which suggests that *in situ* chemical weathering of surface sediments overshadowed the geochemical influence of marine aerosols in these environments (Fig. 5).

TABLE 1

Comparison of the six Canadian Arctic ice shelves. Mean values followed by ±SE in parentheses.

Ice Shelf	Serson	Petersen	Milne	Ayles	Ward Hunt	Markham
Position	82°20′N, 86°00′W	82°31′N, 81°45′W	82°40′N, 81°20′W	82°50′N, 80°30′W	83°02′N, 74°00′W	83°03′N, 71°20′W
Length (km)	21	17	21	10	17	9
Width (km)	18	12	14	8	55	5
Total area (km^2)	204.7	51.2	205.9	84.1	448.1	49.5
Basement ice (km^2)	119.1	—	0	61.1	130.0	42.4
Iced firn (km^2)	0?	—	129.2	23.0	318.1	7.1
Glacier Ice (km^2)	85.6	—	76.7	0	0	0
Ice shelf fragments[a] (km^2)	6.2	—	0	1.5	19.1	3.3
MLSI[a] (km^2)	50	>100	>100	15.5	39.8	0
Water area[b] (km^2)	11.2 (0.8)	7.3	28.8 (2.1)	—	82.7 (4.7)	9.0 (0.7)
Habitat area[b] (km^2)	2.4 (0.4)	—	4.1 (0.4)	8.7[c]	43.6 (6.2)	24.2 (0.9)
Estimated chlorophyll *a* (Mg)	0.060 (0.022)	—	0.16 (0.12)	—	7.6 (1.8)	6.2 (1.1)
Estimated organic matter (Gg)	0.189 (0.032)	—	0.924 (0.66)	0.394[c]	16.0 (2.4)	16.5 (3.2)
Estimated sediment (Gg)	38.6 (26)	—	26.4 (11.4)	81.2[c]	141.1 (22.5)	128.9 (27.8)

[a] Multiyear landfast sea ice (MLSI) Not considered to be a part of the ice shelf.

[b] Includes ice shelf fragments, but not MLSI.

[c] Estimated from an average of the other four ice shelves with transect data.

The dominant taxa in the ice shelf microbial mats were Oscillatorian cyanobacteria, specifically morphotypes Osc. 3 and Osc. 1 followed by Osc. 2, the diatom *Chamaepinnularia begeri*, and the palmelloid green alga cf. *Bracteacoccus* sp. The former three taxa are all filamentous in habit and produce extracellular polymeric substances (EPS) which suggests that the overall structure of the microbial mat is influenced by the intertwining of their trichomes and the cohesive, binding effect of the EPS (see Fig. 3e in Vincent et al., 2000). In all, 32 taxa were found (Table 3), and samples frequently contained empty diatom frustules of taxa that were observed with cellular contents elsewhere in the sample or in other samples in this study. The planktonic diatom *Asterionella* sp. and unidentified cysts were occasionally observed in samples but with no visible cellular contents. A list of each observed taxon and their relative abundance is given in Table 3. There were no significant differences between the ice shelves with regards to the number of species (F = 2.3, $P = 0.10$) or Simpson's diversity index (F = 2.6, $P = 0.072$).

The multivariate test ANOSIM, revealed that the microbial mat relative abundance was significantly different (Global R = 0.142, $P = 0.048$) among the five ice shelves. A pairwise comparison indicated that Markham and Serson ice shelves have the most dissimilar communities ($P = 0.012$) while Markham and

TABLE 2

Ice shelf water column nutrients, major ions, and suspended particulates. Averages followed by standard error in parentheses; sample sizes are as follows: Markham Ice Shelf major ions 2, nutrients 6; Ward Hunt Ice Shelf major ions 15, nutrients 21 (except PP: 19 and Total P: 18); Ayles 1; Milne Ice Shelf major ions 3, nutrients 4; Serson Ice Shelf major ions 2, nutrients 4.

Ice Shelf	Serson	Milne	Ayles	Ward Hunt	Markham
Particulates					
POC (mg L^{-1})	0.11 (0.041)	0.080 (0.0079)	0.043	0.090 (0.011)	0.010 (0.014)
PON (mg L^{-1})	0.01 (0.0053)	0.011 (0.0020)	0.0040	0.012 (0.0019)	0.013 (0.0026)
PP (mg L^{-1})	0.0038 (0.0019)	0.00047 (0.0022)	0.00040	0.0042 (0.0016)	0.0019 (0.00098)
Chl. *a* (μg L^{-1})	0.14 (0.10)	0.11 (0.07)	0.001	0.16 (0.04)	0.18 (0.10)
Dissolved Nutrients					
DOC (mg L^{-1})	0.25 (0.05)	0.22 (0.048)	0.20	0.36 (0.020)	0.38 (0.040)
DIC (mg L^{-1})	0.9 (0.13)	0.65 (0.16)	0.6	0.98 (0.17)	1.9 (0.033)
Total N (mg L^{-1})	0.17 (0.10)	0.065 (0.012)	0.019	0.070 (0.0077)	0.087 (0.0055)
NH_4^+ (mg N L^{-1})	0.0065 (0.0023)	0.0088 (0.00075)	0.009	0.016 (0.0032)	0.016 (0.0041)
NO_3^- (mg N L^{-1})	0.026 (0.0039)	0.021 (0.0037)	0.018	0.016 (0.0012)	0.014 (0.0024)
NO_2^- (mg N L^{-1})	0.0035 (0.00029)	0.002 (0.00058)	0.002	0.0011 (0.0001)	0.0011 (0.0002)
Total P (mg L^{-1})	0.0016 (0.00041)	0.0017 (0.00034)	0.0022	0.0095 (0.0045)	0.0030 (0.00054)
SRP (mg L^{-1})	0.0013 (0.00045)	0.0009 (0.00027)	0.0012	0.0023 (0.00022)	0.0018 (0.00025)
Major Ions					
Cl^- (mg L^{-1})	51.8 (5.5)	4.52 (4.0)	132	119 (40)	994 (6.5)
SO_4^{2-}	13 (0.95)	0.73 (0.54)	21	18 (6.1)	158 (18)
SiO_2 (mg L^{-1})	0.015 (0.005)	0.017 (0.0033)	0.01	0.04 (0.14)	0.08 (0.01)
Ca^{2+} (mg L^{-1})	1.9 (0.14)	0.62 (0.52)	3.02	2.9 (0.86)	24 (3.3)
K^+ (mg L^{-1})	1.4 (0.14)	0.083 (0.064)	2.9	2.5 (0.79)	22 (2.4)
Mg^{2+} (mg L^{-1})	3.7 (0.88)	0.25 (0.22)	8.7	7.6 (2.5)	69 (3.1)
Na^+ (mg L^{-1})	35.9 (5.0)	2.25 (2.1)	78.0	67.0 (22)	571 (41)
HCO_3^- (mg L^{-1})	0.84 (0.13)	0.49 (0.23)	0.23	0.69 (0.18)	1.6 (0.36)

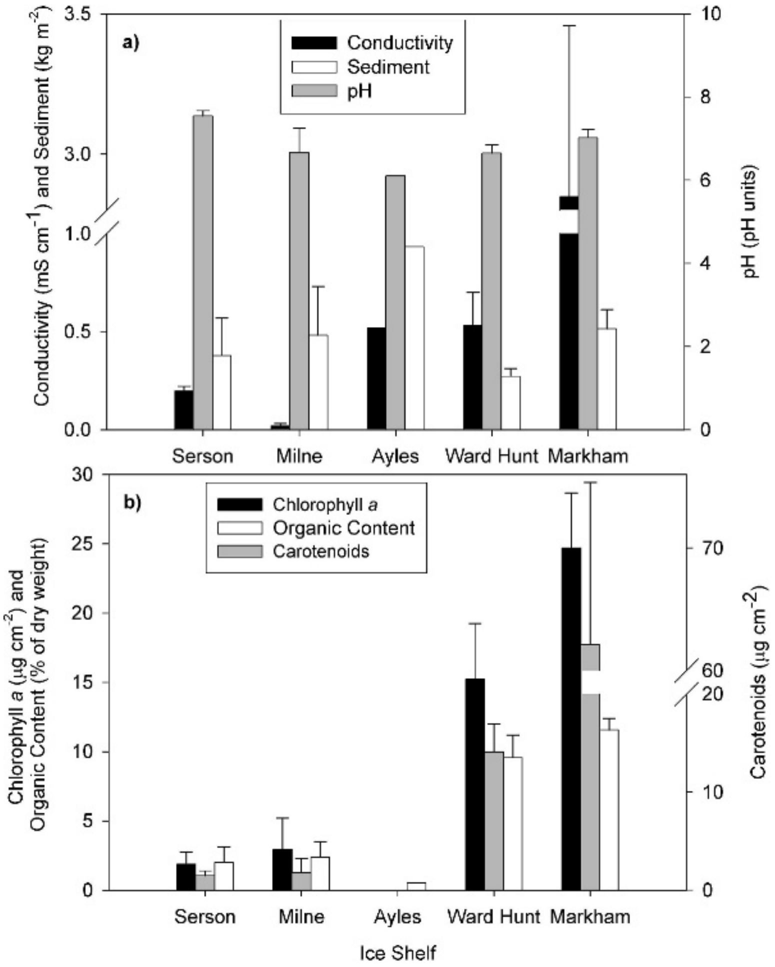

FIGURE 4. Comparisons of cryoecosystem characteristics by ice shelf. (a) Conductivity, pH, and sediment concentration. (b) Pigments and percent organic matter in the microbial mats. Pigments were not measured for the Ayles Ice Shelf.

Milne ice shelves also had significantly different microbial communities ($P = 0.036$). For environmental variables, as well as organic matter content and pigment data, the Global R was 0.408 ($P = 0.001$) with four significantly different pairs (Markham and Milne, $P = 0.01$; Markham and Serson, $P = 0.005$; Ward Hunt and Milne, $P = 0.002$; Ward Hunt and Serson, $P = 0.003$).

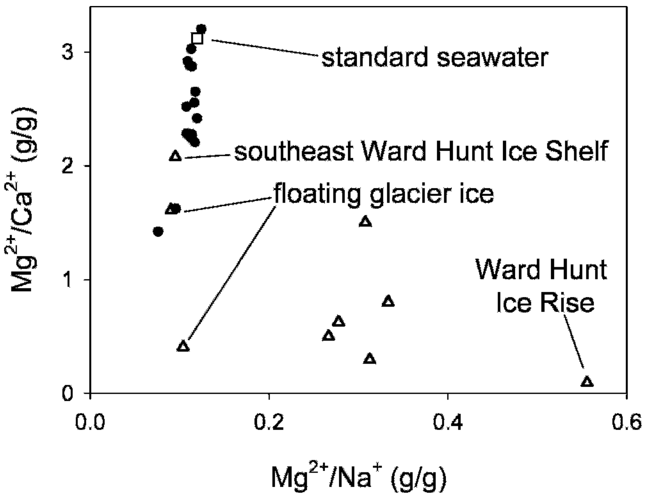

FIGURE 5. Cation ratio plot for surface meltwater samples. Evaporative environments are found to the top left of the plot, whereas rock-dominated environments are found to the bottom right of the plot (Vincent and Howard-Williams, 1994). Marine ice types are denoted by black circles, open triangles indicate meteoric ice types as defined in this study. The ionic composition of standard seawater is displayed as an open square.

Direct ordination of the taxon relative abundance data and the 13 environmental variables revealed a non-significant association between these data matrices, with 53% of the relative abundance explained by variation in the environmental variables ($P = 0.32$). After a manual forward selection procedure, a more parsimonious model using 4 environmental variables (Conductivity, NO_3^-, NH_4^+, and SRP) was constructed that explained 40% of the relative abundance variance ($P = 0.003$).

ICE TYPE AND MAT TYPE COMPARISONS

Samples from marine ice areas had significantly higher ($P < 0.05$) water column nutrient concentrations (except total phosphorus), conductivity, and pH as well as biodiversity indicators, microbial mat pigment concentrations, and organic content than their meteoric ice counterparts (Table 4). The ANOSIM result (Global R = 0.447, $P = 0.001$) also indicated that these ice types differed significantly in their habitat characteristics. The taxon relative abundance was also significantly different between these two habitat types (Global R = 0.187, $P = 0.016$).

The microbial mat types had significantly different pigment and organic matter concentrations; however, the sediment concentration was not significantly different among these groups (three-level ANOVA, not including the "no mat" category). A four-level ANOVA revealed that water that was not underlain by microbial mats was significantly colder, less saline, and had lower pH than water overlying sediment. However, among the three mat

TABLE 3

Abundance of taxa found in Arctic ice shelf microbial mats. All samples: average and standard error for all samples. Ice shelf, Ma: Markham Ice Shelf, WH: Ward Hunt Ice Shelf, IR: Ward Hunt Ice Rise, Di: MLSI near Discovery Ice Rise, Ay: Ayles Ice Shelf, Mi: Milne Ice Shelf, Se: Serson Ice Shelf. Ice Type: Marine: basement ice and MLSI, Meteoric: iced firn and glacier ice. Mat Types: Matlet (small flakes of microbial mat), Orange (thick mat with orange surface layer), Sediment (no discernable biological aggregates). Osc. = oscillatorian cyanobacteria. Taxon relative abundance is coded as follows: 5 indicates dominant (>50% of total algal counts in the sample), 4 indicates subdominant (50–25%), 3 indicates common (25–5%), 2 indicates rare (<5%), 1 indicates not detected (0%).

	All Samples		Ice Shelf							Ice Type		Mat Type		
Taxon	Average	SE	Se	Mi	Ay	Di	IR	WH	Ma	Marine	Atmos.	Matlet	Orange	Sed.
Coccoid cyanobacterium spp.	1%	1%	2	3	1	2	2	2	2	2	2	2	2	2
Colonial coccoid cyanobacteria spp.	1%	0.2%	1	2	1	1	1	2	2	2	2	2	2	2
cf. *Aphanocapsa* sp.	0.1%	0.1%	1	1	1	1	1	2	2	2	1	2	2	1
Gloeocapsa sp.	0.1%	0.05%	1	2	1	1	1	2	2	2	2	1	2	2
Osc. 1	27%	4%	2	3	**5**	**4**	3	3	**4**	**4**	3	3	**5**	3
Osc. 2	4%	1%	1	3	3	2	1	2	3	2	2	3	2	2
Osc. 3	53%	5%	**5**	**5**	3	**4**	**4**	**5**	**4**	**4**	**5**	**5**	3	**5**
cf. *Pseudanabaena* sp.	1%	0.4%	2	2	1	1	1	2	2	2	2	2	2	2
Phormidium sp.	1%	0.5%	2	2	1	2	2	2	2	2	2	2	2	2
Unknown Nostocales sp.	0.2%	0.2%	1	2	1	1	1	1	1	1	2	1	1	2
cf. *Aulosira* sp. 1	0.4%	0.1%	1	2	1	2	1	2	2	2	2	2	2	2
cf. *Aulosira* sp. 2	0.1%	0.1%	1	2	1	1	1	2	2	2	2	2	1	2
Nostoc sp.	0.1%	0.1%	1	2	1	1	1	2	2	2	2	2	2	2
Unknown diatom spp.	0.02%	0.02%	1	1	1	1	1	1	2	1	2	2	1	1
Unknown Achnanthales sp.1	0.03%	0.02%	2	1	1	1	1	2	1	2	2	2	1	2
Unknown Achnanthales sp.2	0.2%	0.1%	1	1	1	1	1	2	2	2	2	2	1	2
Navicula sp. 1	0.1%	0.1%	2	1	1	1	1	2	2	2	2	2	2	2
Navicula sp. 2	0.1%	0.1%	2	1	1	2	1	2	2	2	2	2	2	2
Navicula sp. 3	0.1%	0.1%	2	1	1	1	1	2	1	2	2	1	1	2
Navicula cf. *phyllepta*	1%	0.3%	2	1	1	1	1	2	2	2	2	2	2	2
Chamaepinnularia begeri	3%	1%	2	1	3	2	1	2	2	2	2	2	2	2
Nitzschia cf. *homburgiensis*	0.02%	0.02%	1	1	1	1	1	2	1	2	1	2	1	1
Nitzschia sp.	0.03%	0.02%	1	1	1	2	1	2	1	2	1	2	1	2
Unknown chlorophyte spp.	1%	0.2%	1	2	2	2	1	2	2	2	2	2	2	2
cf. *Bracteacoccus* sp.	2%	0.4%	2	2	2	2	3	2	2	2	2	2	2	2
Nonmotile coccal green algal colony	1%	0.2%	1	2	2	1	1	2	2	2	2	2	2	2
Palmelloid colony	0.3%	0.1%	1	1	2	1	1	2	2	2	1	2	2	2
Ancyclonema nordenskioldii	2%	2%	1	1	1	1	**4**	1	1	1	2	1	1	2
Cylindrocystis cf. *brebissonii*	0.3%	0.1%	1	2	1	1	1	2	2	2	2	2	2	2
Ciliate spp.	1%	0.3%	2	2	1	2	1	2	2	2	2	2	2	2
Rotifera	0.04%	0.02%	1	1	1	1	1	2	2	2	1	2	2	1
Unknown	0.1%	0.04%	1	2	1	1	1	2	2	2	2	2	1	2

TABLE 4

Comparison of ice shelf ecosystem characteristics based on ice type and mat type. Averages followed by standard error in parentheses, for *n* = 13–14 (meteoric ice), 20–24 (marine ice), 9–11 (orange mat), 7–10 (matlet), 11–12 (sediment), 5 (no mat).

	Ice Type		Mat Type			
Variable	Meteoric Ice	Marine Ice	Orange	Matlet	Sediment	None
Water Column						
Conductivity (mS cm^{-1})	0.041 (0.018)	1.26 (0.28)	2.2 (0.61)	0.78 (0.26)	0.16 (0.058)	0.033 (0.027)
Water temperature (°C)	0.58 (0.20)	0.76 (0.13)	1.2 (0.27)	0.64 (0.13)	0.76 (0.20)	0.07 (0.040)
pH	6.4 (0.25)	7.0 (0.15)	7.2 (0.20)	6.5 (0.15)	7.0 (0.28)	6.0 (0.50)
DOC (mg L^{-1})	0.28 (0.025)	0.36 (0.020)	0.36 (0.029)	0.42 (0.02)	0.3 (0.028)	0.2 (0.032)
DIC (mg L^{-1})	0.61 (0.065)	1.3 (0.18)	1.6 (0.27)	0.99 (0.14)	1.0 (0.28)	0.44 (0.024)
Total N (mg L^{-1})	0.054 (0.0066)	0.12 (0.030)	0.088 (0.0090)	0.15 (0.058)	0.058 (0.0072)	0.12 (0.088)
Total P (mg L^{-1})	0.0036 (0.0016)	0.0076 (0.0038)	0.012 (0.0088)	0.0044 (0.0016)	0.0022 (0.00032)	0.0062 (0.0043)
Microbial Mats						
Chlorophyll *a* (mg cm^{-2})	3.4 (1.6)	19.5 (3.4)	32.9 (4.5)	10.9 (2.0)	3.7 (0.91)	
Carotenoids (mg cm^{-2})	1.9 (0.70)	29.9 (6.0)	52.3 (8.9)	14.3 (2.2)	2.3 (0.5)	
Organic content (mg cm^{-2})	14.2 (4.8)	43.2 (5.9)	53.0 (9.6)	46.2 (4.4)	16.2 (4.5)	
Sediment (g cm^{-2})	0.34 (0.092)	0.38 (0.051)	0.42 (0.077)	0.34 (0.050)	0.52 (0.090)	
Number of taxa	6.9 (1.8)	12.8 (1.3)	16.4 (1.2)	13.9 (0.88)	8.3 (1.4)	
Simpson's D	1.4 (0.34)	2.5 (0.26)	3.1 (0.35)	2.6 (0.25)	1.8 (2.5)	

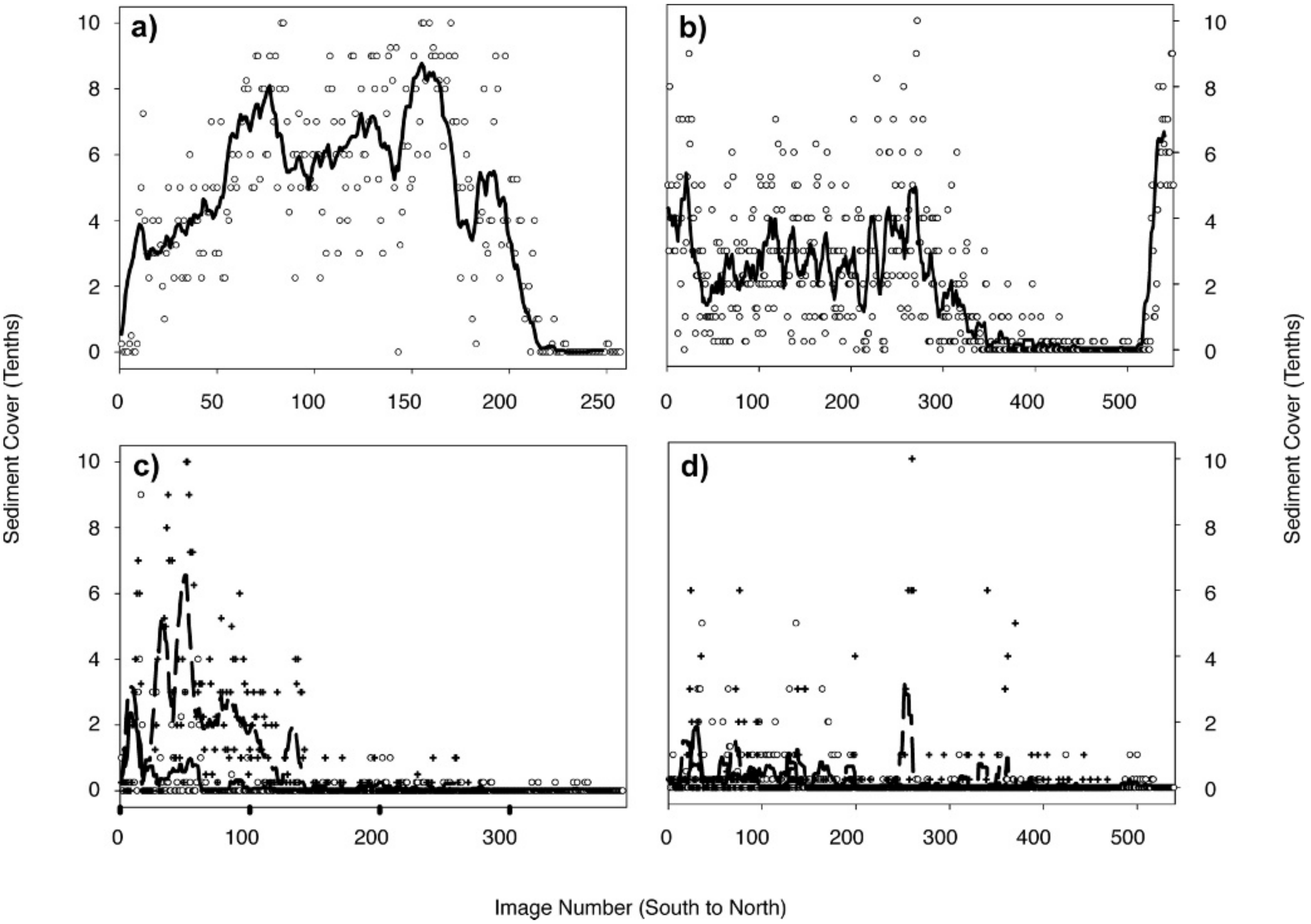

FIGURE 6. Sediment cover determined by over-flight transects. Points are cover estimates (in tenths) for individual images in the transect. Data were also smoothed with a running mean ($n = 10$) and represented by lines. (a) Markham Ice Shelf. (b) Ward Hunt Ice Shelf, Central Transect. c) Ward Hunt Ice Shelf, East Transect (open circles, solid line) and Ward Hunt Ice Shelf, West Transect (crosses, dashed line). d) Milne Ice Shelf (open circles, solid line) and Serson Ice Shelf (crosses, dashed line).

types, conductivity was significantly different, whereas temperature and pH did not differ significantly. With the exception of total phosphorus, nutrient levels were significantly different from each other among the four groups and among the three mat types there were significant differences in both the number of taxa and Simpson's diversity index (Table 4). The ANOSIM analysis indicated a significant difference among the three mat types for relative abundance (Global R = 0.463, $P = 0.001$) with significant pairwise differences between ''orange mat'' and ''matlet'' ($P = 0.002$) as well as ''orange mat'' and ''sediment'' ($P = 0.001$). Significant differences were also found for both the three-level (Global R = 0.334, $P = 0.001$) and the four-level (Global R = 0.488, $P = 0.001$) ANOSIMs on environmental and pigment data among microbial mat categories. All pairwise comparisons were significantly different for each of these tests.

SEDIMENT PATTERNS

Over-flight transect estimates of percent sediment cover (Markham, 44%; Ward Hunt Middle, 19%; Ward Hunt East, 2%; Ward Hunt West, 12%; Milne, 2%; Serson, 3%) and meltwater cover (Markham, 17%; Ward Hunt Middle, 14%; Ward Hunt East, 22%; Ward Hunt West, 16%; Milne, 18%; Serson, 14%) indicated that substantial differences exist among ice shelves with regards to potential microbial habitat. The percent cover of sediment varied markedly throughout each transect, but overall patterns can be seen in Figure 6. Markham Ice Shelf had very little sediment cover at its northern and extreme southern end (Fig. 6a), the Ward Hunt Ice Shelf had greater sediment cover in the southern portions of all transects, and only the central transect, which terminated at Ward Hunt Island showed an increase in sediment cover farther north (Fig. 6b, 6c). The Milne and Serson ice shelves had very little sediment cover throughout, yet the southern portions of these transects did have slightly higher sediment cover (Fig. 6d). When sediment on these latter ice shelves was present in high percentages, it was of glacial origin (moraines), which explained large departures from the overall trend (e.g., Fig. 6d; Serson Ice Shelf, image number 260 on the abscissa).

On a smaller scale, sediment cover point transects also showed a high degree of variability in the ice-shelf surface cover. The point transect on the Ward Hunt Ice Rise revealed that this environment, while not strictly part of the ice shelves, also contained sediments, albeit at very low percentages (Fig. 7d). Meteoric ice (Fig. 7d, 7e) had less sediment exposed at the surface due to snow cover than the other point transects.

Discussion

OVERALL SYSTEM PROPERTIES

The major remnants of the ''Ellesmere Ice Shelf'' surveyed in this study are large masses of ice with substantial yet variable

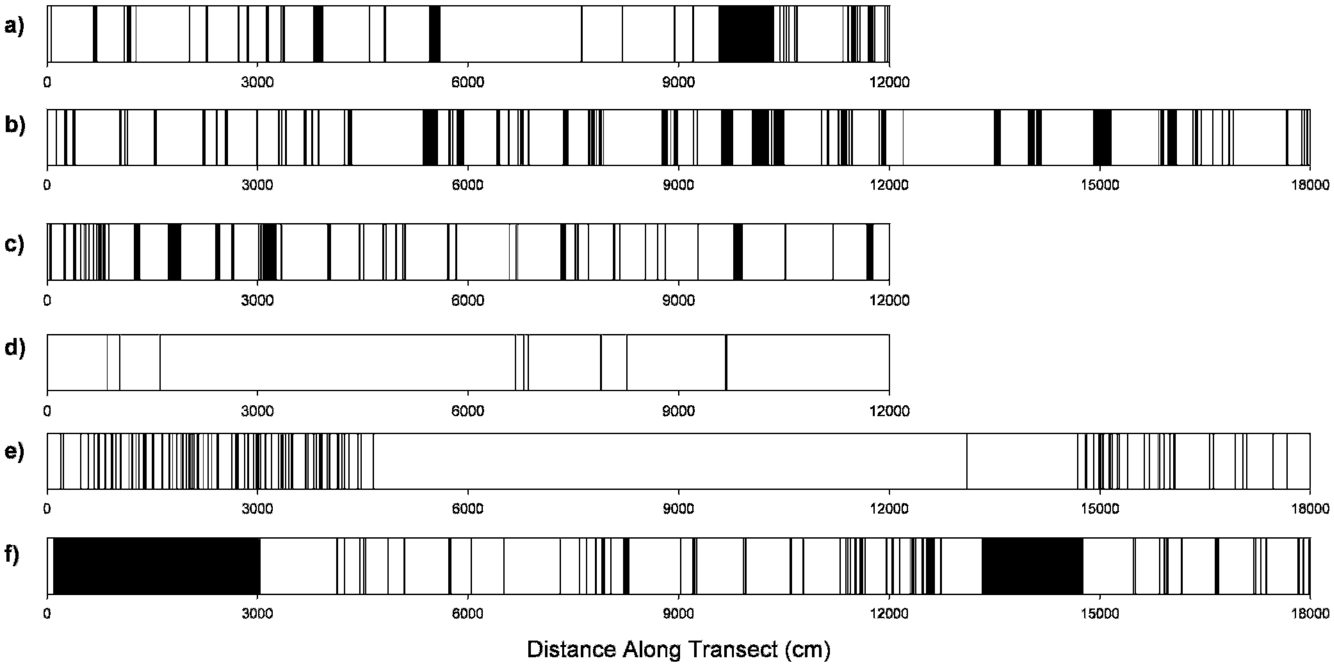

FIGURE 7. Point transect analysis of sediment presence/absence over ice surfaces showing habitat patchiness (black indicates sediment). (a) Ward Hunt Ice Shelf, marine ice area–eastern flank (sediment coverage 15%, SE = 1%). (b) Ward Hunt Ice Shelf, marine ice area–middle transect (only the first 180 m shown; sediment coverage 17%, SE = 1%). (c) Ward Hunt Ice Shelf, marine ice area–western flank (sediment coverage 13%, SE = 1%). (d) Ward Hunt Ice Rise (sediment coverage 1%, SE = 0.3%). (e) Ward Hunt Ice Shelf, meteoric ice area, (sediment coverage 7%, SE = 1%). (f) Markham Ice Shelf, marine ice area (sediment coverage 31%, SE = 1%).

surface water and sediment cover. At the times of sampling the meltwaters had temperatures near freezing, near neutral pH values, and oligotrophic nutrient levels, with the exception of elevated phosphorus levels at some sites (Table 1). The water column seston was also in sparse concentration as indicated by particulate organic carbon and nitrogen and planktonic chlorophyll *a* levels (Table 1). In contrast to the water column, the sediments on the ice surface contained large amounts of organic material and algal pigments. An enumeration of these benthic microbial communities revealed numerous taxa including cyanobacteria, green algae, diatoms, other protists, and microfauna that were common to all habitats in this ensemble of ice shelves. Despite these similarities, there were important and systematic differences across the "Ellesmere Ice Shelf" cryoecosystem, as outlined below.

Total sediment estimates were higher than measurements made by Crary (1958), suggesting that sediment concentration may have increased since these analyses due to ongoing surface wasting of the ice shelf (Braun et al., 2004; Mueller and Vincent, 2006), which would also act to bring immured microbial mats to the surface (Mueller et al., 2005). Spatial variability and sampling bias limit the accuracy and precision of the estimates; however, our results allow a first order approximation of total biomass that can be compared to other ecosystems. In one study, samples from the Central Arctic pack ice averaged an organic carbon content of 112 mg C m^{-2} (Gradinger, 1999), which is more than 2 orders lower than our spatially averaged estimate of ice shelf organic matter. Chlorophyll *a* concentration was 14 mg m^{-2} averaged over all the ice shelf remnants in this study. This compares to a mid-summer chlorophyll *a* concentration in pack ice (>2 m thick) of 1.6 mg m^{-2} (Gradinger, 1999), although far higher chlorophyll *a* biomass may be attained beneath landfast sea ice (Michel et al., 2002). Under optimal conditions, Arctic ice shelf microbial mats have a gross photosynthetic rate of 129 mg C m^{-2} d^{-1} when averaged over the ice shelf (Mueller et al., 2005). This productivity is five times higher than average rates per unit area for the Central Arctic pack ice (Gradinger, 1999) and over ten times higher than the productivity of polar hypolithic communities (Cockell and Stokes, 2004). However, the total surface area of ice shelves is small relative to the 5.5 million km^2 of sea ice found in the Arctic Ocean (Comiso, 2002), and also relative to the vast expanse of Arctic polar desert.

ENVIRONMENTAL GRADIENTS

Consistent with our hypothesis regarding environmental gradients, there was a striking gradient in conductivity, biomass, and pigment concentrations from west to east along 250 km of the coastline. This broad gradient is likely due to the more common occurrence of marine ice with high sediment content in the eastern two ice shelves and the greater proportion of meteoric ice with low sediment content in the west. It is also possible, however, that this trend was influenced to some degree by sampling bias towards marine ice sites on the Ward Hunt Ice Shelf (Fig. 2a). Our results indicated that marine ice types were associated with higher amounts of organic matter and pigments as well as increased nutrient concentration and conductivity than meteoric ice types. Sediment mass per unit area of microbial mat is not necessarily greater for marine ice; however, higher sediment percent cover in the marine ice areas of Ward Hunt and Markham ice shelves makes them more important with regards to potential microbial habitat (Table 1).

We suggest that this east-west gradient is due to a combination of two factors: (1) sediment delivery onto the ice shelf, affected by the local availability of sediment and the efficiency of delivery mechanisms such as eolian transport and ice-shelf grounding (see below); and (2) local climatological differences in snowfall, fog cover, ice shelf albedo, and thus ablation rates (Mueller and Vincent, 2006). Highest surface coverage will occur where the supply rates of sediment are high, and where the sediment is exposed and concentrated on the ice surface due to low albedo and perennial net surface ablation (Crary et al., 1955). In this manner, ice-type surface exposures are related to a temporally integrated mass-balance history of the ice shelf. Over time, if the surface mass balance has been negative and basal mass balance has been positive, then marine ice will become exposed at the surface of the ice shelf. If the converse is true, then the surface ice type will be derived from precipitation. Given this set of processes, the exposure of either marine or meteoric ice would reflect historical differences in climatic parameters such as precipitation, cloud cover, albedo, and air temperature. Sediment concentration on the ice shelf surface serves in turn to enhance ablation through reduced albedo and provides more habitat for microbial mats.

The lithology of coastal areas surrounding the ice shelves likely determines the availability and composition of sediments. Markham and Ward Hunt ice shelves are surrounded by the Cape Columbia Group (biotite, feldspar, hornblende), the M'Clintock Group (andesitic and basaltic lava, breccia, tuffs, greywacke) as well as outcrops of limestone and sandstone. The western three ice shelves are bordered by the Cape Columbia Group as well, but also by harder rocks such as granite and gneiss (Christie, 1957; Trettin, 1991). The relative surface area of outcrops and differences in the friability and weathering of these formations determines the grain size distribution and availability of sediment. Prevailing winds move from west to east along the northern coast of Ellesmere Island (Crary, 1960). For eolian transport of these sediments to the ice surface, source areas must be aligned with wind patterns and there must be sufficient fetch and appropriate topography to move sediments efficiently (winds crossing steep-walled fiords will eddy, thereby decreasing the linear transport of materials). Finally, bathymetry may play a role in determining whether marine ice is exposed at the surface of an ice shelf. Marine sediment can be delivered to the ice-shelf surface via basal freezing and subsequent surface ablation. In this manner, intact marine mollusks, sponges, and sediments are raised to the surface of the ice shelf over a period of several decades to centuries. This has been noted on the ice shelf to the east of Ward Hunt Island (Crary, 1960; Jeffries, 1992b), and we have observed the remains of marine invertebrates on the surface of southern Markham Ice Shelf and on the Ward Hunt Ice Shelf to the southwest of Ward Hunt Island. This mechanism is also known in Antarctica (Debenham, 1920; Vincent, 1988), and it occurs in areas where the bottom of the ice shelf touches the sea floor. A high proportion of sediment on the ice surface will also encourage greater surface ablation via an albedo feedback, thereby accentuating this sediment delivery mechanism. Although little is known about the near shore bathymetry of the region (see Fig. 1 in Crary, 1956), it is probable that certain areas near the shore of Ward Hunt Island and Ellesmere Island have a suitable bathymetry for this to play a role in the delivery of sediments to sections of the Ward Hunt and Markham ice shelves.

From an inshore/offshore perspective, sediment cover patterns are consistent with assumed gradients caused by sediment source areas and modes of transport. Over-flight transects confirmed that sediment distribution is skewed towards coastal areas of the ice shelves with the exception of the termini of coalesced glacier tongues that have transported debris far from shore.

ECOLOGICAL GRADIENTS

Gradients also exist in the biological domain of the "Ellesmere ice shelves," as might be expected from such large gradients in the physical characteristics of this cryoecosystem. Greater chlorophyll *a* and organic content was associated with the more saline ice with higher sediment content in the two eastern ice shelves, whereas the western ice shelves had less sediment and lower biomass content. A multivariate approach showed that the relative abundance was strongly associated with environmental variables, which was supported by a significant RDA ordination with the variables conductivity, soluble reactive phosphorus, ammonium, and nitrate. Using ANOSIM, the taxon relative abundance data were found to be significantly different between marine and meteoric ice types; therefore, it is not surprising that the RDA solution shows the influence of conductivity gradients. The oligotrophic nutrient status of the water columns and the inclusion of nutrients in the RDA solution suggest that nutrient supply may be a limiting factor for certain microbial mat species. However, there is evidence that the nutrient status within microbial mats is much less impoverished than the overlying water column and that microbial mat organisms may not in fact be nutrient limited (Bonilla et al., 2005; Mueller and Vincent, 2006). In this case, if diffusion and water column mixing were comparable among samples, the water column nutrient concentrations may be influenced by microbial mat interstitial waters and may serve as a proxy for the relative nutrient status of the mats.

In the present study, we classified mat types in discrete categories, while recognizing that these communities span a continuum in structure and pigmentation. However, there were important taxonomic differences between the "matlet," "orange," and "sediment" mat types, which suggest that these visually discernable mat characteristics may continue to serve as convenient and useful categories for future work. It is possible that these microbial mat types are related to the ice type of the sample site. For instance, orange mat was not found on meteoric ice whereas "matlet" and "sediment" mat types were found in both marine and meteoric ice types. The biodiversity and nutrient data suggest that a progression may exist in microbial mat development. Inorganic sediment may first become colonized with a number of pioneer taxa (notably Osc. 3, Osc 1, and *Ancyclonema nordenskioldii*) and over time this may develop into "matlets" with more biodiversity and biomass. Finally, if conditions are right, an orange surface layer may develop in late succession with an increase in prominence of taxa such as *Chamaepinnularia begeri*, cf. *Bractaeococcus* sp., *Navicula* cf. *phyllepta*, and cf. *Pseudanabaena* sp. Conversely, the microbial mat types may represent three divergent end members that are not successionally related to each other. As well, the ANOSIM results for ice type and mat type were significantly different for both taxonomic and environmental data, suggesting these categories are meaningful and possibly related. It is reasonable to assume that the environmental gradients exert some degree of control on relative abundance of taxa; however, the reverse may also be true in that certain taxa or mat types may influence local conditions, for example through nutrient release, pH control and albedo effects.

ICE TYPE DETERMINATION

The overall area of ice shelves has not changed substantially since the last determination was made in 1998/1999 (Vincent et al., 2001). Two relatively minor changes are the loss of 6 km^2 of shelf ice and 20 km^2 of MLSI from the eastern seaward edge of the Ward Hunt Ice Shelf in 2002 (Mueller et al., 2003). This was preceded by the break-up of the ice shelf into two fragments, although they are still held in place by islands and ice rises. Other discrepancies from the previous literature can be explained by the ice type reclassifications. For example, the inner portion of the Milne Ice Shelf is known to be epishelf lake ice (Jeffries, 2002; Van Hove, 2005) and was therefore not included in this study. As well, we have recently determined that the dark ice at the southern end of the western Ward Hunt Ice Shelf was ice shelf covered by water during our over-flight transects (Figs. 1b, 2a). We therefore include this area as part of the Ward Hunt Ice Shelf in the present study.

Marine and meteoric ice areas were relatively easy to demarcate; however, in the case of one sample in the southeast corner of the Ward Hunt Ice Shelf (Fig. 2a), the ionic composition was closer to marine ice meltwater than any of the other meteoric ice water samples (see Fig. 5). This likely reflects an error in ice type delineation, probably due to a prevalence of ice type unconformities (Lyons et al., 1971) in this particular region. Two other outliers in this graph were from the glacial section of Serson Ice Shelf and the floating portion of the Milne Glacier (see Fig. 5). These samples may have differed from other samples underlain by meteoric ice due to a high degree of flushing with glacial surface meltwaters that had not contacted rock debris and were therefore marine-influenced relative to other meteoric ice meltwater that had longer contact times with eolian sediment.

THE EFFECTS OF HABITAT FRAGMENTATION

Our results show that gradients exist across the extent of the ''Ellesmere Ice Shelf'' cryoecosystem, although these spatial trends are discontinuous because the former ice shelf is now fragmented into several remnant cryohabitats. According to ecological theory, habitat fragmentation affects population dynamics through a reduction in total habitat, fragment size, and connectivity, yet effects due to habitat fragmentation are highly species specific, depending on their dispersal ability and habitat specificity. For this reason, habitat fragmentation is a concern for species with narrow ecological niches, such as certain plants, mammals and birds (e.g., Terborgh et al., 2001) and has been little explored in microbial ecology. The physical disintegration of the largest known ice shelf in the Northern Hemisphere can also be viewed as habitat fragmentation since the remaining ice shelves today form an ''archipelago'' of isolated habitats. However, many microbial mat photoautotrophs that inhabit cryoecosystems are easily wind-dispersed and are physiological generalists with a relatively wide optimum range (Mueller et al., 2005) that may not be adversely affected by habitat fragmentation. It is not possible to compare the ecological properties of the original ''Ellesmere Ice Shelf'' to the ensemble of present-day remnants, however these two competing hypotheses may be evaluated by comparing biodiversity among the isolated fragments.

There were no significant differences in species richness or diversity among these remnants, suggesting that fragment size does not control the biodiversity of the microbial mat phototrophs as would be expected if habitat fragmentation were deleterious. Furthermore, the ice shelf cryohabitat is naturally heterogeneous at the sub-ice shelf scale and microbial mats are distributed in patches as shown in Figure 7. Therefore, the latter hypothesis appears to be more plausible, and there is likely considerable connectivity and dispersal between many of the ice-shelf fragments as well as between habitat patches (especially in the direction of the prevailing wind). In addition, habitats from Ellesmere Island serve as a source for ice-shelf biota. Most of the organisms found in ice mats are present on nearby islands in either microbial mats from tundra ponds (Villeneuve et al., 2001), glacial cryohabitats (Mueller et al., 2001), or soil ecosystems (Elster et al., 1999), although they are not organized into the distinctive assemblage types and mat architectures observed on the ice shelves. It is also possible that other factors masked the effects of habitat fragmentation in our study as was observed in studies on High Arctic soil microarthropod communities (Coulson et al., 2000) and soil decomposers in Finland (Rantalainen et al., 2004), where resource quality and environmental stress overshadowed expected community changes due to habitat patchiness.

The cryosphere in general provides many microbial habitats throughout the biosphere, and the availability of these habitats has varied greatly throughout geologic time. During interglacial epochs, the cryosphere becomes physically fragmented until cryohabitats are relegated to high altitudes and latitudes. This habitat fragmentation may be detrimental to microbial biodiversity and population dynamics or, as we have observed in Arctic ice shelves, the dispersal abilities and broad tolerance ranges of these organisms may overcome the effects of habitat fragmentation and loss and allow the development of similar communities at multiple, noncontiguous sites.

Conclusions

Our observations across the 250-km extent of the ''Ellesmere Ice Shelf'' cryoecosystem show that each of the five remnants sampled contains a rich microbial flora. This amounts to an estimated 34 Gg of organic matter, with average areal productivities that are well above values in the Central Arctic pack ice. The surface exposure of meteoric versus marine ice is an important factor in structuring these ice shelf assemblages. However, the optimal habitat appears to be in areas where inorganic sediments have accumulated over exposed marine ice. Regions where such conditions exist, on Ward Hunt and Markham ice shelves, differ greatly from areas elsewhere on the ice shelves that are characterized by sparsely distributed ''sediment'' and ''matlet'' microbial mats in isolated cryoconite holes and glacial debris. Our results underscore the broad gradient of environments that can be found across this ensemble of northern ice shelves and our RDA analysis showed that microbial mat relative abundance was significantly associated with environmental variability. There was no evidence that the 20th century fragmentation of the ''Ellesmere Ice Shelf'' cryohabitat has affected biodiversity and richness of the microbial mat communities, but the continued existence of this extreme Arctic ecosystem is vulnerable to ongoing climate change.

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References Cited

Bonilla, S., Villeneuve, V., and Vincent, W. F., 2005: Benthic and planktonic algal communities in a High Arctic lake: Pigment structure and contrasting responses to nutrient enrichment. *Journal of Phycology*, 41: 1120–1130.

Braun, C., Hardy, D. R., Bradley, R. S., and Sahanatien, V., 2004: Surface mass balance of the Ward Hunt Ice Rise and Ward Hunt Ice Shelf, Ellesmere Island, Nunavut, Canada. *Journal of Geophysical Research-Atmospheres*, 109: D22110.

Britton, G., 1985: General carotenoid methods. *In:* Law, J. H., and Rilling, H. C. (eds.), *Methods in Enzymology: Steroids and Isoprenoids Part B*. New York: Academic Press, 113–149.

Castenholz, R. W., 1992: Species usage, concept, and evolution in the Cyanobacteria (blue-green algae). *Journal of Phycology*, 28: 737–745.

Christie, R. L., 1957: *Geological Reconnaissance of the North Coast of Ellesmere Island, District of Franklin, Northwest Territories.* Geological Survey of Canada: Ottawa.

Clarke, K. R., and Warwick, R., 1994: Similarity-based testing for community pattern—the 2-way layout with no replication. *Marine Biology*, 118: 167–176.

Cockell, C. S., and Stokes, M. D., 2004: Widespread colonization by polar hypoliths. *Nature*, 431: 414.

Comiso, J., 2002: A rapidly declining perennial sea ice cover in the Arctic. *Geophysical Research Letters*, 29: 1956.

Coulson, S. J., Leinaas, H. P., Ims, R. A., and Søvik, G., 2000: Experimental manipulation of the winter surface ice layer: the effects on a High Arctic soil microarthropod community. *Ecography*, 23: 299–306.

Crary, A. P., 1956: Geophysical studies along northern Ellesmere Island. *Arctic*, 9: 155–165.

Crary, A. P., 1958: Arctic ice islands and ice shelf studies, Part I. *Arctic*, 11: 3–42.

Crary, A. P., 1960: Arctic ice islands and ice shelf studies, Part II. *Arctic*, 13: 32–50.

Crary, A. P., Kulp, J. L., and Marshall, E. W., 1955: Evidences of climatic change from ice island studies. *Science*, 122: 1171–1173.

Debenham, F., 1920: A new mode of transportation by ice: the raised marine muds of South Victoria Land. *Quarterly Journal of the Geological Society*, 75: 51–76.

Dowdeswell, J. A., Gorman, M. R., Glaszovsky, A. F., and Macheret, Y. Y., 1994: Evidence for floating ice shelves in Franz Josef Land, Russian High Arctic. *Arctic and Alpine Research*, 26: 86–92.

Elster, J., Lukesová, A., Svoboda, J., Kopecky, J., and Kanda, H., 1999: Diversity and abundance of soil algae in the polar desert, Sverdrup Pass, central Ellesmere Island. *Polar Record*, 35: 231–254.

Garcia-Pichel, F., and Castenholz, R. W., 1991: Characterization and biological implications of scytonemin, a cyanobacterial sheath pigment. *Journal of Phycology*, 27: 395–409.

Gradinger, R., 1999: Vertical fine structure of the biomass and composition of algal communities in Arctic pack ice. *Marine Biology*, 133: 745–754.

Hattersley-Smith, G. F., 1957: The rolls on the Ellesmere Ice Shelf. *Arctic*, 10: 32–44.

Hattersley-Smith, G. F., 1963: The Ward Hunt Ice Shelf: recent changes of the ice front. *Journal of Glaciology*, 4: 415–424.

Hawes, I., Howard-Williams, C., and Pridmore, R. D., 1993: Environmental control of microbial biomass in the ponds of the McMurdo Ice Shelf, Antarctica. *Archiv für Hydrobiologie*, 127: 27–287.

Higgins, A. K., 1989: North Greenland ice islands. *Polar Record*, 25: 207–212.

Holdsworth, G., 1987: The surface waveforms on the Ellesmere Island ice shelves and ice islands. *Workshop on Extreme Ice Features, Technical Memoir 141 (NRCC 28003)*, 385–403.

Howard-Williams, C., Pridmore, R. D., Broady, P. A., and Vincent, W. F., 1990: Environmental and biological variability in the McMurdo Ice Shelf ecosystem. *In:* Kerry, K. R., and Hempel, G. (eds.), *Antarctic Ecosystems: Ecological Change and Conservation*. Berlin: Springer-Verlag, 23–31.

Jeffries, M. O., 1986a: Ice island calvings and ice shelf changes, Milne Ice Shelf and Ayles Ice Shelf, Ellesmere Island, N.W.T. *Arctic*, 39: 15–19.

Jeffries, M. O., 1986b: Glaciers and the morphology and structure of the Milne Ice Shelf, Ellesmere Island, N.W.T., Canada. *Arctic and Alpine Research*, 18: 397–405.

Jeffries, M. O., 1992a: The source and calving of ice island ARLIS-II. *Polar Record*, 28: 137–144.

Jeffries, M. O., 1992b: Arctic ice shelves and ice islands: Origin, growth and disintegration, physical characteristics, structural-stratigraphic variability, and dynamics. *Reviews of Geophysics*, 30: 245–267.

Jeffries, M. O., 2002: Ellesmere Island ice shelves and ice islands. *In:* Williams, R. S., and Ferrigno, J. G. (eds.), *Satellite Image Atlas of Glaciers of the World: North America*. Washington: United States Geological Survey, J147–J164.

Jeffries, M. O., and Serson, H. V., 1983: Recent changes at the front of Ward Hunt Ice Shelf, Ellesmere Island, N.W.T. *Arctic*, 36: 289–290.

Jeffries, M. O., Krouse, H. R., Sackinger, W. M., and Serson, H. V., 1990: Surface topography, thickness and ice core studies of multiyear landfast sea ice and Ward Hunt Ice Shelf, Northern Ellesemere Island, N.W.T. *In:* Harington, C. R. (ed.), *Canada's Missing Dimension: Science and History in the Canadian Arctic Islands*. Ottawa: Canadian Museum of Nature, 229–254.

Koenig, L. S., Greenaway, K. R., Dunbar, M., and Hattersley-Smith, G., 1952: Arctic ice islands. *Arctic*, 5: 67–103.

Legendre, P., and Legendre, L., 1998: *Numerical Ecology*. 2nd ed. Amsterdam: Elsevier, 853 pp.

Lemmen, D. S., Evans, D. J. A., and England, J., 1988: Ice shelves of northern Ellesmere Island, N.W.T., Canadian landform examples. *The Canadian Geographer*, 32: 363–367.

Lovejoy, C., Vincent, W. F., Frenette, J. J., and Dodson, J. J., 1993: Microbial gradients in a turbid estuary: Application of a new method for protozoan community analysis. *Limnology and Oceanography*, 38: 1295–1303.

Lyons, J. B., Savin, S. M., and Tamburi, A. J., 1971: Basement ice, Ward Hunt Ice Shelf, Ellesmere Island, Canada. *Journal of Glaciology*, 10: 93–100.

Lyons, J. B., Ragle, R. H., and Tamburi, A. J., 1972: Growth and grounding of the Ellesmere ice rises. *Journal of Glaciology*, 11: 43–52.

Marshall, E. W., 1955: Structural and stratigraphic studies of the northern Ellesmere Ice Shelf. *Arctic*, 8: 109–114.

Michel, C., Nielsen, T. G., Nozais, C., and Gosselin, M., 2002: Significance of sedimentation and grazing by ice micro- and meiofauna for carbon cycling in annual sea ice (northern Baffin Bay). *Aquatic Microbial Ecology*, 30: 57–68.

Mountfort, D. O., Rainey, F. A., Burghardt, J., Kaspar, H. F., and Stackebrandt, E., 1997: *Clostridium vincentii* sp. nov., a new obligately anaerobic saccharolytic, psychrophilic bacterium isolated from low-salinity pond sediment of the McMurdo Ice Shelf, Antarctica. *Archives of Microbiology*, 167: 54–61.

Mueller, D. R., and Vincent, W. F., 2006: Microbial habitat dynamics and ablation control on the Ward Hunt Ice Shelf. *Hydrological Processes*, 20: 857–876.

Mueller, D. R., Vincent, W. F., Pollard, W. H., and Fritsen, C. H., 2001: Glacial cryoconite ecosystems: A bipolar comparison of algal communities and habitats. *Nova Hedwigia, Beiheft*, 123: 173–197.

Mueller, D. R., Vincent, W. F., and Jeffries, M. O., 2003: Break-up of the largest Arctic ice shelf and associated loss of an epishelf lake. *Geophysical Research Letters*, 30: 2031.

Mueller, D. R., Vincent, W. F., Bonilla, S., and Laurion, I., 2005: Extremotrophs, extremophiles and broadband pigmentation strategies in a High Arctic ice shelf ecosystem. *FEMS Microbiology Ecology*, 53: 73–87.

Nusch, E., 1980: Comparison of different methods for chlorophyll and phaeopigment determination. *Archiv für Hydrobiologie*, 14: 14–36.

Rantalainen, M. L., Kontiola, L., Haimi, J., Fritze, H., and Setala, H., 2004: Influence of resource quality on the composition of soil decomposer community in fragmented and continuous habitat. *Soil Biology & Biochemistry*, 36: 1983–1996.

Strickland, J. D. H., and Parsons, T. R., 1972: *A Practical Handbook of Seawater Analysis.* Fisheries Research Board, Canada: Ottawa.

Suren, A., 1990: Microfauna associated with algal mats in melt ponds of the Ross Ice Shelf. *Polar Biology*, 10: 329–335.

ter Braak, C. J. F., and Smilauer, P., 1998: *CANOCO release 4 reference manual and user's guide to Canoco for Windows—Software for canonical community ordination*. Ithaca, New York: Microcomputer Power, 352 pp.

Terborgh, J., Lopez, L., Nuanez, P., Madhu, R., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G. H., Lambert, T. D., and Balbas, L., 2001: Ecological meltdown in predator-free forest fragments. *Science*, 294: 1923.

Trettin, H. P., 1991: Late Silurian–Early Devonian deformation, metamorphism, and granitic plutonism, Northern Ellesmere and Axel Heiberg Islands. *In:* Trettin, H. P. (ed.), *Geology of the Innuitian orogen and arctic platform of Canada and Greenland*. Ottawa: Geological Survey of Canada, 295–301.

Van Hove, P., 2005: Limnologie du Nord d'île d'Ellesmere: Réponses et Sensibilité aux Changements de Climat dans les Environnements Extrêmes. PhD thesis, Département de biologie, Université Laval: Québec, 119 pp.

Villeneuve, V., Vincent, W. F., and Komárek, J., 2001: Community structure and microhabitat characteristics of cyanobacterial mats in an extreme high Arctic environment: Ward Hunt Lake. *Nova Hedwigia, Beiheft*, 123: 199–224.

Vincent, W. F., 1988: *Microbial Ecosystems of Antarctica*. Cambridge: Cambridge University Press, 304 pp.

Vincent, W. F., and Howard-Williams, C., 1994: Nitrate-rich inland waters of the Ross Ice Shelf region, Antarctica. *Antarctic Science*, 6: 339–346.

Vincent, W. F., Gibson, J. A., Pienitz, R., Villeneuve, V., Broady, P. A., Hamilton, P. B., and Howard-Williams, C., 2000: Ice shelf microbial ecosystems in the High Arctic and implications for life on snowball Earth. *Naturwissenschaften*, 87: 137–141.

Vincent, W. F., Gibson, J. A. E., and Jeffries, M. O., 2001: Ice shelf collapse, climate change, and habitat loss in the Canadian High Arctic. *Polar Record*, 37: 133–142.

Vincent, W. F., Mueller, D. R., and Bonilla, S., 2004: Ecosystems on ice: the microbial ecology of Markham Ice Shelf in the high Arctic. *Cryobiology*, 48: 103–112.

Wetzel, R. G., and Likens, G. E., 2000: *Limnological Analyses*. 3rd ed. New York: Springer-Verlag, 429 pp.

Williams, M., and Dowdeswell, J. A., 2001: Historical fluctuations of the Matusevich Ice Shelf, Severnaya Zemlya, Russian High Arctic. *Arctic, Antarctic, and Alpine Research*, 33: 211–222.

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