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STRUCTURE ET DYNAMIQUE DES CRYO-ÉCOSYSTÈMES :
Plates-formes de glace nordiques

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Résumé

Cette thèse doctorale est la première étude systématique d'une classe d'écosystèmes extrêmes nouvellement découverts dans l'environnement arctique : les communautés de tapis microbiens et leurs habitats sur les plates-formes de glace nordiques. L'objectif principal était d'examiner la structure et la dynamique de ces cryo-écosystèmes à plusieurs échelles et d'étudier l'interaction entre les aspects physiques et biologiques sur les cinq plates-formes de glace principales trouvées dans le Haut Arctique canadien. Cette étude comprend une large gamme de méthodologies, soit : l'énumération microscopique des algues ; la quantification des pigments avec la chromatographie liquide de haute performance ; les mesures automatisées de salinité, d'éclairement et de température ; des survols en hélicoptère accompagnés de prise d'échantillons ; et l'analyse d'images de télédétection. La limnologie chimique et physique des cryo-habitats à travers cet écosystème est hétérogène et une communauté diversifiée de phototrophes a été retrouvée dans les tapis microbiens. La fragmentation de l'habitat a eu peu d'effet sur la biodiversité du cryo-écosystème. Cependant, des gradients environnementaux ont été associés à la structure de la communauté des tapis microbiens. L'hypothèse stipulant que les organismes des tapis microbiens des plates-formes de glace subsistent dans des conditions sub-optimales a été évaluée en examinant des réponses métaboliques aux changements de salinité, d'éclairement et de température. Les micro-organismes hétérotrophes se sont avérés spécialisés aux conditions extrêmes répandues sur la glace, tandis que les micro-organismes photosynthétiques ont toléré une plus large gamme de conditions, suggérant ainsi qu'ils étaient des extrêmotrophes (terme défini dans cette étude comme la tolérance des microbes aux conditions locales mais possédant une croissance *in situ* en dehors de leurs optimums physiologiques) plutôt que des extrêmophiles (la spécialisation aux conditions locales, avec une croissance *in situ* près des limites physiologiques). Un assemblage de pigments accessoires et photoprotecteurs a été associé à la communauté autotrophe, ce qui peut expliquer la gamme de tolérance plus large des extrêmotrophes. Le rapport entre la couverture du tapis microbien et la perte de masse de la surface de la plate-forme de glace a été examiné. Une concentration élevée de sels nutritifs dans les tapis microbiens a indiqué que ce micro-environnement différait considérablement de l'écosystème entier. Ces résultats soulignent l'importance du couplage biotique-physique

sur la plate-forme de glace autant que dans le reste de la cryosphère. Pendant la période d'étude, un événement de détachement d'une partie de la plate-forme de glace Ward Hunt ainsi que le drainage d'un lac épiplate-forme (eau douce barrée par la glace flottant sur l'océan) ont été observé. Une analyse supplémentaire a suggéré que le réchauffement du climat ait contribué à cet événement, ce qui souligne la vulnérabilité des habitats dépendants des plates-formes de glace et de leur valeur comme indicateurs des changements climatiques. Ces cryo-écosystèmes fournissent également de nouvelles connaissances reliées à la vie microbienne dans les milieux polaires extrêmes, ouvrant de nouvelles avenues sur la survie, la croissance et l'évolution pendant les périodes glaciaires du passé, y compris l'ère précambrienne.

Abstract

This doctoral thesis is the first systematic study of a newly discovered class of extreme ecosystems in the arctic environment: microbial mat communities and their habitats on northern ice shelves. The overarching objective was to examine the structure and dynamics of these cryo-ecosystems at several scales and to examine the interaction between physical and biological aspects on the five major ice shelves found in the Canadian High Arctic. This study made use of a broad range of methods including: microscopic enumeration of algal taxa; quantification of pigments with high performance liquid chromatography; automated over-winter measurements of salinity, irradiance and temperature; helicopter-assisted surveys and sampling; and analysis of satellite imagery. The chemical and physical limnology of the cryo-habitats across this entire ecosystem was found to be heterogeneous and a diverse community of phototrophic microorganisms was found within the microbial mats. Habitat fragmentation was shown to have little effect on the biodiversity of the cryo-ecosystem, however environmental gradients were significantly associated with microbial mat community structure. The hypothesis that ice shelf microbial mat organisms subsist in sub-optimal conditions was tested by examining metabolic responses to changes in salinity, irradiance and temperature. Heterotrophic microbiota were found to be optimized for the extreme conditions prevalent on the ice shelf, whereas photosynthetic micro-organisms tolerated a broader range, suggesting they were extremotrophic (defined by this study as tolerance by microbiota to local conditions but with *in situ* growth well outside their physiological optima) rather than extremophilic (a more narrow specialization to local conditions, with *in situ* growth close to physiological maxima). An assemblage of sunscreening and accessory pigments was associated with the autotrophic community, which may account for the extended tolerance range of the extremotrophs. The relationship between microbial mat cover and the surface ablation of the ice shelf was examined and a high concentration of nutrients within the microbial mats indicated that this microenvironment differed greatly from the properties of the bulk ecosystem. These results underscore the importance of biotic-physical coupling on the ice shelf, and in the cryosphere in general. A break-up event on the Ward Hunt Ice Shelf and the drainage of an epishelf lake (ice-dammed freshwater overlying seawater) was discovered during the study period. Further analysis suggested that climate warming

contributed to this event, which highlights the vulnerability of ice shelf dependent habitats and their value as indicators of climate change. These cryo-ecosystems also provide new insights into microbial life under extreme polar conditions, with implications for survival, growth and evolution during glacial periods in the past, including the Precambrian Era.

Avant-propos

Cette thèse est la synthèse culminante de ma recherche doctorale sous la direction du professeur Warwick F. Vincent. Elle est composée de six chapitres, dont quatre sont sous la forme d'article. Après révision par mes évaluateurs de thèse, des corrections mineures ont été apportées sur les articles déjà publiés. Je suis l'auteur principal de tous ces chapitres et j'assume l'entière responsabilité pour toutes les erreurs ou omissions.

Chapitre 1 - Introduction générale

Chapitre 2 - *Environmental gradients, fragmented habitats and microbiota of a northern ice shelf cryo-ecosystem.* D.R. Mueller, W.F. Vincent et M.O. Jeffries, soumis à Arctic, Antarctic, and Alpine Research.

Chapitre 3 - *Extremotrophs, extremophiles and broadband pigmentation strategies in a high arctic ice shelf ecosystem.* D.R. Mueller, W.F. Vincent, S. Bonilla et I. Laurion, est publié dans FEMS Microbiology Ecology (2005) 53:73-87.

Chapitre 4 - *Microbial habitat dynamics and ablation control on the Ward Hunt Ice Shelf.* D.R. Mueller et W.F. Vincent, est sous presse dans Hydrological Processes.

Chapitre 5 - *Break-up of the largest Arctic ice shelf and associated loss of an epishelf lake*. D.R. Mueller, W.F. Vincent et M.O. Jeffries, est publié dans Geophysical Research Letters (2003) 30:2031.

Chapitre 6 - Conclusion générale

Pendant mes études à l'Université Laval, j'ai participé à la rédaction des articles suivants qui sont complémentaires au sujet de ma thèse.

Mueller, D.R., Jeffries, M.O. et Vincent, W.F. (2003) *Ice shelf break-up and ecosystem loss in the Canadian High Arctic*. Eos, Transactions of the American Geophysical Union 84:548,552.

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

Vincent, W.F., Mueller, D.R. et Van Hove, P. (2004) *Break-up and climate change at Canada's northern coast, Quttinirpaaq National Park*, Meridian, pp. 1-6.

Vincent, W.F., Mueller, D.R., Van Hove, P. et Howard-Williams, C. (2004) *Glacial periods on early Earth and implications for the evolution of life*. In: Seckbach J. (ed), Origins: Genesis, Evolution and Diversity of Life. Kluwer Academic Publishers, Dortrecht, pp. 481-501.

Mueller, D.R. et Pollard, W.H. (2004) *Gradient analysis of cryoconite ecosystems from two polar glaciers*. Polar Biology, 27: 66-74.

Vincent, W.F., Van Hove, P., Mueller, D.R. et Jeffries, M.O. (2004) *Sensitivity to climate change in the Canadian High Arctic: Ellesmere Island Lakes, Fiords and Ice Shelf Ecosystems*, Conference Proceedings of the Arctic Climate Impact Assessment Symposium, Reykjavik, Iceland, November 2004.

Fountain, A.G., Tranter, M., Nylen, T.H., Lewis, K J., and Mueller, D.R. (2004) *Evolution of cryoconite holes and their contribution to melt-water runoff from glaciers in the McMurdo Dry Valleys, Antarctica*. Journal of Glaciology, 50: 35-45.

Mueller, D.R. (2005) *Microbial Mats*. Dans: Nuttall, M. (ed), Encyclopedia of the Arctic. Routledge, New York, pp. 1288-1289.

Mueller, D.R. (2005) *Book Review of "Arctic Climate Impact Assessment: Impacts of a Warming Arctic (Overview Report)"*. Écoscience. (sous presse).

Mes études doctorales sont fait le sujet de plusieurs articles dans le media publique, incluant les pages-web suivantes :

http://earthobservatory.nasa.gov/study/wardhunt/
http:/www.nunatsiaq.com/archives/40730/news/features/40730_01.html
http://www.unep.org/geo/yearbook/yb2003/053.htm

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à la mémoire de Malcolm Ramsay et Stuart Innes - chercheurs nordiques

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Chapitre 1 Introduction générale

La cryosphère est la partie de la surface terrestre qui comprend l'eau à l'état de glace. Bien que la vie nécessite l'eau sous forme liquide pour la croissance, la cryosphère réussi à fournir de nombreux habitats à certains micro-organismes. Ces cryo-écosystèmes existent puisque de l'eau liquide est disponible localement et/ou périodiquement pour l'activité microbienne, même lorsque la température de la surface descend sous le point de congélation. On retrouve les cryo-écosystèmes aussi bien sur la neige, la glace de lac, la glace de mer et les glaciers que sur la surface des plates-formes de glace. Ces dernières existent en Antarctique et en Arctique, le long de la côte nordique du Canada. Bien qu'une communauté microbienne ait déjà été découverte sur une de ces plates-formes de glace en 1998 (Vincent *et al.*, 2000), peu était connu au sujet de la structure, de la dynamique et de l'ampleur spatiale de cet écosystème saisissant de l'Haut Arctique canadien avant la présente étude.

Cette thèse doctorale, divisée en quatre chapitres sous forme d'article scientifique, examine l'écologie microbienne des plates-formes de glace nordiques du Canada et discute de la relation entre les aspects biologiques et physiques de ce cryo-écosystème. L'introduction dépasse le cadre des quatre chapitres centraux en présentant une revue de la littérature sur les plates-formes de glace, la tolérance adaptative dans les cryo-écosystèmes et les tapis microbiens. Par la suite, seront présentés les objectifs généraux de cette étude, ainsi que les buts spécifiques accompagnés des hypothèses traitées dans chacun des chapitres.

1.1 Les plates-formes de glace

1.1.1 Définition et emplacement

Les plates-formes de glace sont de denses masses de glace flottante retrouvées le long des côtes avec un franc-bord d'au moins 2 m au-dessus du niveau de la mer (Jeffries, 1987). Elles sont constituées soit par un épaississement de la banquise côtière de plusieurs années, soit par la coalescence de glaciers d'écoulement flottants, ou encore par le résultat de ces deux processus (Jeffries, 1986a ; Jeffries, 1992b). Les plates-formes de glace sont répandues en Antarctique, où elles occupent jusqu'à 45 % de la côte (Figure 1.1 ;

Dowdeswell *et al.*, 1994). Dans l'Hémisphère Nord, on les retrouve le long des côtes de l'île d'Ellesmere, au Canada (Hattersley-Smith *et al.*, 1955), et des côtes des l'îles de Severnaya Zemlya, en Russie (Figure 1.1 ; Zinger et Koryakin, 1965 ; Williams et Dowdeswell, 2001). Plusieurs preuves tendent à montrer que les plates-formes de glace pourraient également être présentes au Groenland (Higgins, 1989) et sur la terre de Franz Josef (Figure 1.1 ; Dowdeswell *et al.*, 1994). Au Canada, il y a cinq plates-formes de glace principales le long de la côte nord de l'île d'Ellesmere. Ces dernières sont les vestiges d'une frange glaciaire plus grande, officieusement appelée la plate-forme de glace d'Ellesmere. Cette dernière aurait atteint une superficie de près de 8900 km^2 en 1906. Cette plate-forme s'étendait de l'anse de Clements Markham jusqu'à l'île d'Axel Heiberg (Peary, 1907 ; Koenig *et al.*, 1952 ; Vincent *et al.*, 2001).

1.1.2 La relation entre le bilan de masse et le climat

Plusieurs chercheurs ont étudié la formation et le développement des plates-formes de glace (Hattersley-Smith, 1967 ; Gow et Epstein, 1972 ; Jeffries, 1986a, 1987), leurs propriétés physiques et glaciologiques (Debenham, 1920 ; Dorrer, 1971 ; Serson, 1979) et leur réponse aux changements climatiques (Vaughan et Doake, 1996 ; Doake *et al.*, 1998 ; Scambos *et al.*, 2000 ; Vincent *et al.*, 2001). La datation au radiocarbone du matériel organique prélevé sur les côtes derrière les plates-formes de glace le long de la côte nord de l'île d'Ellesmere suggère que ces plates-formes de glace se sont développées au cour des trois mille dernières années (Lyons et Mielke, 1973 ; Evans et England, 1992). Cette période correspond à une ère de refroidissement qui aurait commencé il y a environ 3500 ans (Bradley, 1990). Cependant, la tendance actuelle de réchauffement du climat aurait contribué à une réduction de 90 % de l'aire de la plate-forme de glace d'Ellesmere (Vincent *et al.*, 2001). Plusieurs autres études ont également documenté des changements dans l'aire de la plate-forme de glace de Ward Hunt (Hattersley-Smith, 1963 ; Holdsworth, 1971 ; Jeffries et Serson, 1983) de même que des événements de détachements sur d'autres plates-formes de glace arctiques (Jeffries, 1986b). Dans l'Hémisphère Sud, plusieurs plates-formes de glace le long de la péninsule Antarctique ont récemment subi des effondrements attribués à un réchauffement régional (Vaughan et Doake, 1996 ; Scambos *et al.*, 2000 ; Shepherd *et al.*, 2003 ; Vaughan *et al.*, 2003).

La croissance et l'effondrement des plates-formes de glace dépendent de leur bilan de masse glaciologique. Les éléments relatifs au bilan de masse incluent l'advection des glaciers et les détachements des îles de glace de même que les gains et les pertes en surface et sous la plate-forme. Si la somme de ces éléments demeure négative pendant des années successives, la plate-forme de glace risque de s'amincir, de subir des événements de rupture et à la limite, d'effondrement. Ainsi, le climat détermine une partie du bilan de masse en surface (par la précipitation, l'ablation, etc.) tandis que les facteurs océanographiques agissent sous la plate-forme de glace (à cause de la vitesse et de la température des courants océaniques). Le lien indirect entre le climat et les événements de rupture est connu mais peu compris à cause du manque d'observations. La documentation et la prévision de ces événements sont problématiques étant donné que la rupture de glace est un processus non-linéaire largement dicté par des seuils. En outre, la mesure du bilan de masse d'une plate-forme de glace est difficile, particulièrement en ce qui concerne les processus sous la glace (mais c'est possible de les discerner avec certains méthodes de télédétection ; Corr *et al.*, 2002). Dans les années 60 et 70, plusieurs études ont examiné le bilan de masse de la surface de la plate-forme de glace de Ward Hunt (Hattersley-Smith et Serson, 1970 ; Serson, 1979) et son lien avec le climat (Lister, 1962). Ces études, ainsi qu'un article récent (Braun *et al.*, 2004), démontrent à la fois que le bilan de masse de surface à long terme (depuis 1906) a été négatif et que l'importance de la perte en glace est liée à la température de l'air. Cependant, ces études n'ont pas mesuré l'ablation des plates-formes dans les secteurs où les tapis microbiens sont répandus. Par conséquent, l'effet des tapis microbiens sur l'ablation des plates-formes de glace nordiques demeure inconnu.

Plusieurs mécanismes de rupture des plates-formes de glace impliquent un lien avec le climat, soit directement par la fonte de la glace ou indirectement par son amincissement au delà d'un seuil critique, c'est-à-dire là où les risques de rupture augmentent. Dans l'Antarctique, où les afflux glaciaires sont substantiels et les débits sont hauts, les crevasses peuvent se remplir d'eau de fonte, ce qui déstabilise le champ de contraintes et cause un effondrement (Scambos *et al.*, 2000). Un mécanisme alternatif est relié au renversement dynamique des blocs de glace, entre plusieurs crevasses ; ce qui cause l'effondrement catastrophique des plates-formes de glace (MacAyeal *et al.*, 2003). Dans l'Arctique, où l'écoulement des plates-formes de glace n'est pas substantiel (e.g., Dorrer, 1971), les causes

immédiates de la rupture et les événements de détachements ont été attribués aux fluctuations des marées ou aux tremblements de terre (Holdsworth, 1971).

1.1.3 Les écosystèmes dépendent des plates-formes de glace

Les organismes vivants ont colonisé pratiquement chaque paysage physique de la planète. Cela vaut également pour les plates-formes de glace qui structurent plusieurs types d'écosystèmes. Un premier type d'écosystème existe dans les eaux adjacentes aux plates-formes de glace. Ces rares masses d'eaux se nomment lacs épiplates-formes. Ces lacs constituent un habitat pour le plancton d'eau douce, malgré le fait qu'ils soient directement reliés à l'océan. La surface des plates-formes de glace abrite d'autres types d'écosystème. D'abord, il y a des micro-organismes qui vivent directement sur la neige (e.g., *Ancyclonema nordenskioldii* dans la neige sur le « Ward Hunt Ice Rise » adjacente à la plate-forme de glace Ward Hunt, D. R. Mueller, données non publiées), ensuite des espèces planctoniques qui sont présentes dans les eaux de fonte (Hawes *et al.*, 1993) et finalement plusieurs organismes qui forment des tapis microbiens associés aux sédiments. En terme de biomasse, cette dernière communauté microbienne est la composante principale sur plusieurs plates-formes de glace et elle constitue l'axe de recherche biologique de cette thèse doctorale (voir les images en Annexe 1).

1.1.3.1 Les tapis microbiens des plates-formes de glace

Malgré l'intérêt pour les plates-formes de glace nordiques dans le passé, peu de travaux ont traité de leurs aspects biologiques. En Antarctique, les écosystèmes de plate-forme de glace ont suscité un intérêt scientifique considérable au cours des 14 dernières années (Vincent, 1988 ; Howard-Williams *et al.*, 1989 ; Howard-Williams *et al.*, 1990 ; Hawes *et al.*, 1993 ; Hawes *et al.*, 1999). Ces études ont prouvé que les plates-formes de glace pouvaient fournir un habitat pour des « consortiums » microbiens (des assemblages microbiens de plusieurs groupes fonctionnels) complexes et que ces communautés seraient capables d'accumuler une quantité substantielle de matière organique sur la surface de glace. Dans l'Hémisphère Nord, nous ne connaissons que très peu les tapis microbiens des plates-formes de glace. Leur présence a été notée sur deux des cinq principales plates-formes de glace canadiennes (Vincent *et al.*, 2000 ; Vincent *et al.*, 2004a), mais aucune

évaluation de la biomasse de ces tapis ni de la structure de leur habitat n'a été faite pour l'ensemble de l'écosystème des plates-formes de glace d'Ellesmere.

Contrairement à la glace de mer (<4 m d'épaisseur) adjacente, qui est riche en diatomées de façon saisonnière (Spindler, 1994), les étangs de fonte des plates-formes de glace abritent des tapis microbiens renfermant des cyanobactéries. Ces étangs de fonte varient en terme de taille, de profondeur, de salinité, de concentration en sels nutritifs et sont toujours associés aux sédiments (Howard-Williams *et al.*, 1990). À cause de leur albedo relativement faible (Podgorny et Grenfell, 1996), ces sédiments causent une fonte localisée de la glace créant ainsi l'habitat microbien. Ces tapis microbiens subissent un cycle saisonnier prononcé et restent congelés durant une grande partie de l'année. La saison de croissance est généralement limitée aux mois d'été où l'eau liquide est disponible, bien que la période et la durée de la fonte ne soient pas connues pour les tapis microbiens des plates-formes de glace nordiques.

1.1.3.2 Les lacs épiplates-formes

Les lacs épiplates-formes sont des masses d'eau stratifiées présentes du côté terrestre des plates-formes de glace (Heywood, 1977). L'eau douce en surface de ces lacs est maintenue par la présence d'une plate-forme de glace et ne peut donc se mélanger avec l'eau de mer en raison d'un gradient de densité prononcé ou halocline. Ces lacs ont été localisés dans 4 régions de l'Antarctique ainsi que le long de la côte nord de l'île d'Ellesmere dans l'hémisphère nord (Figure 1.1 ; Gibson et Andersen, 2002). Les lacs épiplates-formes sont influencés par la marée, dû à leur raccordement avec l'océan, et sont le plus souvent couverts de glace en permanence. Ils constituent un type d'écosystème unique parce qu'ils peuvent fournir un habitat pour les espèces d'eau douce et saumâtre (telles que les espèces zooplanctoniques arctiques *Limnocalanus macrurus* et *Drepanopus bungei*) et les espèces marines arctiques (par exemple, les espèces zooplanctoniques *Oncaea borealis* et *Oithona similis*), qui peuvent émigrer dans la couche d'eau douce supérieure (Van Hove *et al.*, 2001). Le lac Beaver, un grand lac épiplate-forme en Antarctique, est l'un des lacs les plus ultra-oligotrophes de ce continent. Il abrite malgré tout des nanoflagellées phototrophes et hétérotrophes, des bactéries hétérotrophes, des ciliés, et même une espèce de copépode (Laybourn-Parry *et al.*, 2001). Ces communautés uniques peuvent être remplacées par des

organismes typiquement marins suite à un effondrement de la plate-forme de glace qui permettrait à l'eau douce de surface d'être évacuée. Cela a été démontré à l'aide de carottes de sédiments dans le lac Moutonnée sur la péninsule Antarctique (Bentley *et al.*, 2005).

1.2 Les cryo-écosystèmes

1.2.1 La cryosphère

La cryosphère, définie comme l'ensemble des secteurs sur la surface de la terre qui sont en dessous du point de congélation de l'eau, est maintenant reconnue comme étant un habitat unique pour plusieurs organismes microbiens. Considérant que 8 % de la superficie de la terre se retrouve dans des régions polaires (latitude au-delà de 66.5 º), que 70 % de l'eau douce sur la terre est gelée et que 20 % de la superficie de la terre est localisée sur un pergélisol, il devient évident que la cryosphère représente un habitat très vaste (Priscu et Christner, 2004). La vie a été trouvée dans une grande partie de la cryosphère, incluant la glace de mer (Staley et Gosink, 1999 ; Deming, 2002 ; Gunde-Cimerman *et al.*, 2003), la surface des glaciers (Kohshima, 1984 ; Mueller *et al.*, 2001), le pergélisol (Rivkina *et al.*, 2000), les gouttelettes de nuage surfondues (Sattler *et al.*, 2001), la glace de lac (Psenner et Sattler, 1998 ; Priscu *et al.*, 2005) et les calottes glaciaires (Handfield *et al.*, 1992 ; Christner, 2000). Il semble y avoir des raisons théoriques et physiques expliquant la présence d'eau liquide entre des contours cristallins de glace, même à des températures très basses, ce qui fournissant ainsi un habitat pour la vie microbienne (Price, 2000 ; Price et Sowers, 2004).

1.2.2 Les stratégies éco-physiologiques

Les organismes qui sont étroitement spécialisés (« optimisés ») à des conditions particulières ont, par définition, une tolérance réduite à une variété de conditions (Forbes et Calow, 1997). Pourtant, les espèces tolérantes (ou généralistes) peuvent faire face aux environnements stressants en employant leurs mécanismes physiologiques, mais puisqu'elles ne sont pas spécialisées pour un stress particulier, elles sont moins performantes que les espèces qui sont plus spécialisées vers ces conditions (Vincent et

Quesada, 1997). Cependant, les conséquences de cette spécialisation peuvent être néfastes si les conditions extrêmes ne demeurent pas constantes. Par conséquent, les environnements extrêmes et stables devraient sélectionner plutôt des organismes spécialisés, tandis qu'un environnement avec des stress multiples et variables favorisera des espèces plus tolérants a une large gamme de conditions (Elster, 1999).

Des organismes qui sont spécialisés vers des conditions froides se nomment psychrophiles, par opposition aux psychrotrophes, qui sont des espèces généralistes (Morita, 1975). D'autres spécialistes sont également identifiés dans la littérature scientifique, comme les eutectophiles (organismes qui sont optimisés au point de congélation de l'eau ; Price, 2000 ; organismes qui sont optimisés au point de congélation de l'eau ; Deming, 2002) et les halophiles (organismes spécialisés à une salinité élevée), qui entrent tout deux dans la catégorie des extrêmophiles (organismes optimisés à des conditions extrêmes ; Horikoshi et Grant, 1998). Les cryo-écosystèmes polaires sont connus pour héberger des extrêmophiles, bien que les espèces généralistes pouvant tolérer des conditions environnementales extrêmes puissent être plus répandues dans certains cryo-habitats (Vincent, 1997).

Un objectif de ce projet de recherche était d'examiner la réponse physiologique des organismes des plates-formes de glace aux conditions extrêmes de leur habitat. Cette section brosse un tableau des mécanismes qui peuvent permettre aux micro-organismes d'atténuer les types de stress auxquels ils doivent faire face dans l'environnement de la plate-forme de glace. Les micro-organismes des plates-formes de glace sont soumis aux températures froides, à des niveaux importants d’éclairement solaire et à une disponibilité réduite de l'eau due à la congélation, aux salinités élevées ou à la dessiccation. Cependant, les gammes de tolérance et les stratégies d’adaptation employées par les consortiums microbiens des plates-formes de glace nordiques à leur environnement demeurent inconnues.

1.2.3 Les basses températures

Les basses températures réduisent l'énergie cinétique moléculaire, ce qui réduit les taux de réaction physico-chimiques en fonction de la température (Taylor, 1987). En revanche, les taux de réaction qui sont catalysés par des enzymes sont réduits proportionnellement au

logarithme de la diminution de la température (Russell, 1990). Conséquemment, pour compenser cette diminution d'efficacité, les organismes doivent produire des quantités plus élevées en enzymes limitantes (par exemple, Rubisco ; Tang et Vincent, 1999 ; Thomas et Dieckmann, 2002). Certaines enzymes et autres protéines peuvent également être dénaturées par les températures froides (Taylor, 1987). Ceci nécessite la fabrication par les organismes de protéines qui sont adaptées au froid, telles que les protéines flexibles qui ont des surfaces plus hydrophobes que leurs homologues (Russell et Hamamoto, 1998).

Les membranes des cellules et d'organelles bi-lipides deviennent de plus en plus rigides à des températures basses (Morris et Clarke, 1987), ce qui entrave l'efficacité des protéines membranaires (Thomas et Dieckmann, 2002). Pour augmenter la flexibilité des membranes, les proportions d'acides gras insaturés cis et trans sont augmentées et les chaînes d'acides gras sont davantage reliées et rallongées (Russell et Hamamoto, 1998). L'augmentation de la proportion d'acides gras poly-insaturés mène à une membrane plus liquide qui ne durcira pas autant que les membranes avec des acides gras saturés (McLachlan *et al.*, 1999).

Le stress associé à la réduction fonctionnelle des enzymes soumises à des conditions froides empêche la photosynthèse des algues parce que les voies photosynthétiques deviennent surchargées, causant un déséquilibre entre le transfert de l'énergie d'excitation et l'utilisation ordonnée de cette énergie pour les réactions photosynthétiques (par exemple, Machalek *et al.*, 1996 ; Tang et Vincent, 1999). Une augmentation dans le rapport caroténoïde : chlorophylle *a* été démontrée dans des conditions froides (Tang et Vincent, 1999 ; Fong *et al.*, 2001), ce qui suggère que ce mécanisme puisse atténuer les dommages dans les photosystèmes (Tang et Vincent, 1999) ou encore jouer un rôle dans la stabilisation des membranes (Fong *et al.*, 2001). De plus, la réparation des dommages exige la synthèse de protéines, ce qui est également entravé par des températures réduites (Rae *et al.*, 2000). Par conséquent, une stratégie d'empêchement des dommages est probablement plus efficace qu'un investissement substantiel de ressources vers la réparation.

1.2.4 Le stress hydrique

La congélation, la dessiccation et la salinité élevée sont reliées parce qu'elles mènent toutes à une diminution de la disponibilité intracellulaire de l'eau. Puisque l'eau liquide est nécessaire pour les réactions biologiques, les stratégies atténuant ces stress sont indispensables, sinon le gradient osmotique causerait la plasmolyse de la cellule (Franks, 2000). Plusieurs stratégies sont utilisées pour contrer les effets de la plasmolyse. La première implique l'expulsion des ions de la cellule en employant des protéines de transport et d'énergie (Jeanjean *et al.*, 1993). Une deuxième stratégie implique la synthèse des solutés compatibles qui équilibre le gradient osmotique mais qui n'est pas défavorable au métabolisme, même à des concentrations élevées (Russell et Hamamoto, 1998 ; Thomas et Dieckmann, 2002). Les solutés compatibles sont des « osmolytes », typiquement de faible poids moléculaire, tels que les sucres (Golldack *et al.*, 1995), le « dimethylsulphoniopropionate » ou DMSP (Stefels, 2000), le glycérol (Wynn-Williams, 2000) et la glycine (Ladas et Papageorgiou, 2000). Pendant la période d'acclimatation, les protéines qui sont responsables de la fabrication des solutés compatibles, aussi bien que celles qui sont impliquées dans d'autres stratégies, sont synthétisées (Molitor *et al.*, 1990 ; Golldack *et al.*, 1995). Une troisième stratégie est la sécrétion de substances polymériques extracellulaires (EPS, de l'anglais *Extracellular Polymeric Substances*) dans l'environnement qui entoure la cellule, ce qui ralenti la plasmolyse en agissant comme une barrière contre l'écoulement de l'eau (Vincent, 1988 ; Decho, 1994 ; Wynn-Williams *et al.*, 1997 ; Liu et Buskey, 2000 ; Wynn-Williams, 2000). L'augmentation de la concentration en caroténoïdes serait une réponse à la dessiccation et à une hausse de salinité, probablement en raison de leur capacité à diminuer la fluidité des membranes autour de l'appareil photosynthétique (Fong *et al.*, 2001) ainsi que leur capacité d'empêcher l'endommagement des photosystèmes (Schubert *et al.*, 1993 ; Chen et Lai, 1996).

La congélation des cellules combine les risques de la déshydratation et du stress osmotique pouvant potentiellement induire une croissance incontrôlée des cristaux de glace qui peuvent rompre les membranes cellulaires (Lock, 1990). Une stratégie pour éviter la formation des cristaux de glace consiste à empêcher la congélation intracellulaire par la synthèse d'antigels cellulaires (Sheath *et al.*, 1996 ; Stefels, 2000 ; Wynn-Williams, 2000). Ces solutés compatibles (protéines, glycérols ou autres composés) abaissent le point de

congélation dans le cytoplasme (Lock, 1990). Une autre stratégie pour réduire la croissance cristaux de glace est l'utilisation d'une classe de protéines appelées substances anti-glaces (« ice-active »), qui font fondre la surface des cristaux de glace mais qui ne sont pas associées avec la dépression du point de congélation (Raymond et Fritsen, 2000). On a également suggéré que les EPS produit par les diatomées de glace de mer attirent le sel qui agrandit les canaux de saumures et les pores de ce cryo-habitat (Krembs *et al.*, 2000 ; Krembs *et al.*, 2003). Une autre stratégie utilisée par certains organismes pour éviter des dommages cellulaires en dessous de zéro degré Celsius est d'encourager la surfusion du cytoplasme. Cet état métastable perdure seulement en l'absence des agents de nucléation et devient de plus en plus instable avec la diminution de la température. En dépit de cette précarité, le métabolisme de certaines bactéries a été observé à -20 °C, dans un état surfondu (Franks, 1985 ; Sattler *et al.*, 2001).

1.2.5 L'éclairement solaire

L'éclairement élevé surcharge les voies photosynthétiques avec un excès d'énergie et cause la photoinhibition, soit une réduction du taux photosynthétique (Vincent, 1990). Typiquement, ceci se produit parce qu'une protéine particulièrement sensible mais importante, la D1, se dénature et doit donc être synthétisée *de novo* pour reprendre la photosynthèse (Bhaya *et al.*, 2000). Les cellules d'algues peuvent s'ajuster sur diverses échelles temporelles aux changements de l'éclairement (la photoacclimatation) grâce à une série de modifications physiologiques connues sous le nom de cascade photosynthétique, (Vincent, 1990). Cette réorganisation de l'appareil photosynthétique peut atténuer certains dommages qui se produisent avec un excès de rayonnement photosynthétiquement actif (PAR, pour *Photosynthetically Active Radiation*) mais les dommages sont plus graves si la cellule est soumise à un excès de rayonnement ultraviolet (RUV). Dans des cas extrêmes, l'éclairement de grande énergie peut causer plusieurs dommages cellulaires par la production de photo-oxydants ou de radicaux libres (Vincent et Quesada, 1997).

Pour faire face aux niveaux élevés de RUV, il y a quatre stratégies principales. La première est l'évitement de l'éclairement, ce qui présume que les organismes sont mobiles (Nadeau *et al.*, 1999). La deuxième stratégie est d'employer la protection offerte par les pigments

qui peuvent agir comme un écran solaire (Quesada *et al.*, 1999). Le troisième mécanisme utilise les caroténoïdes pour modérer la formation de radicaux libres d'oxygène (Vincent *et al.*, 1993b). Finalement, les organismes peuvent essayer de réparer l'ADN endommagé en augmentant l'activité des enzymes qui réparent les acides nucléiques (e.g., la photolyase d'ADN, Quesada *et al.*, 1995).

Les pigments sont particulièrement importants pour contrecarrer le PAR et RUV excessif parce que leur utilisation est plus rentable que la réparation des dommages. Des pigments protecteurs peuvent être trouvés à l'intérieur de la cellule, par exemple des acides aminés de type mycosporine (MAA ; Garcia-Pichel et Castenholz, 1993b ; Castenholz, 1994) ou, plus efficacement, ils peuvent entourer les cellules dans des gaines de cyanobactéries (par exemple, le scytonemin ; Stal, 1995). Les caroténoïdes constituent une classe variée de pigments ayant plusieurs fonctions. Plusieurs caroténoïdes sont connus pour dissiper le surplus d'électrons des radicaux libres qui sont produits par l'énergie excessive intracellulaire (Edge *et al.*, 1997). Ils peuvent également agir comme des pigments accessoires non-photosynthétiques qui transfèrent l'énergie de longueurs d'ondes plus courtes aux molécules de chlorophylle *a*, mais ils peuvent également convertir l'éclairement de grande énergie en chaleur, déplaçant ainsi l'excès d'énergie loin de l'appareil photosynthétique (Sakshaug *et al.*, 1997). Cependant, une façon alternative de traiter les RUV de très haute énergie est de réduire la production des pigments qui captent la lumière, ce qui diminue l'effet de la pression d'excitation (Roos et Vincent, 1998).

1.3 Les tapis microbiens

Les tapis microbiens sont une composante importante de plusieurs habitats polaires, y compris le cryo-écosystème de la plate-forme de glace d'Ellesmere. Ces assemblages sont des consortiums de micro-organismes liés dans une matrice sédimentaire (Stal, 1995). Malgré leur apparente simplicité, ces écosystèmes n'en demeurent pas moins complexes en terme de biodiversité, d'éco-physiologie et de voies biochimiques (Castenholz, 1994). Typiquement, ils sont dominés par des cyanobactéries filamenteuses et peuvent être différenciés des films biologiques par l'existence d'au moins deux couche horizontale. Par la production de mucilage et de composés semblables, les cyanobactéries relient les

sédiments et le reste des communautés ensemble, ce qui mène à une structure cohésive de tapis (Decho, 1994 ; Stal, 1995). La juxtaposition des couches, qui contiennent les différents éléments fonctionnels et les différentes communautés, crée souvent de forts gradients biochimiques. En outre, les gradients prononcés peuvent se développer entre la colonne d'eau et la surface sous-jacente des tapis parce que les flux sont ralentis par une couche limite (Jørgensen, 1994 ; Sumner, 2001 ; Villeneuve *et al.*, 2001).

Les cyanobactéries filamenteuses (particulièrement les Oscillatoriaceae) dominent souvent dans les tapis microbiens photoautotrophes. Les tapis microbiens accueillent également une variété d'autres micro-organismes comprenant des procaryotes et les eucaryotes, autant unicellulaires que multicellulaires. Ces petits organismes peuvent être facilement disséminer des longues distances par le vent. La physiologie polyvalente des cyanobactéries couplée à leur tolérance aux conditions extrêmes permettent aux communautés des tapis microbiens de coloniser plusieurs habitats (Castenholz, 1994). Cependant, leur croissance relativement lente les empêche de compétitionner avec d'autres espèces benthiques et les rend très vulnérable au broutage. Par conséquent, les tapis microbiens sont habituellement trouvés en conditions plus strictes où les brouteurs sont en grande partie exclus (Farmer, 1992 ; cité dans Castenholz, 1994).

1.3.1 Les habitats des tapis microbiens

Les tapis microbiens sont capables de croître dans des conditions qui sont trop difficiles pour la plupart des organismes, mais en environnement plus clément ils entrent en compétition avec d'autres espèces qui ont des taux de croissance plus rapides (Vincent, 2000). Cela expliquerait pourquoi les tapis microbiens photosynthétiques sont généralement moins répandus. On retrouve les tapis de cyanobactéries dans des étangs hypersalins, des étangs tidaux (par exemple, lac Solaire et Gavish Sabkha ; Schidlowski *et al.*, 1984), des marais salants (Des Marais *et al.*, 1989), des lacs de soude (Oremland et King, 1989), des sources thermales (Estep, 1984 ; Ward *et al.*, 1989), des lacs, ruisseaux et étangs de toundra (Vincent *et al.*, 1993c ; Sheath et Müller, 1997 ; Vézina et Vincent, 1997), des glaciers (Mueller *et al.*, 2001) et des plates-formes de glace (Howard-Williams *et al.*, 1990 ; Vincent *et al.*, 2000). Cependant, on trouve également les tapis microbiens

dans des endroits moins exotiques tels que les environnements littoraux dans les zones tempérées (Stal, 1994), les deltas (Guerrero *et al.*, 1993) et les lacs oligotrophes (Castenholz, 1994), ce qui prouve qu'ils peuvent également survivre dans des conditions moins extrêmes si le broutage est minimal. Dans chacun des endroits ci-dessus, les stress sont différents. Le lac Solaire présente des niveaux toxiques de soufre (Aizenshtat *et al.*, 1984), les sabkhas (un étang tidal évaporé) sont hypersalins (Lyons *et al.*, 1984), les environnements côtiers et les deltas sont enclins à la turbulence, la perturbation et la salinité fluctuante (Stal, 1994), les lacs antarctiques sont des environnements avec un faible éclairement (Hawes et Schwarz, 1999), tandis que les sources thermiques et les plates-formes de glace imposent des stress liés à la température (Ward *et al.*, 1989 ; Hawes *et al.*, 1993). De plus, plusieurs environnements imposent des stress multiples qui augmentent les dommages physiologiques, potentiellement au-delà de la somme de chaque stress.

1.3.2 Organisation physique et biologique des tapis microbiens

En général, les tapis microbiens bien développées sont stratifiés. La couche supérieure (à peu près 1 à 2 millimètres) se compose en grande partie de cyanobactéries mortes, de gaines vides et de débris sédimentaires qui sont tombés sur le tapis (Stal, 1995). Cette couche contient une proportion très élevée de pigments d'écran solaire tels que la scytonemin et des composantes anti-oxydantes comme les caroténoïdes (Vincent *et al.*, 1993a). En dessous de cette couche, les filaments sont plus adaptés à l'ombre et contiennent plus de chlorophylle, ce qui représente la région la plus productive du tapis. Il s'agit du maximum profond de chlorophylle (DCM pour *Deep Chlorophyll Maximum*) du tapis, où la photosynthèse est la plus élevée et la majorité des cyanobactéries et d'autres photoautotrophes vivent (Vincent *et al.*, 1993b). Sous cette couche, les conditions anoxiques et la pauvreté en éclairement lumineux limitent la croissance des cyanobactéries (Canfield et Des Marais, 1994). La photosynthèse anoxygénique (par exemple, par les bactéries sulfureuses pourpres), la réduction de soufre, la création de méthane et la fermentation sont effectuées dans cette couche noire (indiquant la présence du sulfure de fer), qui peut former différents gradients, qui deviennent imperceptibles au niveau des sédiments (Fauque, 1995).

Malgré ce profil général particulier, les tapis microbiens sont très variables, selon les espèces qui les habitent et les conditions dans lesquelles ils se retrouvent. En particulier, les quelques cyanobactéries qui forment des tapis microbiens sont capables de mouvement (relatif au reste du tapis) et peuvent ajuster leurs positions pour contrôler l'éclairement de façon quotidienne (Vincent *et al.*, 1993b ; Nadeau *et al.*, 1999). Ceci peut mener à des variations sur le thème idéalisé des couches laminaires (c'est pourquoi on les nomme aussi des tapis allongés). Les tapis allongés sont parmi les plusieurs types de tapis observés dans les milieux lacustres de la vallée sèche de l'Antarctique (Wharton *et al.*, 1983). La nécessité de compétitionner pour la lumière, combiné avec la mobilité des organismes, peut produire une formation de pinacle (ou le « conophyton » ; Castenholz, 1994) à cause d'un héliotropisme positif, tandis que la production de gaz dans la matrice du tapis peut faire flotter certains tapis (aussi appelés tapis décollants) et même les déchirer au fond du lac (Wharton *et al.*, 1983). Les tapis bien développés dominés par *Nostoc* sont reconnaissables par leurs vésicules arrondies (Vincent *et al.*, 1993b). Malgré toutes ces études, les tapis microbiens moins cohésifs et mal développés trouvés dans des cryo-habitats ne sont pas encore bien décrits, à part dans les travaux de Takeuchi *et al.* (2001) et de Sabbe *et al.* (2004).

Les tapis microbiens sont souvent dominés par les cyanobactéries (jusqu'à 90 % de la biomasse ; Castenholz, 1994), mais ils peuvent contenir plusieurs groupes d'autres organismes comme les algues vertes (Chlorophyta), les diatomées (Bacillariophyceae) (Vincent *et al.*, 2000), les protistes, et les micro-invertébrés (Suren, 1990). D'autres organismes plus petits mais fonctionnellement importants peuvent inclure les bactéries réductrices de sulfate (par exemple, *Desulfovibrio* ; Fauque, 1995), les bactéries d'oxydation de sulfure (par exemple, les bactéries sulfureuses pourpres et vertes ; Ward *et al.*, 1994), les bactéries méthanogènes (Oremland et King, 1989), les bactéries dénitrifiantes, les bactéries nitrifiantes (Joye et Paerl, 1994), ainsi que d'autres types de bactéries hétérotrophes, et également des champignons (Vincent et Howard-Williams, 1986) et des virus (Short et Suttle, 2005).

Les cyanobactéries de tapis microbiens sont en général filamenteuses et sans hétérocystes (Oscillatoriales - par exemple, *Microcoleus, Oscillatoria, Lygnbya, Leptolyngbya* etc. ;

Parker et Wharton, 1985 ; Vézina et Vincent, 1997 ; Oscillatoriales - par exemple, *Microcoleus, Oscillatoria, Lygnbya, Leptolyngbya* etc. ; McKnight *et al.*, 1998), bien qu'il puisse aussi y avoir des espèces filamenteuses avec hétérocystes (Nostocales - par exemple, *Nostoc, Anabaena, Scytonema, Nodularia, Calothrix, Rivularia* ; Wharton *et al.*, 1983 ; Vincent *et al.*, 1993a ; Sheath et Müller, 1997). Les cyanobactéries non-filamenteuses peuvent également faire partie de l'écosystème des tapis microbiens (Chroococcales - par exemple, *Gleocapsa, Gleothece, Chroococcus, Synechococcus* ; Broady, 1982 ; Wharton *et al.*, 1983 ; Ward *et al.*, 1994 ; Stal, 1995). Les protistes incluent les ciliés, les flagellés, les amibes, tandis que les micro-invertébrés se retrouvent typiquement dans les groupes Rotifera, Tardigrada et Nematoda (Suren, 1990). Ces assemblages sont apparemment inter-dépendants et, tandis que les processus autotrophes dominent, les processus hétérotrophes, comme la décomposition et le recyclage des nutriments (c'est à dire, la boucle microbienne ; James *et al.*, 1998), contribuent à l'écosystème. Les associations mutuelles de différentes populations microbiennes créent des arrangements biogéochimiques qui sont synergiques et qui comprennent des consortiums (Paerl et Pinckney, 1996). Ceci garde l'environnement du tapis microbien relativement autonome grâce au cycle biochimique des nutriments.

Les tapis microbiens montrent une riche biodiversité et compriment verticalement un réseau trophique microbien à l'échelle millimétrique. Cette réduction spatiale a pour conséquence la présence de forts gradients biochimiques dans le tapis, ce qui crée beaucoup de niches écologiques pour des organismes avec des capacités physiologiques différentes. Les rapports syntrophiques dans les tapis microbiens sont répandus (van den Ende et van Gemerden, 1994). Ceci permet aux micro-organismes d'abaisser les besoins physiologiques de l'ensemble du consortium (c'est à dire, moins d'importation de nutriments, de matière organique) ce qui est aussi avantageux pour abaisser les dépenses thermodynamiques (Jackson et McInerney, 2002). Parmi les exemples de ces rapports syntrophiques on compte : la réduction de sulfate (bactéries réductrices de sulfate) avec l'oxydation de sulfure (photosynthèse anoxygenique) ; les photoautotrophes oxygéniques avec la phosphorylation oxydante (la respiration aérobie par des hétérotrophes) ; et la désamination (par les hétérotrophes) avec la nitrification.

La protection fournie par les tapis microbiens est un autre avantage de la vie dans ces consortiums. La pigmentation des couches supérieures garde les habitants des strates inférieures loin de l'éclairement de haute énergie (Quesada *et al.*, 1999), alors que les EPS synthétisées par beaucoup d'organismes de tapis microbiens amènent la stabilité contre la perturbation physique et empêchent le broutage (Stal, 1994). Un des inconvénients pour les organismes des tapis microbiens est que la couche limite empêche l'importation des substances requises et l'exportation des déchets (Jørgensen, 1994 ; Sumner, 2001). La pénétration de la lumière, nécessaire pour la photosynthèse, peut même être accrue à l'intérieur de la surface du tapis, dû à la rétrodiffusion (Jørgensen, 1989). Cependant, les niveaux d'éclairement chutent rapidement (dans moins de 800 µm ; Jørgensen, 1989) de même que les changements spectraux à cause de l'augmentation de la profondeur dû au filtrage efficace du RUV par des pigments d'écran solaire et du PAR par la chlorophylle *a*, la phycocyanine et d'autres pigments accessoires du DCM (Vincent *et al.*, 1993b).

1.3.3 L'origine et l'évolution des tapis microbiens

Pendant que la vie commençait et évoluait durant l'ère précambrienne, les tapis de cyanobactéries ont joué un grand rôle en façonnant le monde d'aujourd'hui (Habicht et Canfield, 1996 ; Smith, 1997 ; Hoehler *et al.*, 2001). Ces tapis ont dominé la biosphère pendant les 2 premiers milliards d'années de son existence (Schidlowski *et al.*, 1984). Il a été suggéré que la proximité étroite et l'interaction forcée entre les micro-organismes dans les tapis microbiens ont catalysé l'évolution endosymbiotique (Nisbet et Fowler, 1999 ; Vincent *et al.*, 2000). Les tapis microbiens apparaissent dans les fossiles géologiques comme stromatolites et sont l'un des indices critiques de la vie pendant le précambrien (Fairchild, 1991). Les géologues et les biologistes évolutionnistes ont employé des biomarqueurs dans ces fossiles pour explorer les conditions environnementales et la productivité biologique de par le passé (Nisbet et Fowler, 1999 ; Rosing et Frei, 2004). Cependant, plusieurs de ces extrapolations sur le passé sont basées sur une connaissance des tapis microbiens modernes (Des Marais, 2003). Par exemple, les tapis microbiens des plates-formes de glace offrent des analogues aux conditions au cours des événements connus sous le nom de « Terre boule de neige » (de l'anglais *Snowball Earth*) qui réfèrent à une glaciation sévère, possiblement globale (Hoffman *et al.*, 1998 ; Vincent *et al.*, 2000 ;

Vincent et Howard-Williams, 2000 ; Kirschvink, 2002 ; Vincent *et al.*, 2004c). L'ère des tapis microbiens s'est terminé pendant le cambrien, suggérant une hausse dans la pression de broutage ou la concurrence avec d'autres espèces (Parker *et al.*, 1981). Aujourd'hui, les tapis microbiens luxuriants sont confinés aux habitats spécialisés, loin des brouteurs et des compétiteurs. Les tapis microbiens modernes sont méconnus, et cela limite nos connaissances non seulement sur un des types d'écosystème moderne, mais également sur le fonctionnement écologique d'une majeure partie du passé évolutionnaire sur notre planète. Il est primordial d'apprendre davantage au sujet de ces communautés pour prévoir le rôle et la réponse future des tapis microbiens, bien qu'il semble certain que ces écosystèmes diversifiés et aux grandes capacités d'adaptation pourront survivre pendant longtemps.

1.4 Objectifs poursuivis

L'objectif général de cette étude est d'évaluer la structure et la dynamique des plates-formes de glace nordiques en tant que cryo-écosystèmes pour les organismes microbiens. La méthodologie combine les mesures physiques, chimiques et biologiques. Plus spécifiquement, ce travail caractérise, sur plusieurs échelles spatiales, un habitat récemment découvert. Le travail permettra d'évaluer la tolérance de deux groupes d'organismes dans les tapis microbiens (la communauté autotrophe et la communauté hétérotrophe) à une gamme des conditions qui recouvrent celles trouvées sur les plates-formes de glace et il examinera les stratégies microbiennes qui ont été adoptées pour faire face à ces conditions. Les conditions environnementales dans les tapis microbiens seront déterminées pendant la saison de fonte estivale mais aussi durant l'hiver et l'ablation sur la surface de la plate-forme de glace sera examinée. En guise de conclusion, les changements sans précédent qui ont pris place sur la plate-forme de glace Ward Hunt qui ont été observés seront relatés, de même que les grandes conséquences pour l'écosystème des lacs épiplates-formes. Ce dernier objectif permet de relier ces changements à une importante hausse de température dans la région.

Cette thèse est divisée en six chapitres. Le chapitre 2 examine l'ensemble du cryo-écosystème des plates-formes de glace de l'Arctique canadien. Précisément, il était crucial

de savoir à quel point la fragmentation de l'habitat de la plate-forme de glace d'Ellesmere aurait pu être la cause des différences dans la biodiversité entre les cinq plates-formes de glace restantes. Le chapitre 3 examine la physiologie des organismes dans les tapis microbiens et évalue l'hypothèse que les populations photoautotrophes et hétérotrophes diffèrent en relation avec leur tolérance et leur performance physiologique dans les conditions ambiantes. Le chapitre 4 caractérise la nature dynamique de l'environnement physico-chimique des tapis microbiens et s'interroge sur l'influence des tapis microbiens sur l'ablation de la surface de la plate-forme de glace. Le chapitre 5 rend compte d'un événement important qui s'est produit entre deux saisons de terrain pendant cette étude et qui a affecté l'intégrité du plus grand écosystème de plate-forme de glace nordique et du lac épiplate-forme maintenu derrière lui. Enfin, la conclusion de cette thèse synthétise les résultats de la recherche et identifie des volets de recherche pour le futur.

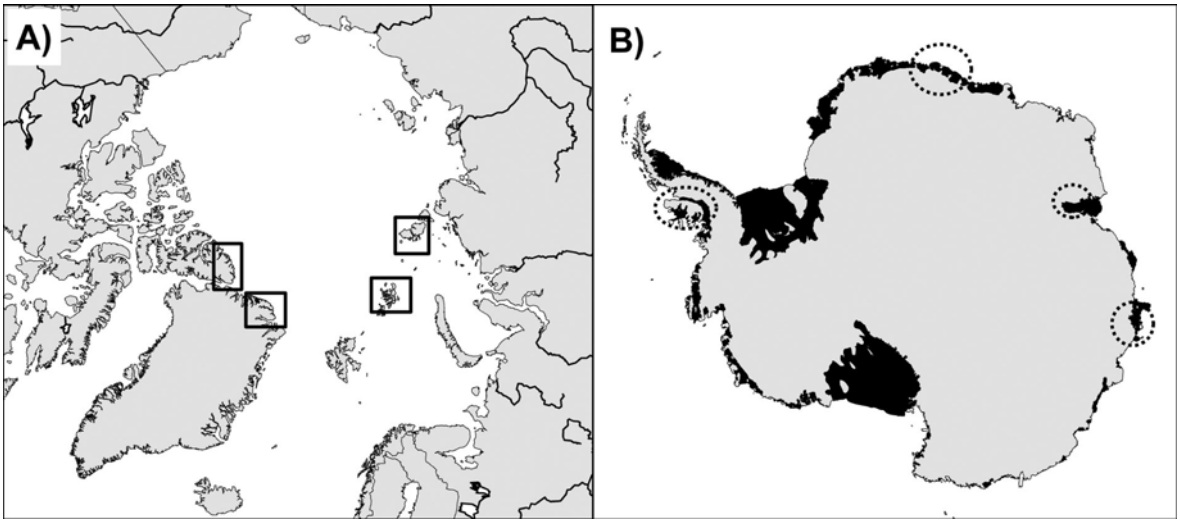

Figure 1.1 Répartition géographique des plates-formes de glace et des lacs épiplates-formes dans l'Hémisphère Nord et l'Hémisphère Sud.

A) Région Arctique. Les secteurs avec des plates-formes de glace sont délimités par des rectangles. De plus, plusieurs lacs épiplates-formes ont été rapportés le long de la côte de l'île d'Ellesmere (le rectangle gauche ; Jeffries, 2002). B) Région Antarctique. Les plates-formes de glace sont colorées noires et les secteurs qui contiennent les lacs épiplates-formes (Gibson et Andersen, 2002) sont encerclés. Les données des plates-formes de glace de l'Hémisphère Sud ont été fournies par l'Antarctic Digital Database (version 4.1, 2004). L'échelle des deux cartes est 1:50 000 000.

Chapitre 2 Environmental gradients, fragmented habitats and microbiota of a northern ice shelf cryo-ecosystem

2.1 Résumé

En 1906, la plate-forme de glace d'Ellesmere s'étendait sur 9000 km^2 (82-83ºN, 64-90ºW), mais au cours du dernier siècle, la plate-forme s'est désintégrée en 5 plates-formes de glace principales qui présentement possèdent au total une superficie de 992 km^2. Cet assemblage d'environnements de glace épaisse, retrouvé le long de la côte nord de l'île d'Ellesmere (Haut Arctique canadien), procure un cryo-habitat pour les communautés microbiennes associées avec les sédiments de la surface de glace. L'analyse comparative des caractéristiques physiques, chimiques et biologiques de ces 5 plates-formes de glace inclut la cartographie des types de glace. Chacune de ces 5 parties est une épaisse masse de glace (> 20 m) recouverte d'une quantité substantielle de sédiments qui favorisent la formation d'eau de fonte oligotrophe pendant l'été. Des micro-organismes ont été observés dans tous les types de sédiment. Ceux-ci forment des tapis microbiens pigmentés d'abondance variable, passant d'agrégats clairsemés d'organismes jusqu'aux tapis présentant une relative cohésion. En utilisant des images numériques des radiales de vol, nous avons déterminé que 8,4 % de l'aire de l'ensemble des plates-formes représentent un habitat potentiel pour les tapis microbiens qui contiendrait environ 34 Gg (34000 tonnes) de matière organique. Les valeurs de concentration en chlorophylle *a,* de contenu organique et de conductivité augmentent d'ouest en est, ce qui est probablement relié au type de glace (marine ou météorique) et à la disponibilité du sédiment sur la surface de la glace. Nos résultats ont indiqué que l'abondance relative des micro-organismes était associée avec le type de glace et le type de tapis microbien. En outre, la structure de la communauté a été associée aux gradients environnementaux de la conductivité, la concentration de phosphore soluble, de nitrate et d'ammoniaque. Le réchauffement du climat continue encore de nos jours à dégrader ce cryo-écosystème unique. En dépit des différences entre chaque plate-forme de glace, celles-ci montrent des similarités en terme de biodiversité microbienne, et ce, peu importe la taille de ces fragments.

2.2 Abstract

Over the course of the last century, the 9000 km^2 'Ellesmere Ice Shelf' (82-83ºN, 64-90ºW) fragmented into 5 main ice shelves now totaling 992 km^2. This ensemble of thick ice environments lies along the northern coast of Ellesmere Island in the Canadian High Arctic and provides a cryo-habitat for microbial communities that occur in association with aeolian and glacially entrained sediments on the ice surface. We undertook a comparative analysis of physical, chemical and biological characteristics of the 5 remnant ice shelves including 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 8.4 % of the combined ice shelf area was suitable microbial mat habitat, and contained an estimated 34 Gg (34000 tons) 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 (marine versus meteoric) and to the relative availability of sediment. Our results indicated that differences in relative abundance of micro-organisms were associated with different ice type and microbial mat type. In addition, community structure was significantly associated with environmental gradients of conductivity, soluble reactive phospohorus, nitrate and ammonium concentrations. There were distinct differences between each ice shelf with regards to ice type and sediment availability, however these remnants showed little difference in microbial biodiversity with respect to fragment size. This suggests that habitat fragmentation has not affected algal diversity as measured by morphotypes. However this unique cryo-ecosystem remains vulnerable to habitat attrition and complete loss with ongoing climate warming.

2.3 Introduction

Ice shelves, thick masses of coastal ice floating on the sea, are found in both the North and South Polar Regions and have been traditionally viewed as abiotic components of the cryosphere. However, over the last several decades, 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. 83ºN, long. 74ºW) 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 four other substantial ice shelves in Arctic Canada: Markham, Ayles, Milne and Alfred Ernest Ice Shelves (Figure 2.1). In addition to the five main ice shelves, there are a few minor ice shelves (a few km^2 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 north-western 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, many calving and break-up events have taken place, further fragmenting this feature into smaller pieces (Hattersley-Smith, 1963; Jeffries and Serson, 1983; Jeffries, 1986b; Mueller *et al.*, 2003b).

The existence of ice shelves in the Northern Hemisphere is limited to the five 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 stark contrast with Antarctica that has 40 % of its coastline fringed with ice shelves, some as large as half a million km^2 (Jeffries, 1992b). There, they are typically formed by floating glacier tongues that aggregate into broad expanses of thick (100s of metres) ice. However, in the Arctic they 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 regular undulating morphology becomes more chaotic closer to coastlines (Hattersley-Smith, 1957) and its cause has not yet been conclusively determined (Holdsworth, 1987). In this northern region, air temperatures can approach or exceed zero 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 aeolian 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 (organo-sedimentary 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 ºC for 300 days of the year reaching minimum temperatures of -17 ºC (Mueller and Vincent, 2005). Oscillatorian cyanobacteria dominate the microbial assemblage but diatoms, green algae, heterotrophic bacteria and viruses are also present. In addition, micro-invertebrates 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).

Over the last decade, there has been much interest in the effects of habitat fragmentation on ecosystem dynamics and functioning as well as the success of individual species. These concerns stem from the theory of island biogeography (MacArthur and Wilson, 1967) and subsequent theoretical and experimental work in ecology (e.g., Robinson *et al.*, 1992; e.g., Tilman *et al.*, 1994; With and Crist, 1995). Experimental results vary considerably depending on methodology, species considered, as well as spatial and temporal scales (Debinski and Holt, 2000), and this has engendered much debate. The majority of these studies focus on temperate and tropical ecosystems and primarily document changes in plant and animal species (Wolff *et al.*, 1997; Terborgh *et al.*, 2001). The fragmentation of the largest known ice shelf in the Northern Hemisphere can also be viewed in this context since the remaining ice shelves today form an 'archipelago' of isolated habitats. This microbial ecosystem is a unique feature of the High Arctic, and is threatened by further fragmentation of habitat and eventual loss. However, many microbial mat photoautotrophs that inhabit cryo-ecosystems are easily wind-dispersed and are physiological generalists with a relatively wide optimum range (Mueller *et al.*, 2005a). Therefore, these communities may be structured by environmental conditions in their immediate habitat, rather than the habitat fragmentation of the Ellesmere Ice Shelf.

The cryo-habitats of Arctic ice shelves have been little characterized and all work to date has focused on the Ward Hunt and Markham Ice Shelves (Vincent *et al.*, 2000; Vincent *et al.*, 2004a; Mueller and Vincent, 2005; Mueller *et al.*, 2005a). No analysis has been undertaken to assess how much habitat exists across all these ice shelves, the limnological properties of the meltwater lakes nor the spatial variability in the microbiota. In the present study, we hypothesized that the biological properties of this ensemble of ice shelves would vary according to environmental gradients and, as in fragmented ecosystems elsewhere, the size of each remnant ice shelf would affect the diversity of habitats and microbiota. We addressed these hypotheses by way of detailed transects, remote sensing and sampling of microbial mats and surface waters.

2.4 Methods

2.4.1 Sampling

Fieldwork was undertaken in late July and early August of 2001 and 2002. In 2001, all 5 major ice shelves were visited by helicopter. We did not visit 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 (Figure 2.2), with sample sizes reflecting the area of each ice shelf and logistical constraints. In addition to the samples from each ice shelf, an auxiliary samples 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 (Figure 2.2a). *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. Microbial mat type was noted at the time of sampling and classified into four categories: 'orange', 'matlet', 'sediment' and 'none' if no mat or sediments were present. This crude mat classification system was designed as a rapid, visual census only (Figure 2.3).

2.4.2 Community structure

Subsamples of microbial mat were preserved with a gluteraldehyde/formaldehyde solution (Lovejoy *et al.*, 1993) and refrigerated prior to analysis. 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. 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. The analysis focused on cyanobacteria, green algae, diatoms, other protists and micro-invertebrates, thereby excluding heterotrophic bacteria, archaea and viruses. 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 looking, sheath. Given the uncertain taxonomy of oscillatorians, molecular analysis would be required to define these taxa at a more precise level (Castenholz, 1992).

2.4.3 Microbial mat and water analyses

Microbial mats were sampled for chlorophyll *a* 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-second bursts with a pause of 30 seconds between sonication steps or samples were homogenized using a tissue grinder (Camafro R2R1, Wiarton, Ontario) for 1 minute (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 hour at 4 ºC and terminated with centrifugation at 4000 rpm for 5 minutes at 4 ºC. 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 not initially corrected for absorbance by scytonemin by scanning at 384 nm; however we post-corrected our data based on a spectrophotometric data and trichromatic equations of similar samples (Garcia-Pichel and Castenholz, 1991), which indicated an overestimate of carotenoid content by 57 % (SE = 4 %, n = 70). Meltpond water (420 ml) was filtered onto GF/F equivalent filters for determination of water column chlorophyll *a* by boiling ethanol extraction using a model 450 Sequoia-Turner fluorometer (Turner Corporation, Mountain View, CA) (Nusch, 1980).

Microbial mat organic content was determined for samples 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 ºC. The mass of organic and inorganic fractions were determined by loss on ignition at 500 ºC for 7 hours. 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 samples by the National Laboratory for Environmental Testing (NLET), 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-indophenol, nitrate/nitrite- cadmium reduction, soluble reactive phosphorus- ammonium molybdate-stannous chloride). Sample water (420 ml) was filtered through GC-50 filters (GF/C equivalent, AMD Manufacturing, Mississauga, ON) to remove particulate carbon and nitrogen, which was 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' was 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).

2.4.4 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 non-floating 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 (Alfred Ernest Ice Shelf: r1_24186_211, June 22, 2000; r1_22728_211, March 12, 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 taken with standard beam with the exception of one fine beam image (r1_35605_210). 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):

$$(A - B)/2)+128 \quad (1)$$

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.

2.4.5 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 (Figure 2.2; Markham,

Ward Hunt East, Ward Hunt West, Ward Hunt Middle, Milne, Alfred Ernest). Images were extracted from a digital video sequence (every 40th frame, or 1 image every ~1.3 sec, 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 up-scaled 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).

2.4.6 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 (Figure 2.2). The substrate was characterized at 10 cm intervals by recording the presence or absence of snow and sediment visually. 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.

2.4.7 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 λ = 0, Chlorophyll *a* and Carotenoids λ = 0.25, NH_4^+ λ = -0.25). Some variables were not transformable and therefore remained unaltered (Temperature, DOC, NO_3^- and NO_2^-). Taxa 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 taxa 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 taxa abundance data and normalized Euclidean distances for environmental and pigment data (the latter matrix contained several samples that did not have equivalents in the taxa 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.

2.5 Results

2.5.1 Ice shelf comparisons

The five largest remnant ice shelves in the Canadian High Arctic totaled 992 km^2 at the time of observation, and 8.4 % of their surface provided a sediment cryo-habitat for microbiota. The area of each ice shelf and their constituent ice types are given in Table 2.1. 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 2.1). This trend was also reflected in the estimates of sediment load for each ice shelf.

The five ice shelves had fairly constant values in many of their limnological properties (Table 2.2) and differed greatly in others (Figure 2.4). The three western ice shelves had less chlorophyll *a*, carotenoids and organic matter per unit area than the Ward Hunt and Markham Ice Shelves (Figure 2.4b; 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 density ($H = 5.8$, $p = 0.22$) and pH ($F = 1.4$, $p = 0.25$) among the ice shelves (Figure 2.4a). 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 2.2), 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 Alfred Ernest Ice Shelf samples, whereas 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 2.2). Major ion concentrations (except SiO_2) covaried with conductivity (Table 2.2). 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 (Figure 2.5).

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. In all, 32 taxa were found (Table 2.3), 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 2.3. 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 community structure was significantly different (Global $R = 0.142$, $p = 0.048$) among the five ice shelves. A pairwise comparison indicated that Markham and Alfred Ernest Ice Shelves have the most dissimilar communities ($p = 0.012$) whereas Markham and 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 & Milne, $p = 0.01$; Markham & Alfred Ernest, $p = 0.005$; Ward Hunt & Milne, $p = 0.002$; Ward Hunt & Alfred Ernest, $p = 0.003$).

Direct ordination of the community structure data and the 13 environmental variables revealed a non-significant association between these data matrices, with 53 % of the community structure 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 community structure variance ($p = 0.003$).

2.5.2 Ice type and mat type comparisons

Samples from marine ice areas had significantly higher ($p < 0.05$) water column nutrients (except total phosphorus), conductivity and pH as well as biodiversity indicators, microbial mat pigment concentrations and organic content than their meteoric ice counterparts (Table 2.3). The ANOSIM result (Global $R = 0.447$, $p = 0.001$) also indicated that these ice types differed significantly in their habitat characteristics. The community structure 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 overtop sediment. However, among the three mat 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 2.3). The ANOSIM analysis indicated a significant difference among the three mat types for community structure (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.

2.5.3 Sediment patterns

Over-flight transect estimates of total sediment cover (Markham, 44 %; Ward Hunt Middle, 19 %; Ward Hunt East, 2 %; Ward Hunt West, 12 %; Milne, 2 %; Alfred Ernest, 3 %) and meltwater cover (Markham, 17 %; Ward Hunt Middle, 14 %; Ward Hunt East, 22 %; Ward Hunt West, 16 %; Milne, 18 %; Alfred Ernest, 14 %), indicated that substantial differences exist among ice shelves with regards to potential microbial habitat. The percent cover of sediment varied dramatically over the length of each transect, but overall patterns can be seen in Figure 2.6. Markham Ice Shelf had very little sediment cover at its northern and extreme southern end (Figure 2.6a), 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 further north (Figure 2.6b and c). The Milne and Alfred Ernest Ice Shelves had very little sediment cover throughout, yet the southern portions of these transects did have slightly higher sediment cover (Figure 2.6d). 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., Figure 2.6d; Alfred Ernest 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 (Figure 2.7d). Meteoric ice (Figure 2.7d and e) had less sediment exposed at the surface due to snow cover than the other point transects.

2.6 Discussion

2.6.1 Overall system properties

Each of the five major remnants of the 'Ellesmere Ice Shelf' is a large mass of ice with substantial yet variable 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 2.1). The water column seston was also in sparse concentration as indicated by particulate organic carbon and nitrogen and planktonic chlorophyll *a* levels (Table 2.1). 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, and 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' cryo-ecosystem 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), which would also act to bring immured microbial mats to the surface (Mueller *et al.*, 2005a). 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, Central Arctic pack ice had an organic carbon concentration of 112 mg C m^{-2}, which was more than 2 orders lower than our spatially averaged estimate of ice shelf organic matter (Gradinger, 1999). 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 under 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.*, 2005a). 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.

2.6.2 Environmental gradients

Consistent with our hypothesis, 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 (Figure 2.2a). 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 accumulation per unit area of microbial mat is not necessarily greater for marine ice; however, sediments are far more widespread in the marine ice areas of Ward Hunt and Markham Ice Shelves making these ice shelves more important with regards to potential microbial habitat (Table 2.1).

We suggest that this east-west gradient is due to a combination of factors, specifically: 1) Local climatological differences (such as fog cover and ice shelf albedo) along the Ellesmere Island coastline act to maintain areas of high surface ablation, which promotes the exposure of marine ice (see Mueller and Vincent, 2005). 2) Sediment availability (which depends largely on local topography and lithology) and delivery mechanism (aeolian or otherwise) control the potential surface sediment coverage. This potential is realized when available sediment (the second factor) is exposed and concentrated on the ice

surface due to perennial net surface ablation caused by the first factor (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 albedo feedback and provides more habitat for microbial mats.

The lithology of coastal areas surrounding the ice shelves determines the availability of sediment. 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 also bordered by the Cape Columbia Group, but also 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 aeolian 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 works in areas where the bottom of the ice shelf is in close proximity to the sea floor and where the ice shelf is relatively thin to allow

conduction of heat upwards from the basal freezing front. 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 Figure 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.

2.6.3 Ecological gradients

With such important gradients in the physical characteristics of this cryo-ecosystem, it is noteworthy that gradients also exist in its biological domain. For instance, greater chlorophyll *a* and organic content was associated with the more saline ice of higher sediment content in the two eastern ice shelves, whereas the western ice shelves had less sediment and biomass content. A multivariate approach showed that the community structure was strongly associated with environmental variables, which was supported by a significant RDA ordination with the variables conductivity, and soluble reactive phosphorus, ammonium and nitrate concentration. Using ANOSIM, the taxa 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 controlling influence of conductivity gradients. The oligotrophic nutrient status of the water column and the inclusion of nutrients in the RDA solution suggest that nutrient concentration may be a limiting factor for certain microbial mat species. However, there is evidence that the nutrient status within microbial mats is 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, 2005). In this case, if diffusion and water column mixing were

comparable among samples, the water column nutrient concentration may reflect microbial mat interstitial waters and may serve as a proxy for nutrient accumulation within the mats.

In the present study we classified mat type in discrete categories; however, the mat type actually spans a continuum in microbial mat development. There are important community structure differences between the 'matlet', 'orange' and 'sediment' mat types, which suggest that these visually discernable mat characteristics may serve as convenient 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 continuum 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. *Pseudoanabaena* 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 taxa abundance data and environmental data, suggesting these categories are meaningful and possibly related.

2.6.4 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.*, 2003b). 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 (Figure 2.2a and 2.1b). 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 (Figure 2.2a), the ionic composition was closer to marine ice meltwater than any of the other meteoric ice water samples (see Figure 2.5). 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 Alfred Ernest Ice Shelf and the floating portion of the Milne Glacier (see Figure 2.5). 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 long contact times with aeolian sediment.

2.6.5 The effects of habitat fragmentation

According to ecological theory, habitat fragmentation impacts population dynamics through a reduction in total habitat, fragment size and connectivity. Deleterious effects include reduced dispersal rates and population size as well as increased extinction rates (Krebs, 1994). Habitat fragmentation is highly species specific (depending on their dispersal ability and habitat specificity) and hinges on the fragmentation pattern in the spatial and temporal domains (Levin, 1992). Isolating the effects of habitat fragmentation from other processes is viewed as exceedingly difficult due to the complex and chaotic nature of ecosystems (Bissonette and Storch, 2002).

It is not possible to compare the ecological properties of the original 'Ellesmere Ice Shelf' to the ensemble of present-day remnants. However, comparing the isolated fragments to each other is instructive. There were no significant differences in species richness or diversity among these remnants, suggesting that, contrary to our hypothesis, fragment size is not a controlling variable. Given the ability of microbial mat organisms to disperse, it seems probable that there is considerable connectivity between many of the ice shelf fragments (especially in the direction of the prevailing wind), or more likely, that 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 cryo-habitats (Mueller *et al.*, 2001) or soil ecosystems (Elster *et al.*, 1999), although not organized into the assemblage types observed on the ice shelves.

The 'Ellesmere Ice Shelf' cryo-ecosystem is fragmented at the large scale but dispersal may be also limited by habitat patchiness at the local scale, due to surface sediment distribution. Organisms are either randomly distributed among the fragments and landscape patches (null hypothesis), dispersal-limited due to habitat fragmentation, or their relative abundance is associated with environmental gradients. The RDA ordination indicates that 40 % of the community structure was associated with 4 environmental variables, leaving 60 % of the variance to be explained by unmeasured gradients or other factors. The ANOSIM analysis of community structure indicated that the Markham Ice Shelf community structure differed from communities from 2 other ice shelves. Aside from the differences in environmental habitat characteristics that may explain this, the large patches of sediment observed on the Markham Ice Shelf (and to a lesser extent on the Ward Hunt Ice Shelf; Figure 2.6b and c), may account for some of this discrepancy (Figure 2.6a and 2.7f). In this manner, habitat patchiness may be important to the overall patterns observed.

2.7 Conclusions

Our observations across the 250 km extent of the Ellesmere Ice Shelf cryo-ecosystem shows that each of the 5 main remnants that exist today 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 a substantial sediment cover accumulates on exposed marine ice. Regions where such conditions exist, on Ward Hunt and Markham Ice Shelves, differ greatly from areas elsewhere 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 indicates that microbial mat community structure is largely controlled by this environmental variability.

Any effect of fragmentation on Ellesmere ice shelf microbial mat habitats appears to be masked by the strong environmental gradients and high dispersal ability of constituent microbiota. This result is consistent with habitat fragmentation 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. However, ice shelf habitat fragmentation may become an important factor in microbial mat community dynamics in the future after further ice shelf disintegration has taken place. In order to detect this change as well as provide a more detailed analysis of microbial diversity, it will be useful to apply molecular techniques to extend beyond microscopic analyses. Remote sensing, however, will continue to play a vital role in the long term monitoring of this microbial ecosystem.

2.8 Acknowledgements

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Table 2.1 Comparison of the five Canadian Arctic ice shelves.

Ice Shelf	Alfred Ernest	Milne	Ayles	Ward Hunt	Markham
Position	82º20'N, 86º00'W	82º40'N, 81º20'W	82º50'N, 80º30'W	83º02'N, 74º00'W	83º03'N, 71º20'W
Length (km)	21	21	10	17	9
Width (km)	18	14	8	55	5
Total Area (km^2)	204.7	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	15.5	39.8	0
Water Area[b] (km^2)	11.2 (0.8)	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] 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. Mean values followed by ± SE in parentheses.

Table 2.2 Ice shelf water column nutrients, major ions and suspended particulates.

Ice Shelf	Alfred Ernest	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-} (mg l^{-1})	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)

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, Alfred Ernest Ice Shelf major ions 2, nutrients 4.

Table 2.3 Comparison of ice shelf ecosystem characteristics based on ice type and mat type.

	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 (ºC)	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)	

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).

Table 2.4 Abundance of taxa found in arctic ice shelf microbial mats.

Taxon	All Samples		Ice Shelf							Ice Type		Mat Type		
	Average	SE	AE	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. *Pseudoanabaena* 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
Non-motile 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

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, AE: Alfred Ernest 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 abundance is coded as follows: **5** indicates dominant (> 50 %), **4** indicates subdominant (50 to 25 %), 3 indicates common (25 to 5 %), 2 indicates rare (< 5 %), 1 indicates not detected (0%).

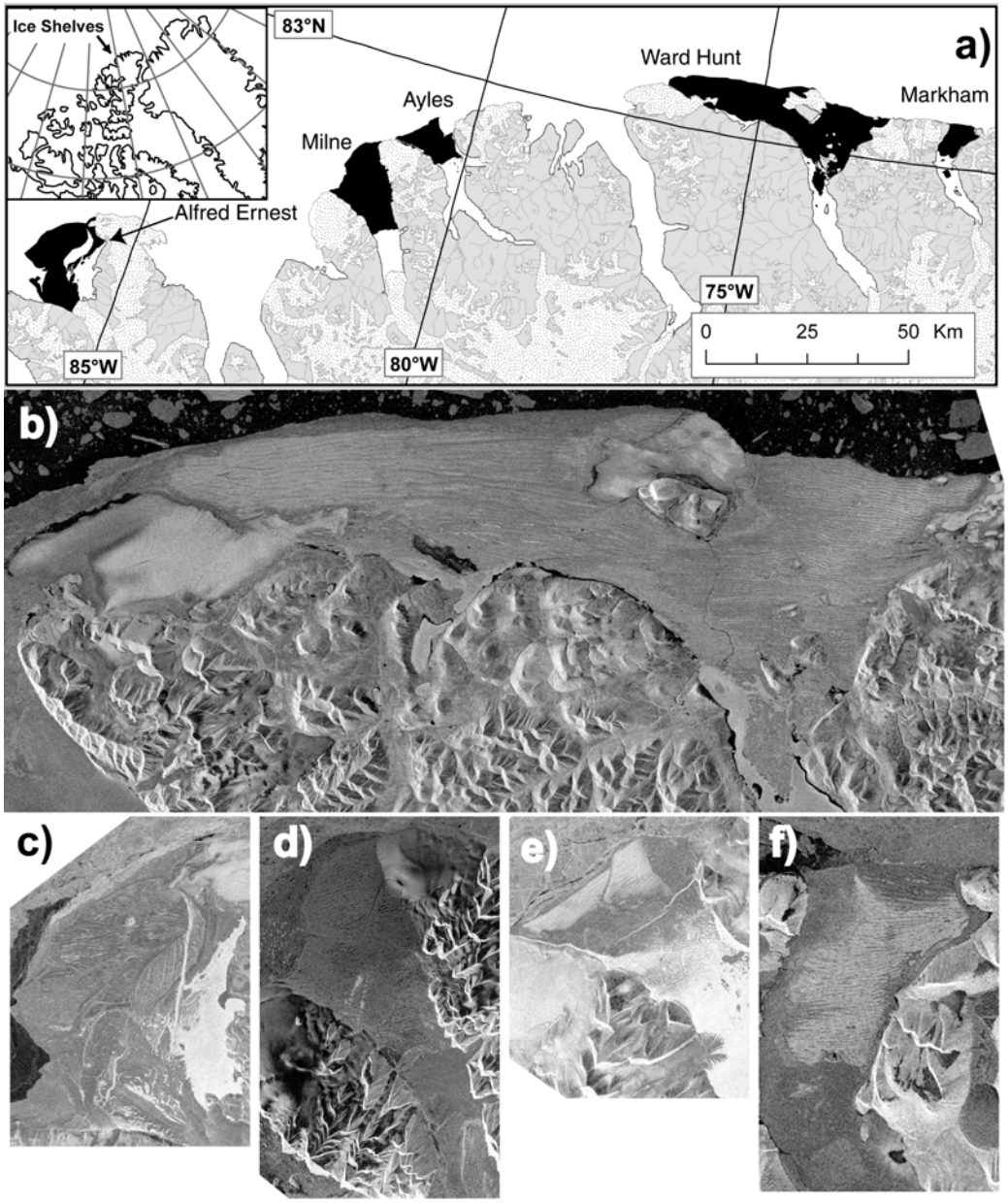

Figure 2.1 Map and RADARSAT images of ice shelves in the Canadian High Arctic that were the subject of this study.

a) The location of ice shelves along the coast of Ellesmere Island. 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, August 21, 2002. c) Alfred Ernest Ice Shelf, image number r1_22728, March 12, 2000. d) Milne Ice Shelf, image number r1_29859, July 25, 2001. e) Ayles Ice Shelf, image number r1_37462, January 7, 2003. f) Markham Ice Shelf. image number r1_35261, 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 Figure 2.1a).

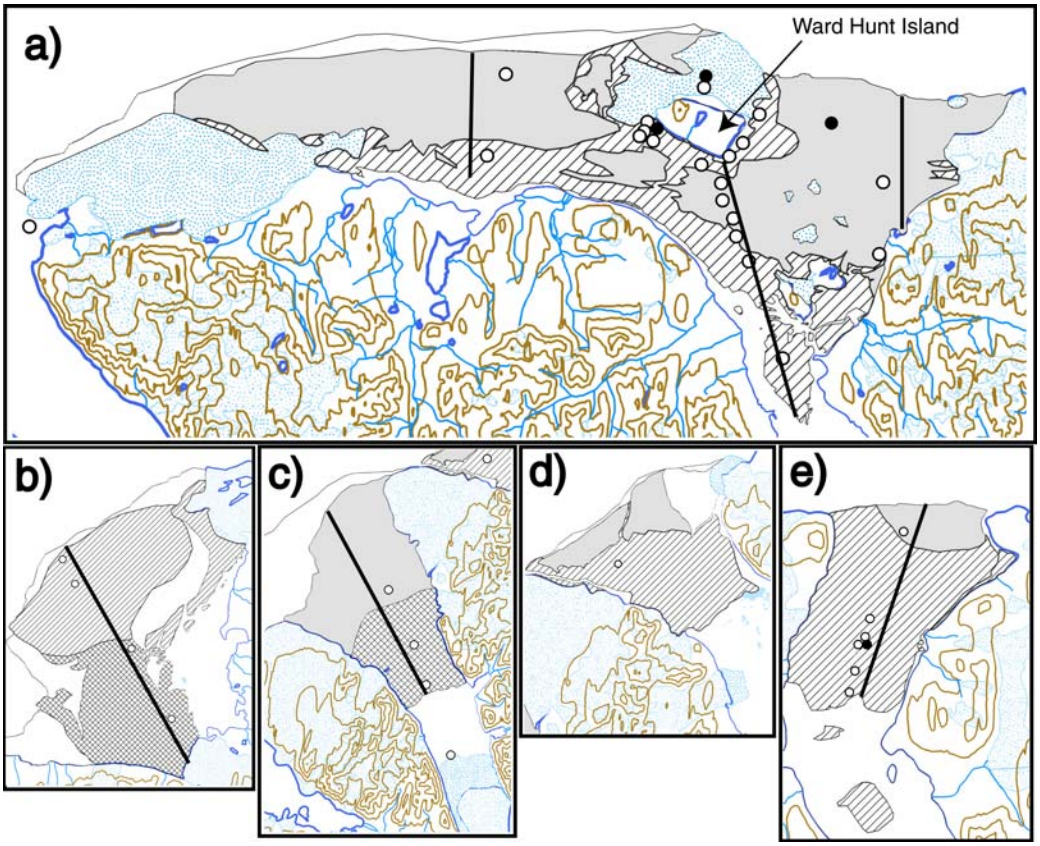

Figure 2.2 Ice types, sample sites and transect locations used in this study.

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. 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) Alfred Ernest 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 2.1a for scale.

Figure 2.3 Microbial mat types found on the ice shelves along the northern coast of Ellesmere Island.

a) Orange mat type: a luxuriant, thick (> 0.5 cm) loosely cohesive mats with a thin surface layer of orange pigmentation. b) Matlet type: 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 type: no visible biological aggregates in a fine to coarse sediment. The white scale bar in Figure 2.2c is approximately 10 cm wide.

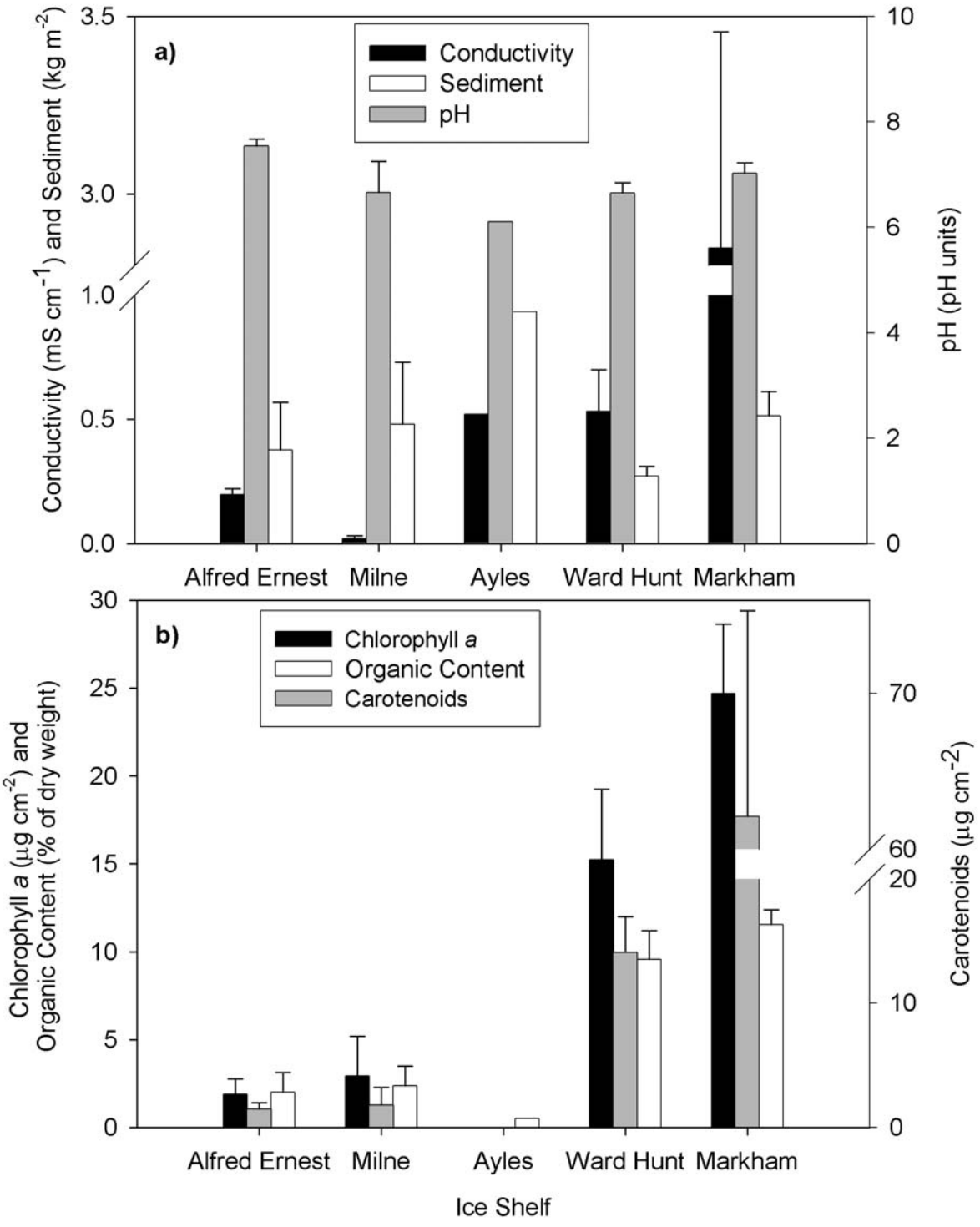

Figure 2.4 Comparisons of cryo-ecosystem characteristics by ice shelf.

a) Conductivity, pH and sediment concentration. b) Pigments and percent organic matter. Pigment data are missing for Ayles Ice Shelf.

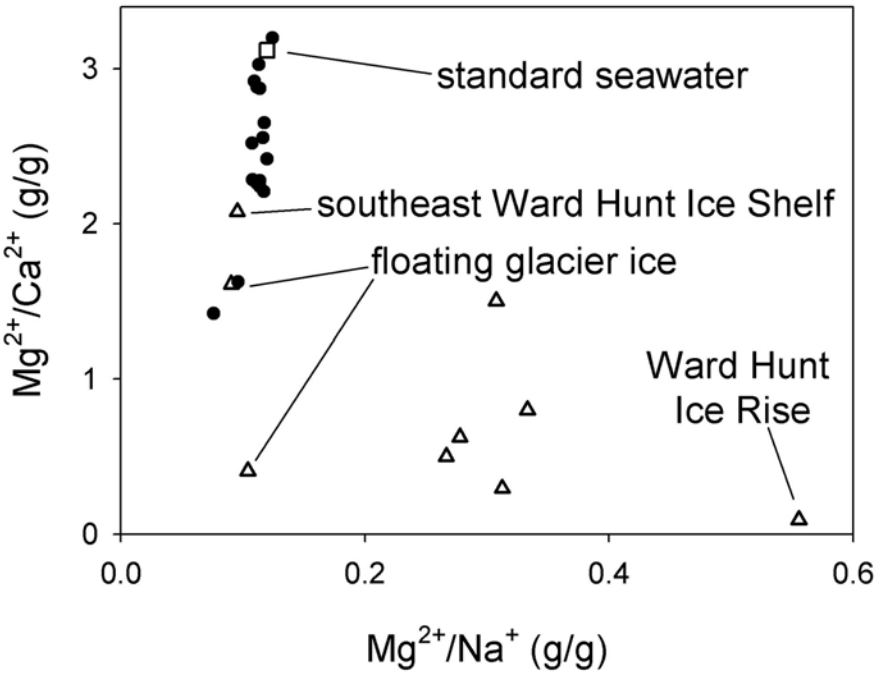

Figure 2.5 Cation ratio plot for surface meltwater samples.

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.

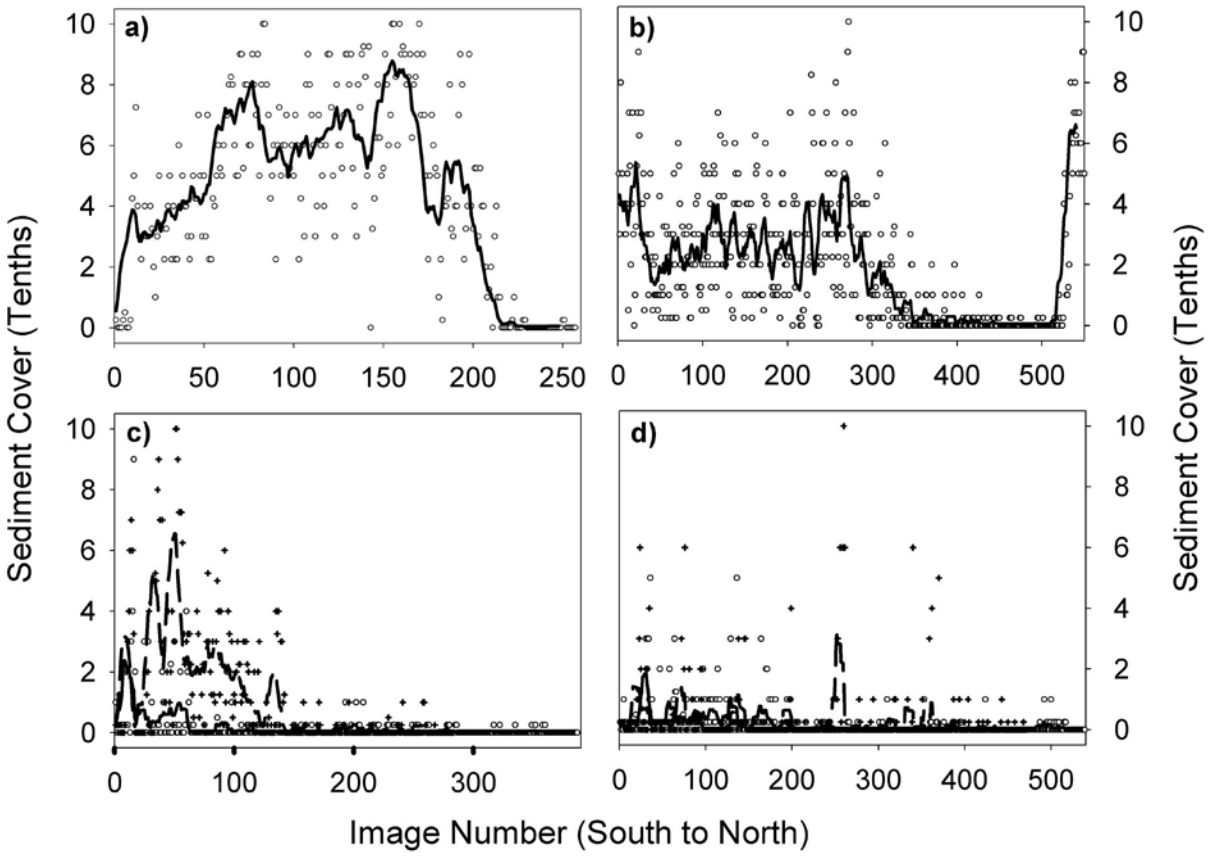

Figure 2.6 Sediment cover determined by over-flight transects.

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 Alfred Ernest Ice Shelf (crosses, dashed line).

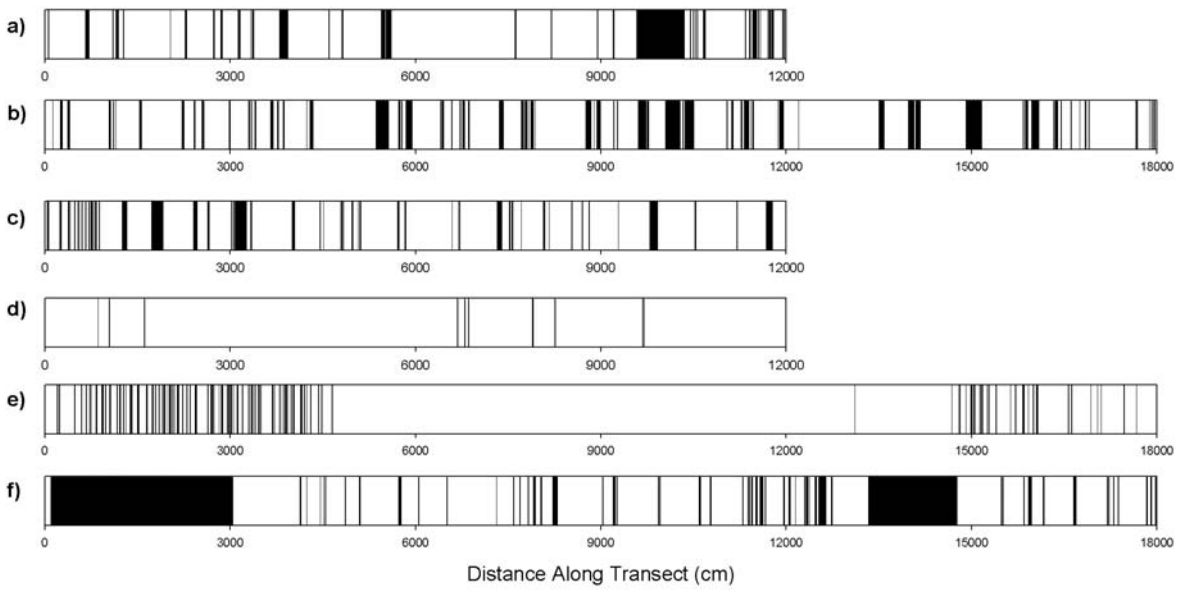

Figure 2.7 Point transect analysis of sediment presence/absence over ice surfaces showing habitat patchiness.

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 %).

Chapitre 3 Extremotrophs, extremophiles and broadband pigmentation strategies in a high arctic ice shelf ecosystem

3.1 Résumé

Les plates-formes de glace qui subsistent encore le long de la côte nord de l'île d'Ellesmere, Nunavut, Canada (~83^{o}N) fournissent un habitat pour les communautés de tapis microbiens cryo-tolérantes. Des bioessais de production primaire et de production bactérienne ont été faits pour mesurer la réponse physiologique à court terme des tapis aux changements des principales variables caractérisant ce cryo-écosystème (salinité, éclairement et température). Les réponses aux perturbations expérimentales des hétérotrophes ont nettement différé des réponses de la communauté d'autotrophes. Les bactéries hétérotrophes ont été qualifiées comme étant des extrêmophiles spécifiquement spécialisés aux conditions ambiantes de la plate-forme de glace. La communauté autotrophe, tant qu'à elle, a démontré un plus large intervalle de tolérance et un optimum de production en dehors des conditions ambiantes. Cette réponse, qualifiée d'extrêmotrophe, peut être partiellement due à la présence de pigments divers comprenant des acides aminés de type mycosporine liées à des oligosaccharides, des scytonemins, des caroténoïdes, des phycobiliprotéines et des chlorophylles qui absorbent dans l'ultra-violet B jusqu'aux longueurs d'ondes de la lumière rouge. Ces pigments fournissent une stratégie efficace pour contrer les effets néfastes d'un trop fort éclairement, d'une grande variation de la salinité et des basses températures de ce cryo-environnement.

3.2 Abstract

Remnant ice shelves along the northern coast of Ellesmere Island, Nunavut, Canada (~83^{o}N) provide a habitat for cryo-tolerant microbial mat communities. Bioassays of bacterial and primary production were undertaken to quantify the short-term physiological response of the mats to changes in selected variables that characterize this cryo-ecosystem (salinity, irradiance and temperature). The heterotrophic versus autotrophic community responses to these stressors differed markedly. The heterotrophic bacteria were extremophilic and specifically adapted to ambient conditions on the ice shelf, whereas the autotrophic community had broader tolerance ranges and optima outside the ambient range. This latter, extremotrophic response may be partly due to a diverse suite of pigments including oligosaccharide mycosporine-like amino acids, scytonemins, carotenoids, phycobiliproteins and chlorophylls that absorb from the near UV-B to red wavelengths. These pigments provide a comprehensive broadband strategy for coping with the multiple stressors of high irradiance, variable salinity and low temperatures in this extreme cryo-environment.

3.3 Introduction

Microbial phototrophs occur in a wide range of ice-bound environments including sea ice, glaciers and snow (Priscu and Christner, 2004). More recently, another type of cryo-ecosystem has been discovered in the North Polar Region. Similar to their Southern Hemisphere equivalents, arctic ice shelves provide an extreme habitat for microbiota. Microbial mats constitute the dominant biomass on the Ward Hunt Ice Shelf, High Arctic Canada (latitude 83º04' N, longitude 74º25' W). These are complex microbial consortia dominated by cyanobacteria (notably the genera *Phormidium*, *Leptolyngbya*, *Nostoc* and *Gloeocapsa*) but also containing a wide variety of other taxa including viruses, heterotrophic bacteria, green micro-algae and diatoms, as well as micro-invertebrates (Vincent *et al.*, 2000; Vincent *et al.*, 2004a).

Polar microbial mat communities retain a large over-wintering biomass and then grow slowly during the brief season of liquid water availability (Vincent, 2000). The micro-organisms on the Ward Hunt Ice Shelf deal with a combination of physiological stresses imposed by their ambient environment, including cold temperatures (< 5 ºC), high levels of solar radiation (including ultraviolet radiation) and 10-fold variations in salinity. The conjunction of these conditions makes arctic ice shelves an extreme habitat type, however the physiological optima and tolerance ranges of 'ice-mat' communities in relation to these stressors have not been quantified.

Many polar microbial mat cyanobacteria are cold-tolerant (psychrotrophic) rather than cold-adapted (psychrophilic) with their thermal optima for photosynthesis and growth lying well above their ambient range (Tang *et al.*, 1997; Nadeau and Castenholz, 2000). By extension, polar phototrophs may respond to several aspects of their habitats in the same way, with tolerance to extremes in various environmental dimensions (extremotrophs) rather than adaptation towards optimal growth at or near the extreme conditions experienced *in situ* (extremophiles). Microbial mats elsewhere are known to reduce the effects of high ultraviolet (UV) radiation with photo-protectants that quench free radicals or act as screening pigments (Cockell and Knowland, 1999; Ehling-Schulz and Scherer, 1999). Polar microbial mats are simultaneously exposed to high UV irradiances, high

photosynthetically active radiation (PAR) and low temperatures, leaving them particularly prone to photodamage (Roos and Vincent, 1998), and suggesting that photoprotection may be especially important in these systems. In this multi-stressor environment, a broadband pigment strategy that efficiently reduces photodamage might also free up resources for osmoregulation, thereby assisting in salinity, freeze-thaw and desiccation tolerance, and preventing serious damage when these other stressors inhibit metabolic activity and cellular repair mechanisms.

The purpose of this paper is to evaluate the physiological attributes of mats in the Ward Hunt Ice Shelf cryo-ecosystem and to address the question of how these consortia respond to physical and chemical stresses in their high arctic environment. These communities occur today in the Arctic and Antarctica, but may have been more widespread during periods of glaciation and extreme cooling in the past (Vincent *et al.*, 2004c). We first quantified the primary production and bacterial heterotrophic production of northern ice shelf microbial mat consortia under representative mid-melt season conditions. We then addressed the hypothesis that these mats subsist in sub-optimal conditions by determining their metabolic response to short-term changes in light regime, temperature, salinity and hydration. We identified and quantified pigments (including UV absorbing compounds, some of which may be transparent in the PAR waveband) in these microbial mats, specifically chlorophylls, carotenoids, scytonemins and mycosporine-like amino acids (MAAs), to determine to what extent the potential for photoprotection exists within these communities.

3.4 Methods

3.4.1 Study site

The Ward Hunt Ice Shelf is a ~ 40 m thick free-floating mass of ice that accreted *in situ* over the last 4500 years (Jeffries, 2002). The surface of the ice shelf is marked by a ridge and trough morphology that is associated with meltwater lakes (up to 15 km long, ~3 m deep and 10 to 20 m wide), which run parallel to the Ellesmere Island coastline (Figure 3.1).

The distribution of microbial mats across the ice shelf is highly variable. Typically, microbial mats occur in conjunction with sparse sediment deposits either on the ice surface or in discrete depressions in the ice surface termed cryoconite holes (approximately 7 % cover; D.R. Mueller, unpublished data). In certain areas, where sediment has been concentrated over time (Debenham, 1920), microbial mats appear to be more developed and are relatively abundant (18 to 31 % cover over scales of hundreds of metres; D.R. Mueller, unpublished data).

Arctic ice shelf microbial mats are typically composed of small olive-green flakes or 'matlets' that accumulate to a thickness of several millimetres to centimetres. In more developed communities, the surface layer (100 to 500 μm) is a conspicuous orange colour (Vincent *et al.*, 2004a). Aside from a surface layer, seen in developed communities and a black, anoxic layer, observed in very thick sediments, these microbial mats do not appear to be further stratified as found in many microbial mats (Stal, 1995).

Microbial mats from northern ice shelves are subjected to a variety of environmental stressors. Furthermore, these stressors vary both temporally and spatially, necessitating physiological acclimation on several timescales. A pronounced seasonality at this high latitude site causes gradual but extreme changes in light photoperiod (147 days of continuous darkness in winter and 147 days of continuous light in summer) and irradiance (0 to 1200 μmol photons m^{-2} s^{-1} downwelling PAR), temperature (average mat temperature = -8.6 ºC, maximum = 1.7 ºC, minimum = -15.7 ºC; D.R. Mueller, unpublished data from automated *in situ* dataloggers) and the availability of liquid water.

During the summer months, the ice shelf environment is more dynamic due to temperature shifts across the freezing point of water. Microbial mats emerge sporadically from under melting snow and ice over the course of the summer months resulting in a ~10 fold increase in light levels. Periods of high irradiances due to low solar angles and reflection from high albedo surfaces such as snow and ice are punctuated by periods of intense fog in which ambient irradiances are much reduced. In spring, meltwater influx reduces the salinity of water that overlies the microbial mats, with conductivities ranging from fresh (0.5 mS cm^{-1}) during periods of open water to saline (>10 mS cm^{-1}) during freeze-up. During summer, in

the absence of turbulent mixing, density stratified waters near to the microbial mat surface can be 4 to 10 times more saline than surface waters (Vincent *et al.*, 2004a). Summer air temperatures rarely exceed 10 ºC over the Ward Hunt Ice Shelf and the temperature of the water that immerses microbial mats does not rise higher than a few degrees, yet the temperature of microbial mats that are not overlain by water can exceed 5 ºC (D.R. Mueller, unpublished data). Environmental variables change on timescales from minutes to seasons, yet many of these changes are event-driven and occur on relatively short timescales (minutes to hours). Therefore our short-term acclimation experiments capture some but not all of the possible acclimation scenarios for ice shelf micro-organisms. While a short-term acclimation response will not elucidate the full tolerance range of these micro-organisms, it will serve as a proxy indicator to determine if physiological optima occur within the range of conditions that are prevalent in their cryo-habitat.

3.4.2 Primary productivity assays

Microbial mats from the Ward Hunt Ice Shelf were collected in August of 2002 and July 2003, with sampling focused on the thickest, most developed communities. Mats were placed in plastic trays, covered and returned to a nearby field laboratory, where they were prepared for assay.

Microbial mats were cored at random using a 1 cc syringe (area = 0.2 cm^2) with the tip removed. Five replicates per treatment were placed in separate Whirl-Paks (Nasco, Fort Atkinson, WI), which contained 20 ml of ice shelf surface meltwater, spiked with ^{14}C labelled $NaHCO_3$ yielding a final activity of 0.6 μCi ml^{-1}. Each core of microbial mat partially disintegrated in the incubation water due to a lack of mat cohesion, so the observed rates may represent an overestimate relative to mats in which diffusion limitation is more severe, such as intact cohesive mats. The dissolved inorganic carbon (DIC) concentration of the incubation water was determined by acidification and infrared gas analysis (IRGA) by the National Laboratory for Environmental Testing, Burlington, Ontario.

Whirl-Paks were sealed, gently mixed and placed in plastic neutral density filter envelopes. The absorption spectra of the filters and Whirl-Paks were determined using a Hewlett

Packard 8452A diode-array spectrophotometer (Palo Alto, CA) equipped with an integrating sphere. The filter envelopes did not affect the spectral distribution of light between 400 and 700 nm. The treatments reduced PAR levels to 0 (dark), 1, 6, 10, 22, 45 and 82 % of ambient light. UV-A (320-400 nm) levels were 5, 8, 11, 17, 35 and 80 % of ambient and UV-B (300-320 nm, in this case) levels were 26, 28, 34, 36, 42 and 85 % of ambient light. Samples were placed outside on snow or in white Styrofoam incubators for a period of 4 to 5 hours. Downwelling and scalar PAR irradiances were monitored at regular intervals throughout the experiment using a Licor 190SA quantum sensor (Licor Biosciences, Lincoln, NE), a QSL100 quantum scalar sensor (Biospherical Instruments, San Diego, CA) and a LI 1440 datalogger (Licor Biosciences, Lincoln, NE). The microbial mat samples were exposed to light from all directions and therefore, 4π irradiance was used for further calculations and when the 4π irradiance was not available (2002), it was estimated from 2π irradiance using the empirical relationship ($4\pi = 3.6(2\pi)$, $R^2 = 0.66$, n = 293), determined in 2003. Temperature was measured inside the incubators by using Stowaway temperature loggers (Onset Computer Corporation, Bourne, MA). The incubations were stopped by filtering microbial mats onto GC50 glass-fibre filters (AMD Manufacturing, Mississauga, ON) and acidification with 200 µl of 0.1 N HCl. Filters were stored frozen until analysis.

In the laboratory, filters were placed in scintillation vials and further acidified by fumigation for 24 hours. Liquid scintillation cocktail (Beckman Ready Safe, Fullerton, CA and OptiPhase 'HiSafe' 2, PerkinElmer, Boston, MA) was added and samples were homogenized using glass rods prior to determination of specific activity on a Beckman LS 6500 scintillation counter (Fulerton, CA). Treatments were corrected for β-carboxylation by subtracting dark ^{14}C uptake (Sakshaug *et al.*, 1997), and data were fitted to the hyperbolic equation of Platt *et al.* (1980) using an iterative non-linear approach (Sigma Plot 8.0, Systat Software, Point Richmond, CA). Values for the light saturation index (E_k) were calculated from the relationship $E_k = P_{max}/\alpha$. P_{max} was calculated by using the method outlined by Platt *et al.* (1980).

3.4.3 Bacterial productivity assays

Heterotrophic bacterial productivity was determined by tritiated leucine uptake (Kirchman, 1993b). Samples were prepared as above with a leucine concentration of 10 nM and an activity of 0.5 μCi ml^{-1}. Incubations were carried out on 5 replicates in darkness and were terminated with the addition of trichloroacetic acid (TCA) to a final concentration of 5 % (v/v) followed by heating to 80 ºC for 15 minutes and then filtration onto cellulose acetate filters (JGOFS, 1996). Filters were rinsed twice with 5 % TCA (3 ml) and then twice with 80 % ethanol (2 ml), placed in scintillation vials to dry and were frozen for transport (Kirchman, 1993b). Filters were dissolved with 0.5 ml of ethyl acetate and radioactivity was determined 24 hours following the addition of scintillation cocktail and glass rod homogenization. Samples were corrected for leucine adsorption by using the scintillation counts of TCA killed replicates (dead counts were typically 3 % of live counts). Bacterial carbon production was then estimated using a conversion factor of 3.1 kg C mol $leucine^{-1}$ and an isotope dilution of 2 (Kirchman, 1993b).

3.4.4 Temperature effects

Microbial mat primary and bacterial production were assayed at 0, 5, 10, 15 and 20 ºC, using the methodology outlined above. Water baths were prepared at the correct temperatures and microbial mat samples (acclimated to ~4 ºC) were immersed in the water baths in their hermetically sealed Whirl-Paks, while the temperature was constantly monitored for the incubation period using a hand-held temperature probe (Digithermo 4550, IMEC GmbH, Heilbronn Germany). Additional temperature measurements made with 4 Stowaway temperature loggers indicated that conditions inside the filters were actually 2.6, 5.2, 10.4 and 15.3 ºC for the first four treatments. For primary productivity, only a dark and 45 % filter treatment (average irradiance = 1596 μmol photons m^{-2} s^{-1}) were used (to capture photosynthetic rate in the plateau region of the P vs E curve), whereas bacterial productivity was determined with dark live and dead treatments.

3.4.5 Salinity effects

Mat productivity was determined at 4 different salinities (0.1, 2.9, 10 and 29 mS cm^{-1}), which were obtained by mixing de-ionized water, ice shelf water (0.4 mS cm^{-1}) and locally

sampled Arctic Ocean seawater (29 mS cm^{-1}) at the appropriate ratios. Arctic ice shelves are partly derived from sea ice and the ionic composition of ice shelf surface water is consistent with the dilution of seawater (Vincent *et al.*, 2004a). We did not account for differences in nutrient concentration between these treatments, however, based on the nutrient-replete status of the microbial mats, this unquantified addition did not likely bias these short-term assays (Mueller and Vincent, 2005). For primary production, dark and 45 % PAR treatments were used (average irradiance = 1607 μmol photons m^{-2} s^{-1}), while bacterial production was determined with live and dead treatments. Differences in incubation water DIC between the treatment groups were accounted for in the primary productivity calculations.

3.4.6 Desiccation effects

Microbial mats were collected in plastic trays and dried in the sun over the course of 5 days (water content was reduced to 3 % (w/w), SE = 0.8 %, n = 3). Approximately five minutes prior to the experiment, the dried mats were re-wet using ice shelf water and were incubated along with fresh, moist mats (water content = 48 % (w/w), SE = 1.6 %, n = 3) according to the methodology above. Primary productivity was measured with the 5 filters, full PAR and dark treatments, and bacterial productivity was determined with live and dead treatments.

3.4.7 Light transition effects

Microbial mats were collected from two contrasting micro-habitats on the ice shelf. The first micro-site was exposed to full sunlight whereas the second micro-site contained microbial mats that were shaded from direct sunlight by a ~ 20 cm cover of snow. The latter micro-site had irradiances of approximately 10 % of ambient PAR due to the overlying snow cover. Exposed and shaded mats were returned to the field laboratory in dark containers, but upon arrival they were placed either on top of snow or buried under snow to simulate the two micro-sites on the ice shelf. There were two light transitions, 1) exposed to shaded and 2) shaded to exposed to simulate changes in light levels during melt-out and freeze-up, respectively. These experimental groups were accompanied by control groups, 1) exposed to exposed and 2) shaded to shaded. After an 18-hour acclimation

period, cores of these mats were incubated for primary productivity (P vs E) determination using the methodology described above. For the exposed to shaded group, treatments 1, 6, 11, 22 % had 3 replicates, 45 % had 1 replicate and the 82 % treatment was not performed due to the lack of radiolabel.

3.4.8 Biomass and chlorophyll *a* determination for productivity

Microbial mats were sampled for chlorophyll *a* determination using a 0.64 cm^2 core. These samples were stored frozen and in the dark for transport. In the laboratory, samples were thawed in 6 ml 90 % acetone:water (v/v) and sonicated (Microson XL2000, Misonix, Farmingdale, NY) at approximately 10 W for two 30-second bursts with a pause of 30 seconds between sonication steps. Pigment extraction took place in the dark for 1 hour at 4 ºC and terminated with centrifugation at 4000 rpm for 5 minutes at 4 ºC. The supernatant was removed and chlorophyll *a* concentrations were determined at 663 nm and 750 nm, before and after acidification, in a Cary 300 Bio UV-Visible spectrophotometer (Varian, Mulgrave, Australia) (Strickland and Parsons, 1972). This procedure was carried out 3 times to ensure complete extraction and total chlorophyll *a* content was determined by summing each extraction (Villeneuve, 2000). Microbial mat free water content and biomass were determined from 4.15 cm^2 cores that were collected and frozen for transport. In the laboratory, the cores were weighed and then dried to constant weight at 100 ºC. The mass of organic and inorganic fractions were determined by loss on ignition at 500 ºC for seven hours.

3.4.9 HPLC pigment composition determination

For determination of pigment composition three ice shelf sites were visited on the northern Ellesmere Island coastline (Figure 3.1): Ward Hunt Ice Shelf Site A (83º 05.6’ N, 75º 08.0’ W), Ward Hunt Ice Shelf Site B (83º 05.0’ N, 74º 25.3’ W) and Markham Ice Shelf (83º 02.4’ N, 71º 26.5’ W). Site A was characterized by sparse sediment in cryoconite holes, whereas the other two sites had thick microbial mats with orange surface layers. Site B mats were also used in the productivity assays. At each main site, 7 replicate cores (0.64 cm^2) were taken from micro-sites in the immediate vicinity. Cores were frozen, transported

to Quebec and transferred into -80 ºC storage until analysis by reverse-phase high performance liquid chromatography (HPLC).

Microbial mat cores were thawed, ground with a Caframo R2R1 tissue grinder (Wiarton, Ontario) and sonicated as described above in 5 ml 90 % acetone:water (v/v). Pigments were left to extract under argon at -20 ºC for 20 hours and then centrifuged. The supernatant was filtered on a 0.2 μm pore size PTFE Acrodisc filter (Pall Corporation, Ann Arbor, MI) and 50 μl of the sample was injected into a Varian ProStar HPLC (Mulgrave, Australia) at a flow rate of 1 ml min^{-1}. The mobile phase was a gradient of two eluents, methanol:acetonitrile:aqueous pyridine solution (50:25:25, v/v/v) and methanol:acetonitrile:acetone (20:60:20, v/v/v) (Zapata *et al.*, 2000). The stationary phase consisted of a Symmetry C_8 column (3.5 μm pore size, 4.6 x 150 mm) at 25 ºC with a Symmetry C_8 guard column (5 μm pore size, 3.9 x 20 mm) (Waters Corporation, Milford, MA). Pigments were detected and quantified using two photodiode array channels (450 nm for carotenoids and 384 nm for scytonemins) and a fluorescence channel (excitation at 440 nm and emission at 650 nm) for chlorophylls. Pigments were identified by retention time and verified by absorption spectra (350-750 nm), for all pigments except chlorophyll *c2*, pheophorbide-like and a chlorophyll *b*-related peak, which were identified by retention time only. Purchased standards (chlorophyll *a*, chlorophyll *b*, chlorophyll *c2*, β-carotene, echinenone, canthaxanthin, lutein, zeaxanthin, violaxanthin, diadinoxanthin, myxoxanthophyll and fucoxanthin) were used to convert peak areas to pigment concentrations for these compounds and related chlorophylls. Other carotenoids were quantified by using peak areas in conjunction with published extinction coefficients of closely related pigments (4-keto-myxol-2'-methylpentoside-like, 125.3 L g^{-1} cm^{-1}; myxoxanthophyll-related, 125.3 L g^{-1} cm^{-1}; canthaxanthin-related, 207.5 L g^{-1} cm^{-1}), spectrally modified extinction coefficients (oscillaxanthin, 54 L g^{-1} cm^{-1} at 450 nm from 75 L g^{-1} cm^{-1} at 490 nm; (Hertzberg and Liaan-Jensen, 1969), or the extinction coefficient of β-carotene (250 L g^{-1} cm^{-1}) for unknown carotenoids (Jeffrey *et al.*, 1997). Scytonemin and related pigments were quantified with an extinction coefficient of 112.6 L g^{-1} cm^{-1} at 384 nm (Garcia-Pichel *et al.*, 1992).

3.4.10 MAA determination

Mycosporine-like amino acids were separated, identified and quantified by reverse-phase isocratic HPLC (Shick *et al.*, 1999). Microbial mat cores were sampled, ground and sonicated as described in the previous section, but were extracted using 5 ml 25 % aqueous methanol (v/v) at 45 ºC for 2 hours (Sommaruga and Garcia-Pichel, 1999). Extracts were centrifuged, filtered with 0.2 μm nylon Acrodisc filters (Pall Corporation, Ann Arbor, MI) and stored under argon prior to HPLC analysis. A 50 μl aliquot of each sample was injected into the HPLC at a flow rate of 0.5 ml min^{-1}. The mobile phase was 25 % aqueous methanol (v/v) with 0.1 % acetic acid (v/v), and the stationary phase consisted of a Phenosphere C_8 column (5 μm pore size, 4.6 x 250 mm) (Phenomenex, Torrance, CA) at 26 ºC preceded by a Brownlee RP-8 Spheri-5 guard column (4.6 x 30 mm) (Perkin-Elmer, Shelton, CT). MAA compounds were detected and quantified using 5 photodiode array channels (310, 320, 330, 334 and 360 nm). Oligosaccharide mycosporine-like amino acids (OS-MAA) peak areas at 310 nm were converted to concentration units by using the extinction coefficient 17 L g^{-1} cm^{-1} (Böhm *et al.*, 1995). This group of compounds is heterogeneous and not fully separable from each other using standard MAA methods, a problem that may have been aggravated by our choice of column (which showed poor separability with MAA secondary standards). Therefore, absolute quantities of OS-MAA should be interpreted with caution (Böhm *et al.*, 1995).

3.5 Results

3.5.1 Primary and bacterial productivity

The ice shelf microbial mat had a maximum photosynthetic rate (P_{max} for non-treatment groups) ranging from 0.059 to 0.17 g C g Chl a^{-1} h^{-1} (mean = 0.10, SE = 0.025, n = 5) on a per unit chlorophyll *a* basis giving production rates on a per area basis of 27.3 to 105 mg C m^{-2} h^{-1} (mean = 63.7 SE = 15.2, n = 5) (Table 3.1). The bacterial productivity was three orders of magnitude lower than primary productivity, ranging from 0.085 to 0.38 μg C g $biomass^{-1}$ h^{-1} (mean = 0.23, SE = 0.15, n = 2) yielding 0.037 to 0.21 mg C m^{-2} h^{-1} (mean = 0.12, SE = 0.087, n = 2), on a per area basis. The relative contribution of these processes reflects the overwhelming dominance of autotrophic biomass relative to heterotrophic

bacteria in the mats. Photosynthesis versus irradiance models revealed very small α values, (Table 3.1) while photoinhibition was minor, with one exception (Figure 3.2a), suggesting that excess light did not cause considerable damage to the photosynthetic mechanism.

3.5.2 Effects of temperature

The primary productivity of microbial mats increased monotonically with increasing temperature, suggesting that the physiological tolerance limits lay at temperatures > 20 ºC, more than 15 ºC above maximum ambient temperatures we have recorded in this environment. The treatment at 10.4 ºC showed a rate twice that of the normal or ambient (0 to 5 ºC) internal microbial mat temperatures (Figure 3.3). In contrast, no coherent relationship was found between bacterial productivity and temperature, with maximum rates at 2.6 and 15.3 ºC (Figure 3.3).

3.5.3 Effects of salinity

Primary productivity tripled between the lower salinity treatments and 10 mS cm^{-1} and then returned to a minimum photosynthetic rate at 29 mS cm^{-1} (Figure 3.4). Bacterial productivity was maximal at the lowest salinity and dropped by more than 50 % over the salinity range (Figure 3.4). This suggests that the phototrophic community had a broader salinity optimum range, with peak productivity at higher salinities than mid-season conditions, while the heterotrophic bacterial community appeared to be closely adapted to ambient salinities and poorly adapted to fluctuations relative to the phototrophs.

3.5.4 Effects of desiccation

Microbial mat desiccation and re-hydration produced inconclusive results for primary productivity with the experimental group departing from the general P vs. E model response; this precluded the estimation of photosynthetic parameters (Table 3.1). However, the general trend of both the control and treatment response suggested that there is no apparent effect of desiccation (not shown). After drying and re-hydration, the bacterial productivity showed a 10-fold significant decrease ($t = -19.8$, $p < 0.001$, $n = 5$) versus the

control (Table 3.1) suggesting that the heterotrophic community was adversely affected by desiccation.

3.5.5 Effects of light transition

The light acclimation experiment showed only minor differences between control and experimental groups. This suggests that the microbial mats acclimated quickly and effectively to the new light regime under which they were assayed. Some differences include a slightly lower P_{max} for the exposed to shaded transition relative to the shaded to shaded control group (Figure 3.2c), and a slightly higher P_{max} and β for the shaded to exposed transition relative to the exposed to exposed control group (Figure 3.2d). Despite this, the P_{max} values for all four groups in the light transition experiments were very close.

3.5.6 Microbial mat pigments

A diverse assemblage of pigments was identified and quantified from the ice shelf microbial mats (Table 3.2 and Figure 3.5). These include chlorophylls, such as chlorophyll *a*, *b,* and *c2*, plus various degradation products (pheophorbide-like, chlorophyllide-like and pheophytin-like pigments). Cyanobacterial carotenoids such as echinenone, canthaxanthin (Figure 3.6c), oscillaxanthin, myxoxanthophyll and a related pigment, the 4-keto-myxol-2'-methylpentoside-like carotenoid (Figure 3.6b) (Francis *et al.*, 1970; Goodwin, 1980; Schülter *et al.*, 2004) were separated. There were also carotenoids indicating the presence of other taxonomic groups such as chlorophytes (violaxanthin-like carotenoid and lutein), diatoms (fucoxanthin and diadinoxanthin) as well as generally occurring carotenoids such as β-carotene (Jeffrey *et al.*, 1997). A bacterial carotenoid, tentatively identified as okenone (Fujii *et al.*, 1998), was found in one sample on the Markham Ice Shelf and in all samples at Ward Hunt Ice Shelf Site B (Figure 3.6d). The pigment scytonemin was found in many of the microbial mat samples and was often accompanied by its reduced form, red scytonemin (Figure 3.6a). A pigment with a spectrum similar to scytonemin (maximum absorbance at 384 nm), but with a retention time about 4 minutes later, was observed in several samples and may represent a more non-polar derivative of scytonemin (see Squier *et al.*, 2004b). All samples of the ice shelf microbial mats fluoresced strongly red under

green excitation when examined by epifluorescence microscopy, indicating the dominance of phycobiliprotein-rich cyanobacteria.

3.5.7 Microbial mat mycosporine-like amino acids

No 'typical' mycosporine-like amino acids (MAAs) were isolated from the ice shelf microbial mats, such as those found in many species of algae and lower animals (Karentz *et al.*, 1991). However, there was an abundance of a class of compounds that resembled oligosaccharide MAAs (OS-MAA). These compounds are composed of two chromophores (mycosporine-glycine and likely another MAA) that are linked into a saccharide chain (Böhm *et al.*, 1995). No method yet exists to separate these compounds completely, and therefore they are treated as a mixture, both here and in the literature (Hill *et al.*, 1994b; Ehling-Schulz *et al.*, 1997). The predominant spectral signature of the OS-MAA (peak at 312 and a shoulder at 335 nm) can be seen in Figure 3.7 (inset, spectrum 1). As the HPLC retention time increased, several less polar molecules appeared with different spectra, some with differing proportions of the MAA chromophores (Figure 3.7, inset, spectrum 3) and others having a secondary peak between 265 and 280 nm (Figure 3.7, inset, spectrum 2). This secondary peak may represent a degradation product of the original compound as suggested by others (Ito and Hirata, 1977; Böhm *et al.*, 1995) or this may be the spectral signature of OS-MAA and water stress proteins as shown by Hill *et al.* (1994a).

3.6 Discussion

3.6.1 Microbial mat productivity

Several studies of polar microbial mats have been undertaken in Antarctica where conditions are comparable to the Ward Hunt Ice Shelf. In Antarctic ponds, streams and ice shelves cyanobacterial mat gross primary productivity has been measured at rates between 3 to 40 mg C m^{-2} h^{-1} (0.05 to 0.9 g C g Chl a^{-1} h^{-1}) (Howard-Williams *et al.*, 1986; Howard-Williams and Vincent, 1989; Vincent and Howard-Williams, 1989; Vincent *et al.*, 1993a; Hawes and Howard-Williams, 1998). In the Northern Hemisphere, microbial mats taken from Ward Hunt Lake (adjacent to the Ward Hunt Ice Shelf) had primary productivities of 3.0 to 6.5 mg C m^{-2} h^{-1} (~0.04 g C g Chl a^{-1} h^{-1}) (Villeneuve, 2000). Our measured primary

production rates for the Ward Hunt Ice Shelf mats lie within the range of polar microbial ice mat literature for chlorophyll specific productivity but had relatively high productivity per unit area possibly reflecting the relatively high standing stocks of pigments in these mats. Low chlorophyll *a* specific photosynthetic rates in microbial mats have been attributed to inactive yet intact chlorophyll *a* preserved in senescent cells (Vincent and Howard-Williams, 1989), although this could also be due to self-shading in thick mats.

The maximum light utilization coefficient (α) and the light saturation index (E_k) may be used to assess photo-acclimation status when compared to closely analogous systems. Our estimates are similar to those found by Vincent *et al.* (1993a) in microbial mats from Antarctic ponds, streams and lakes (0.0003 to 0.0089 g C g Chl a^{-1} h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$). Levels of E_k varied substantially and, except for the shaded experiment, greatly exceeded those found by Vincent *et al.* (1993a) suggesting high light acclimated physiology. Photoinhibition exhibited in our study may be due to loss of microbial mat integrity and our method of placing mats in water above a highly reflective surface (snow and Styrofoam), which likely increased irradiance to levels beyond what the microbial mats may naturally receive.

Despite the ubiquitous presence of heterotrophic bacteria in microbial mat consortia, bacterial productivity is rarely measured (Tuominen, 1995). Bacterial productivity as measured by thymidine uptake in Antarctic microbial mats was found to be 0.2 to 0.45 pmol thymidine cm^{-2} h^{-1} (Vincent and Howard-Williams, 1989). Using empirical conversion factors of 2.0 x 10^{18} cells mol thymidine^{-1} and 10 fg C cell^{-1} (Bell, 1993) a productivity of 0.04 to 0.09 mg C m^{-2} h^{-1} can be estimated. This rate is quite close to the results from the present study. Further methodological improvements such as determination of substrate saturation (Fischer and Pusch, 1999), isotope dilution (Kirchman, 1993b) and conversion factor determination (Kirchman, 1993a) are necessary to ensure complete inter-comparability between ecosystems. Given the potential for high concentrations of leucine within the arctic ice shelf microbial mat environment, the use of generic isotope dilution factors, developed for bacterioplankton, may underestimate productivity substantially.

A first order estimate of the annual production of this community can be made from the measurements reported here. The standing stock of microbial mat biomass on the Ward Hunt Ice Shelf attains levels of 464 g m^{-2} (SE = 38, n= 26). Assuming a representative microbial mat primary productivity of 64 mg C m^{-2} h^{-1} (from mean P_{max} for non-treatment groups, SE = 15, n = 5), a growing season of 70 days (D.R. Mueller, unpublished data) and ignoring any potential diel or seasonal effects, the annual gross photosynthesis is approximately 108 g C m^{-2}. With a carbon to biomass ratio of 0.5, the time required to accumulate present standing stocks would be just over 2 years. Respiration rates in microbial mats typically exceed half of the gross photosynthetic rate (Moorhead *et al.*, 1997) and would extend the accumulation time estimate by at least a further 2 years. During this period, bacterial heterotrophy (mean productivity = 0.1 mg C m^{-2} h^{-1}, SE = 0.09 n = 2) would recycle an estimated 4.3 g m^{-2} of biomass (2.15 g m^{-2} of carbon) within the microbial mat at an average efficiency of 30 % (Fischer and Pusch, 1999). These first-order approximations are likely to be sensitive to inter-annual climate variability and changes to the ice shelf surface mass balance (Lister, 1962; Serson, 1979).

3.6.2 Effects of temperature

Ward Hunt Ice Shelf photosynthetic rates increased with temperature up to at least 20 ºC, suggesting a growth optimum above 15 ºC (i.e., psychrotrophic, *sensu* Morita, not psychrophilic), which is common for polar microbial mats (Tang *et al.*, 1997). The heterotrophic bacterial production did not respond coherently to temperature increases, suggesting that some members of the community were psychrophilic, while others were psychrotrophic with perhaps even some mesophilic organisms. The average Q_{10} value for photosynthesis was 1.88 (S.E. = 0.15). This value is close to the theoretical value of 2 for temperature dependent kinetic effects (Davison, 1991; Falkowski and Raven, 1997). These values also compare with those found by Vincent *et al.* (1989) (Q_{10} = 1.6 to 3.2), while a much higher degree of temperature responsiveness was found by Tang *et al.* (1997) (Q_{10} = 4.85, but with large variability).

3.6.3 Effects of salinity

The effect of salinity on primary productivity suggests a broad growth optimum between 3 and 29 mS cm^{-1} for these ice-mat autrotrophs. Our results suggest that these microbial mats can not only tolerate higher salinities, but also prefer them to ambient conditions. Many microbial mats are found in saline (Stal, 1994; Yallop *et al.*, 1994) and hypersaline conditions (Wieland and Kuhl, 2000; Sorensen *et al.*, 2004). These include Antarctic ice shelf mats, where Hawes *et al.* (1999) investigated the microbial mat response to gradual increases in salinity (from 5 to 160 mS cm^{-1}) and found no change in photosynthetic rate (relative to controls) up to 20 mS cm^{-1}. In contrast to the autotrophic community, the heterotrophic bacterial production did not respond favourably to increased salinity, suggesting that the bulk of this community was much more closely adapted to ambient conditions at the time of sampling. We suggest that this community may undergo a seasonal succession due to sharper growth optima relative to the more generalist phototrophs.

3.6.4 Effects of desiccation

Ward Hunt Ice Shelf microbial mats are not likely to dry out *in situ*, as they are relatively thin (1 to 2 cm), lie directly on the ice, and continuously receive moisture from the ice surface during the melt season. However, the effects of drying on mat organisms have implications for their dispersal from land to the ice shelf. In addition, the lowering of water activity associated with desiccation is analogous to the effects of freezing. Hawes *et al.* (1992) found that microbial mat metabolic activity returns within minutes to hours after re-hydration. Mat-forming cyanobacteria are protected against freezing and dehydration by extrapolymeric substances (EPS) and water stress proteins contained within their sheaths (Decho, 1994; Hill *et al.*, 1994a; Hill *et al.*, 1994b). These polysaccharide sheaths provide a physical barrier against the flow of water and may also play a role in repelling bacterial and viral attack. If heterotrophic bacteria were located outside the cyanobacterial sheaths, they may not have benefited from intra-sheath moisture retained during the drying period, and would have been unduly affected by the desiccation of their immediate environment. A mid-season bacterial community specifically adapted to high water availability could

also explain the different responses to desiccation between the autotrophic and heterotrophic bacterial communities, but this was not tested in this study.

3.6.5 Effects of light transition

Changes from snow-shaded to ambient light levels and the reverse did not affect the P_{max} of microbial mat photosynthesis. However, the photoinhibition parameter (β) was higher under low irradiances (at least by a factor of 10) in the light transition experiments and β was also higher in the low irradiance assay versus the high irradiance assay (Figure 3.2a and b). This parameter shifted in concert with values of E_k and α, which is indicative of a reorganization of the photosynthetic apparatus to increased efficiency at lower irradiances, leaving the community prone to photoinhibition outside its acclimation window (Behrenfeld *et al.*, 2004).

The relative stability of P_{max} across all treatments demonstrates that the mats can acclimate to light conditions associated with snow accumulation and ice-over, as well as with melting. Depending on the winter snowfall pattern and the following summer melt regime, we have observed that the microbial mats may remain buried under snow for one or possibly several summer seasons. The annual surface mass balance of the Ward Hunt Ice Shelf is positive when snowfall exceeds melting, and is negative when the opposite is true. As climate fluctuates over time scales of decades to centuries, the thickness of the ice shelf may change appreciably. After successive years of positive surface mass balance, microbial mats may reach a depth where they do not thaw or receive light in the summer. However, these microbial mats may be re-exposed and re-commence their metabolic activity after successive years of negative surface mass balance melts overlying ice and snow. Therefore, the present day ice shelf microbial mats are likely to be a heterogeneous community of variable age, composed of modern micro-organisms as well as ancient microbial mats that lived some time ago and have come to the surface due to climatic shifts since the end of the Little Ice Age (Crary *et al.*, 1955).

3.6.6 Pigments

Chlorophyll *a* levels from mats in high biomass areas of the Ward Hunt and Markham Ice Shelves were high relative to other microbial mats from many ponds and lakes throughout the polar regions, including meltwater ponds on the McMurdo Ice Shelf, Antarctica. One possible explanation is the cold temperatures on ice shelves preserve the chlorophyll molecules inside senescent cells for long periods. Low rates of heterotrophic bacterial productivity and small proportions of chlorophyllides and pheophytins support this low degradation hypothesis. McMurdo Ice Shelf microbial mats often lie atop relatively thick sediment, which likely warm to temperatures not experienced on northern ice shelves. The disparity between the McMurdo Ice Shelf and the northern ice shelves in this study may also be explained by sampling strategy (McMurdo sampling was randomized; (Howard-Williams *et al.*, 1989; Howard-Williams *et al.*, 1990) unlike our targeting of the highest available biomass) and extraction methods (Howard-Williams *et al.*, 1989; Howard-Williams *et al.*, 1990). Finally, there may be extra accumulation of chlorophyll *a* on the northern ice shelves due to recent climatic shifts that allowed buried microbial mats to re-emerge.

Carotenoids serve as photosynthetic accessory pigments and as cellular protection against reactive oxygen species (Hirschberg and Chamovitz, 1994). They were found in abundance in northern ice shelf microbial mats, and in some cases, they exceeded the range of carotenoid concentration reported from Antarctica (Vincent *et al.*, 1993b), and the Arctic (Villeneuve *et al.*, 2001) including those previously measured on Markham Ice Shelf (Vincent *et al.*, 2004a). However, the ratio of carotenoids to chlorophyll *a* was not as high as in Antarctica (Vincent *et al.*, 1993b; Sabbe *et al.*, 2004) and in nearby arctic mats (Villeneuve *et al.*, 2001), possibly reflecting the preservation and accumulation of large standing stocks of chlorophyll *a* on northern ice shelves.

Scytonemin is a cyanobacterial sheath pigment that is known to protect against UV-A radiation (Garcia-Pichel *et al.*, 1992) and is found in very high concentrations in microbial mats containing Nostocales (up to 420 μg cm^{-2}: Vincent *et al.*, 1993b). In the ice shelf mats, concentrations were variable, and ranged up to a maximum of 262 μg cm^{-2}. We also observed high values of red scytonemin, indicating that scytonemin was reduced and

accumulating on the ice shelf. The ratio of scytonemin to red scytonemin may be an indicator of reducing conditions for the site, as suggested for other environments (Garcia-Pichel and Castenholz, 1991; Vincent *et al.*, 2004a) and it may be formed following the loss of cellular integrity (Squier *et al.*, 2004a; Squier *et al.*, 2004b). The relative temporal stability of these sheath pigments supports the hypothesis that the Markham Ice Shelf site and Ward Hunt Site B are older and/or more reduced than Site A, as evidenced by the red scytonemin to chlorophyll *a* ratio and the scytonemin to red scytonemin ratios (Table 3.2). However, this assumes a constant species composition and comparable pigment production rates across space and time. High proportions of red scytonemin may also be indicative of site-specific surface ablation history. If microbial mats were buried at sometime during the past millennium and were kept in reducing conditions, this pigment could re-emerge along with ancient microbial mat material, as discussed above, and could be a valuable paleoglaciological tool for discerning past climates on the ice shelf.

3.6.7 Mycosporine-like amino acids

Mycosporine-like amino acids are compounds that absorb in the UV-B and UV-A wavebands (Karentz *et al.*, 1991), and there is considerable evidence that they play a role in UV screening in a variety of organisms (Garcia-Pichel and Castenholz, 1993b; Neale *et al.*, 1998). To date, OS-MAAs have been isolated from the sheaths of *Nostoc commune* (Scherer *et al.*, 1988), and this compound has been reported in related species (*Calothrix* sp. and cf. *Diplocolon* sp.; (Garcia-Pichel and Castenholz, 1993a) but has not been previously reported from microbial mat consortia. However, the presence of this class of compounds in our sampling sites is to be expected since these ice shelf microbial mats have been found to contain a large proportion of *Nostoc* spp. (Vincent *et al.*, 2004a). OS-MAA concentrations in these microbial mats are almost two orders of magnitude lower than reported elsewhere (up to 2 % of cellular dry weight; (Ehling-Schulz *et al.*, 1997). However, ice shelf microbial mats appear to have very high values of OS-MAA when normalized to chlorophyll *a* relative to this other study (4.6 g OS-MAA (g Chl *a*)$^{-1}$ after 4.5 days of UV-B treatment, versus a control of 0.6 g OS-MAA (g Chl *a*)$^{-1}$(Ehling-Schulz *et al.*, 1997). This was a surprising result (especially for Site A, where the OS-MAA to total scytonemin ratio was ~7 times higher than the other two sites; Table 3.2) since OS-MAA

compounds are water-soluble and do not accumulate as readily as lipophilic scytonemin. High amounts of OS-MAAs at Site A could reflect a difference in community composition or the need for additional UV-B protection in these relatively thin mats.

3.6.8 Broadband pigment strategies

Our HPLC analysis indicates that arctic ice shelf microbial mats contain a broadband pigment assemblage that absorbs from the near UV-B to red PAR, and probably beyond given the pigment indication (okenone) of photosynthetic bacteria. These pigments can be classed as screening compounds (OS-MAAs, scytonemins), light harvesting and accessory pigments (chlorophylls, phycobiliproteins and certain carotenoids), and anti-oxidants (certain carotenoids and perhaps MAAs; (Dunlap and Yamamoto, 1995). As found by Hodgson *et al.* (2004), the presence of these pigments implies that these micro-organisms can spectrally modify their environment for photo-protection and photosynthetic efficiency. Furthermore, the presence of anti-oxidants confers an added mechanism for dealing with a combination of physiological stressors. The extracellular location of OS-MAA and scytonemin greatly enhances the sunscreening factor for the cells over almost the entire naturally occurring UV waveband (Garcia-Pichel and Castenholz, 1993a). A broadband pigment strategy in the arctic ice shelf microbial mats is a means to control the spectral environment and allows the photosynthetic communities to tolerate the changing stresses of their cryo-habitat. This extremotrophic response is likely to be a strategy that also operates in other types of extreme environments. Other microbial inhabitants of the mat consortium, such as the heterotrophic bacteria and non-pigmented protists, may also benefit from the presence of pigments in their surroundings, although possibly not to the same degree as the organisms that produce these compounds.

3.7 Conclusions

Arctic ice shelf microbial mat consortia have relatively high primary productivity and low bacterial productivity, reflecting, in part, the relative proportion of autotrophs to heterotrophs. Consistent with our central hypothesis, the productivity experiments show that the ice shelf autotrophic community subsists in sub-optimal conditions, but can easily tolerate a wider range of environmental conditions including sudden changes in several key

environmental variables in the ice shelf environment. Contrary to this hypothesis, however, the heterotrophic bacteria appeared to be adapted to the ice shelf microbial mat environment at the time of sampling and did not tolerate departures from these conditions as readily as the photosynthetic community. Considering that colonial cyanobacteria and algae in these mats are likely to have much longer generation times by comparison with heterotrophic bacteria, these autotrophic communities may therefore be more dependent upon tolerance rather than close acclimation to ambient conditions (Vincent and Quesada, 1997). This would allow the autotrophic community to retain a large biomass, despite sub-optimal growth, providing that loss rates are small and that there was little competition by extremophilic species with adapted, faster rates of growth under *in situ* conditions (Vincent, 2000). In contrast, the shorter generation times in the heterotrophic bacterial community may allow successional shifts in community structure to be a strategy to deal with seasonal environmental change.

The broadband pigment assemblage, contained within the microbial mats enables the autotrophic community to cope with the combined effect of several environmental stressors, including the synergistic effects of low temperatures and high solar irradiances. The strategic use of these pigments may partly account for their extremotrophic physiological response to changes in environmental conditions. Heterotrophic bacteria appear to be less tolerant of variability and more adapted to the specific, extreme conditions at the time of sampling. These heterotrophic micro-organisms are therefore extremophilic, while the photosynthetic components of the mat consortium would be better classified as extremotrophs.

3.8 Acknowledgements

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Table 3.1 Microbial mat primary and bacterial productivity parameters under different experimental conditions.

Treatment	Productivity Parameter							
	P_s	α	β	P_{max}^1	P_{max}^2	E_k	BP^1	BP^2
T0 Conditions								
Low light	0.105* (0.021)	0.0005* (0.00004)	0.0001* (0.00005)	0.059	27.3	106	-	-
High light	0.057 (0.102)	0.0001* (0.00004)	< 0.000001 (0.00007)	0.057	54.8	566	0.085 (0.007)	0.037 (0.003)
Light Transition 1								
Exposed to Shaded	0.17 (0.078)	0.0054* (0.0011)	0.0004 (0.0007)	0.13	80.4	24.2	-	-
Shaded to Shaded (Control)	0.20* (0.038)	0.007* (0.0012)	0.0003 (0.0003)	0.17	105.2	24.2	-	-
Light Transition 2								
Shaded to Exposed	0.22* (0.011)	0.0005* (0.00001)	<0.00004* (0.000007)	0.17	105.2	332	-	-
Exposed to Exposed (Control)	0.15* (0.031)	0.0004* (0.0001)	< 0.000001 (< 0.00001)	0.15	92.8	367	-	-
Desiccation/Rewetting								
Dry to Wet							0.038 (0.007)	0.021 (0.004)
Wet to Wet (Control)	0.064* (0.021)	0.00015* (0.00003)	< 0.000001 (0.000009)	0.06	38.7	432	0.384 (0.016)	0.212 (0.009)

P_s is the light-saturated maximum photosynthesis in the absence of photoinhibition (g C g Chl a^{-1} h^{-1}), α is the maximum light utilization coefficient (g C g Chl a^{-1} h^{-1} (µmol photons $m^{-2}s^{-1})^{-1}$), β is the photoinhibition parameter (g C g Chl a^{-1} h^{-1} (µmol photons $m^{-2}s^{-1})^{-1}$), P_{max}^1 is the maximum photosynthetic rate per unit Chlorophyll *a* (g C g Chl a^{-1} h^{-1}), P_{max}^2 is the maximum photosynthetic rate per unit area (mg C g m^{-2} h^{-1}), E_k is the light saturation index (µmol photons $m^{-2}s^{-1}$). BP^1 is the bacterial productivity, determined from tritiated leucine uptake per unit biomass (µg C g $biomass^{-1}$ h^{-1}) and BP^2 is the bacterial productivity per unit area (mg C m^{-2} h^{-1}) . Standard errors are in parentheses. * denotes parameter is statistically significant ($\alpha = 0.05$)

Table 3.2 Ice shelf microbial mat pigments, mycosporine-like amino acids and ratios of pigments.

Pigment/ratio	Ward Hunt Ice Shelf A		Ward Hunt Ice Shelf B		Markham Ice Shelf	
	Concentration ($\mu g\ cm^{-2}$) or Ratio ($\mu g\ \mu g^{-1}$)	SE	Concentration ($\mu g\ cm^{-2}$) or Ratio ($\mu g\ \mu g^{-1}$)	SE	Concentration ($\mu g\ cm^{-2}$) or Ratio ($\mu g\ \mu g^{-1}$)	SE
Scytonemin	6.26	1.16	90.47	34.71	6.90	6.05
Red scytonemin	1.66	0.31	137.13	38.37	133.31	39.40
Scytonemin-related	Nd	-	2.58	1.66	nd	-
Total Scytonemins	**7.92**	1.29	**227.6**	49.06	**140.21**	38.99
Fucoxanthin	0.19	0.19	2.08	0.91	0.31	0.31
Oscillaxanthin-like	0.20	0.20	2.35	0.61	0.59	0.45
Violaxanthin-like	nd	-	nd	-	0.35	0.23
4-keto-myxol-2'-methylpentoside-like	nd	-	3.64	0.88	nd	-
Diadinoxanthin	nd	-	nd	-	1.79	0.76
Myxoxanthophyll	nd	-	7.13	1.24	0.22	0.22
Myxoxanthophyll-related	nd	-	1.13	0.21	0.29	0.14
Zeaxanthin	nd	-	0.79	0.12	0.71	0.07
Lutein	1.24	0.37	2.03	0.27	4.86	0.61
Canthaxanthin-related	nd	-	0.50	0.12	0.11	0.03
Canthaxanthin	0.03	0.03	2.56	0.33	0.47	0.12
Echinenone	0.56	0.15	5.95	0.85	1.58	0.22
β-carotene	0.15	0.04	1.88	0.37	0.98	0.13
Unknown carotenoids	nd	-	2.48	0.70	0.39	0.18
Total Carotenoids	**2.36**	0.66	**32.50**	5.26	**12.66**	1.47
Chlorophyll *a*	5.63	0.79	30.58	4.71	17.54	0.96
Chlorophyll *b*	0.80	0.24	1.11	0.13	4.83	0.75
Chlorophyll *c2*	0.29	0.07	0.33	0.10	0.40	0.12
Chlorophyll *a* related1	0.32	0.07	1.47	0.17	0.67	0.10
Chlorophyll *a* related2	0.82	0.35	0.16	0.06	0.36	0.11
Chlorophyll *b* related	0.14	0.05	0.28	0.04	0.19	0.04
Chlorophyllide *a*-like	0.41	0.16	0.94	0.35	0.70	0.07
Pheophytin *a*-like	0.14	0.06	0.11	0.04	0.29	0.08
Pheophorbide-like	nd	-	0.57	0.19	0.19	0.08
Unknown chlorophyll	nd	-	0.05	0.03	nd	-
Total Chlorophylls	**8.55**	1.48	**35.60**	5.36	**25.16**	1.92
Total MAAs	**13.1**	2.79	**62.6**	16.19	**16.6**	6.03

Scytonemin/chlorophyll *a*	1.49	0.61	4.39	2.22	0.38	0.33
Red scytonemin/chlorophyll *a*	0.35	0.08	4.52	1.39	7.22	1.88
Carotenoids/chlorophyll *a*	0.37	0.07	1.07	0.10	0.72	0.08
OS-MAA/chlorophyll *a*	3.34	1.52	2.35	0.74	1.00	0.38
Scytonemins/carotenoids	19.18	16.13	8.13	2.35	10.65	2.42
OS-MAA/scytonemin	1.93	0.44	0.28	0.04	0.26	0.14
Scytonemin/red scytonemin	3.21	0.93	1.42	0.90	0.09	0.06

Ward Hunt Site A was a blue ice area, whereas the Ward Hunt Site B and Markham Ice Shelf Site were sediment rich areas. Data are presented as averages (n =7) and Standard Errors (SE). The totals for each category of compounds are in bold and nd signifies not detected.

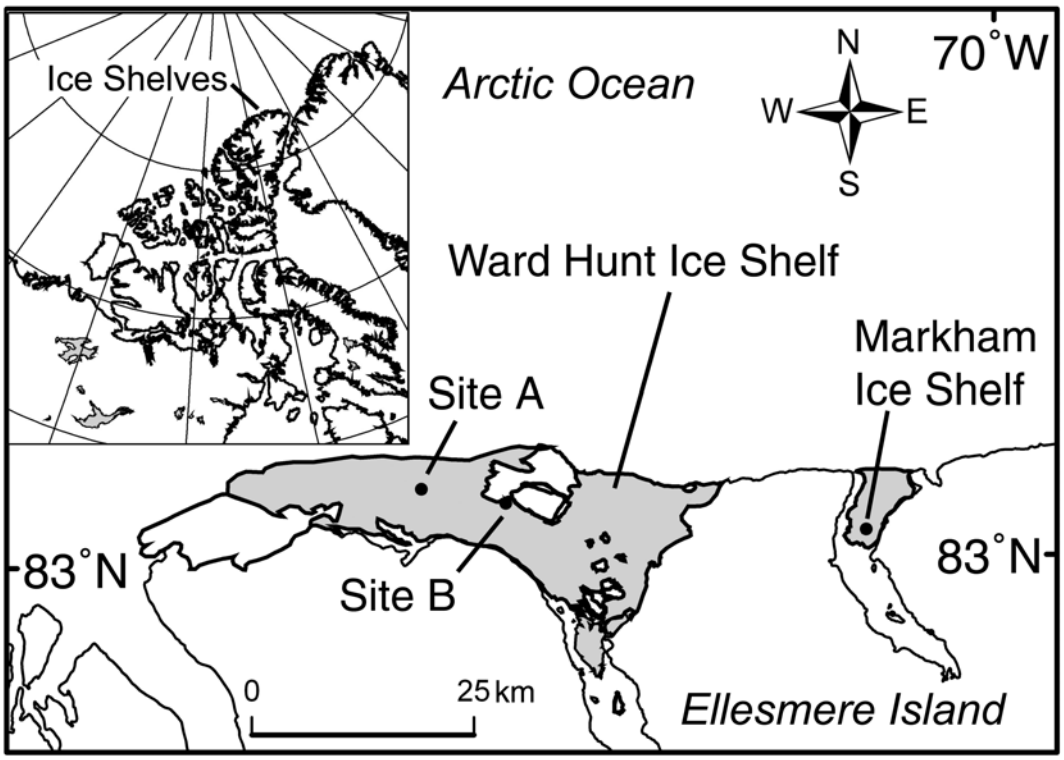

Figure 3.1 Location of ice shelves in Nunavut, Canada.

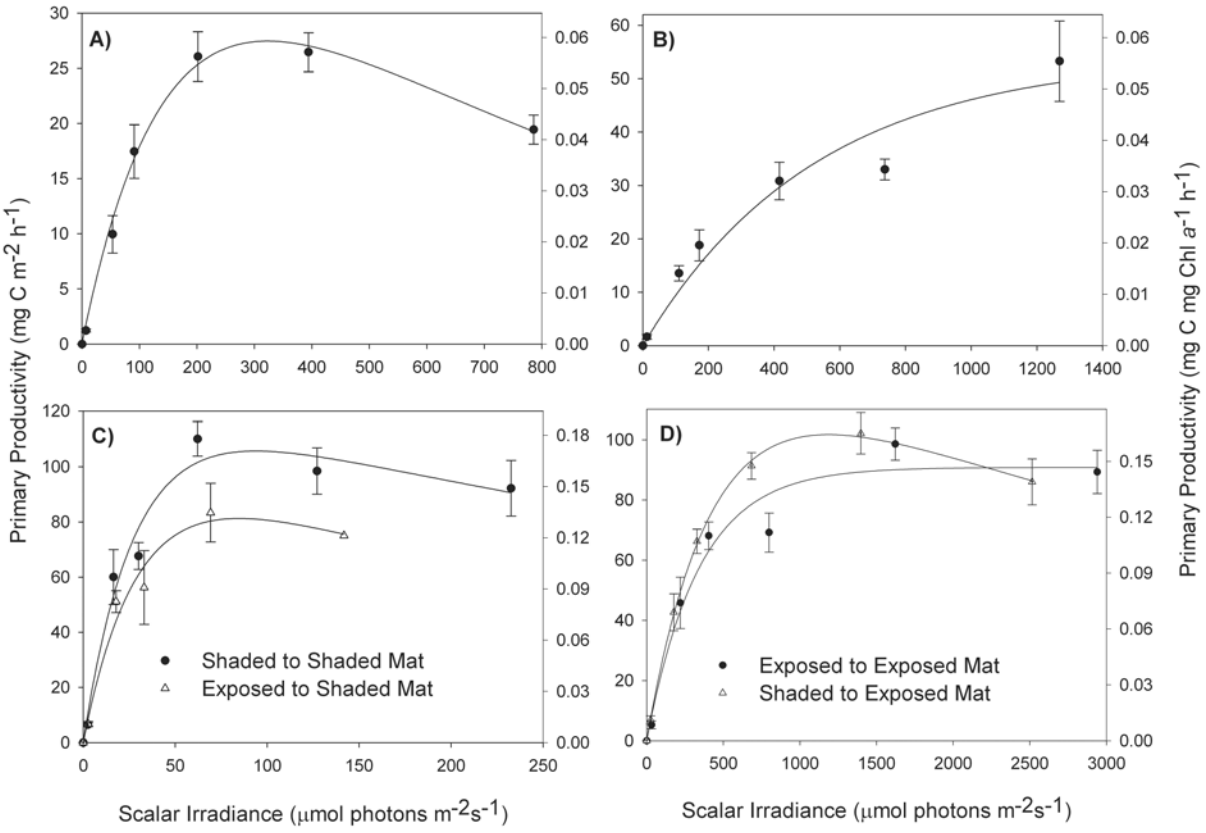

Figure 3.2 Photosynthesis versus irradiance for Ward Hunt Ice Shelf microbial mats.

Low light conditions (A) were caused by intense fog (August 8, 2002), whereas high light conditions (B) refer to clear sky conditions (July 18, 2003). High scalar irradiances are due to reflection from the white Styrofoam incubators (2003) or snow (2002). (C) Mat acclimatization to high irradiance (shaded to exposed) versus control (exposed to exposed). (D) Mat acclimatization to low irradiance (exposed to shaded) versus control (shaded to shaded).

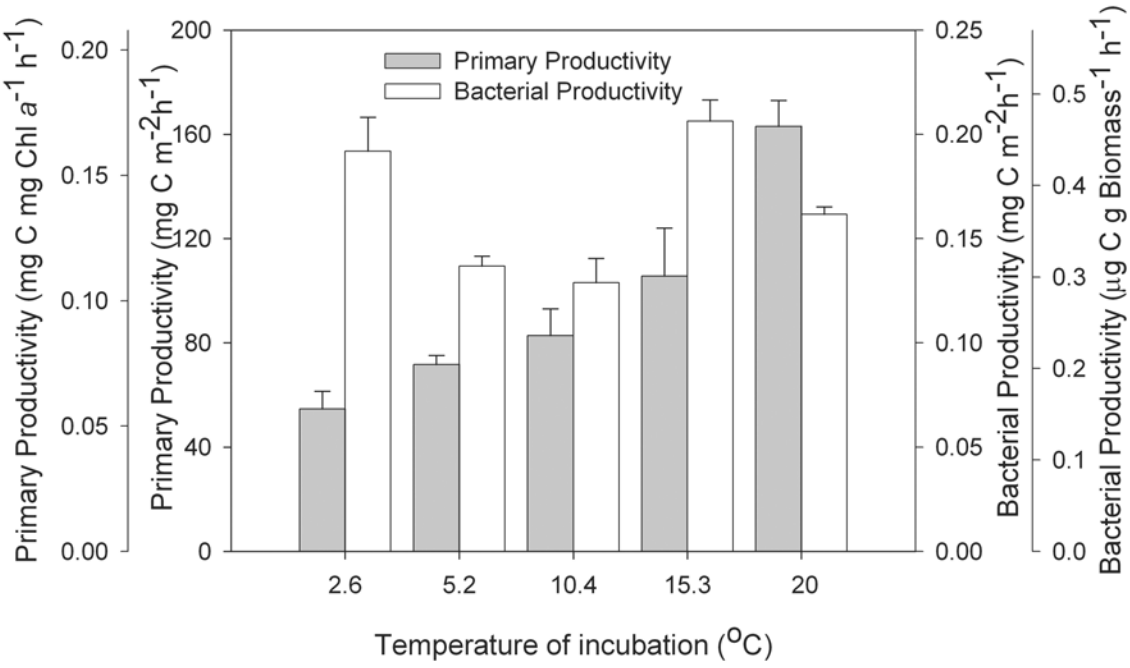

Figure 3.3 Effect of temperature on microbial mat productivity on the Ward Hunt Ice Shelf.

The primary productivity was measured at ~45 % ambient PAR (1596 µmol photons m^{-2} s^{-1}) to avoid potential artifacts due to photoinhibition.

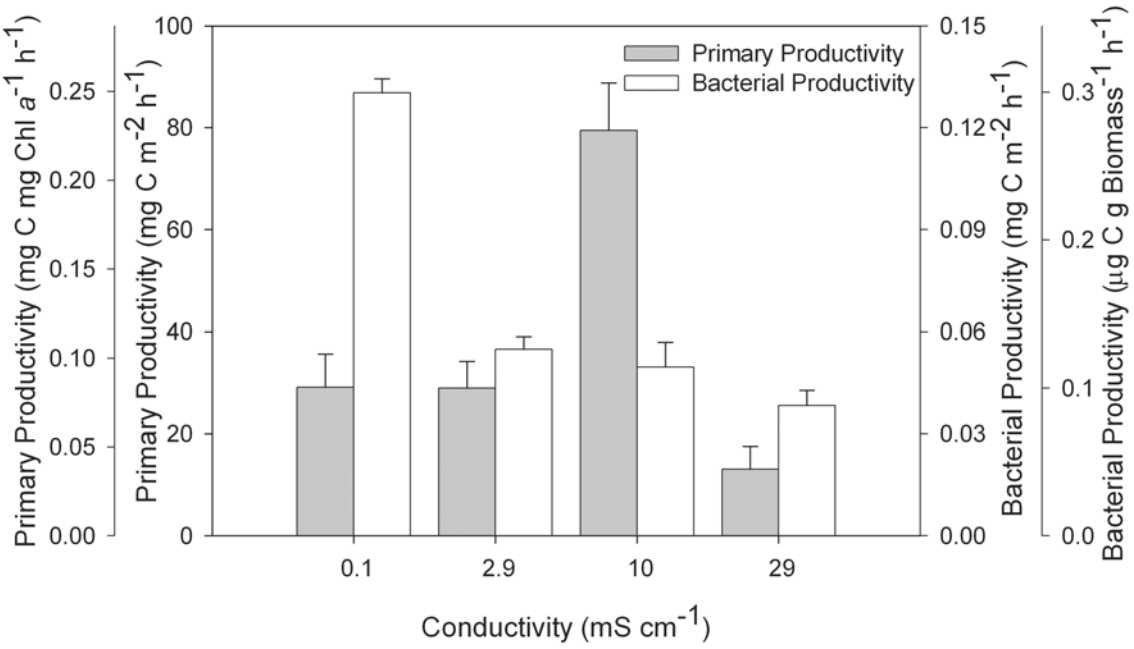

Figure 3.4 Effect of conductivity on microbial mat productivity on the Ward Hunt Ice Shelf.

The primary productivity was measured at ~45 % ambient PAR (1607 µmol photons m^{-2} s^{-1}) to avoid potential artifacts due to photoinhibition.

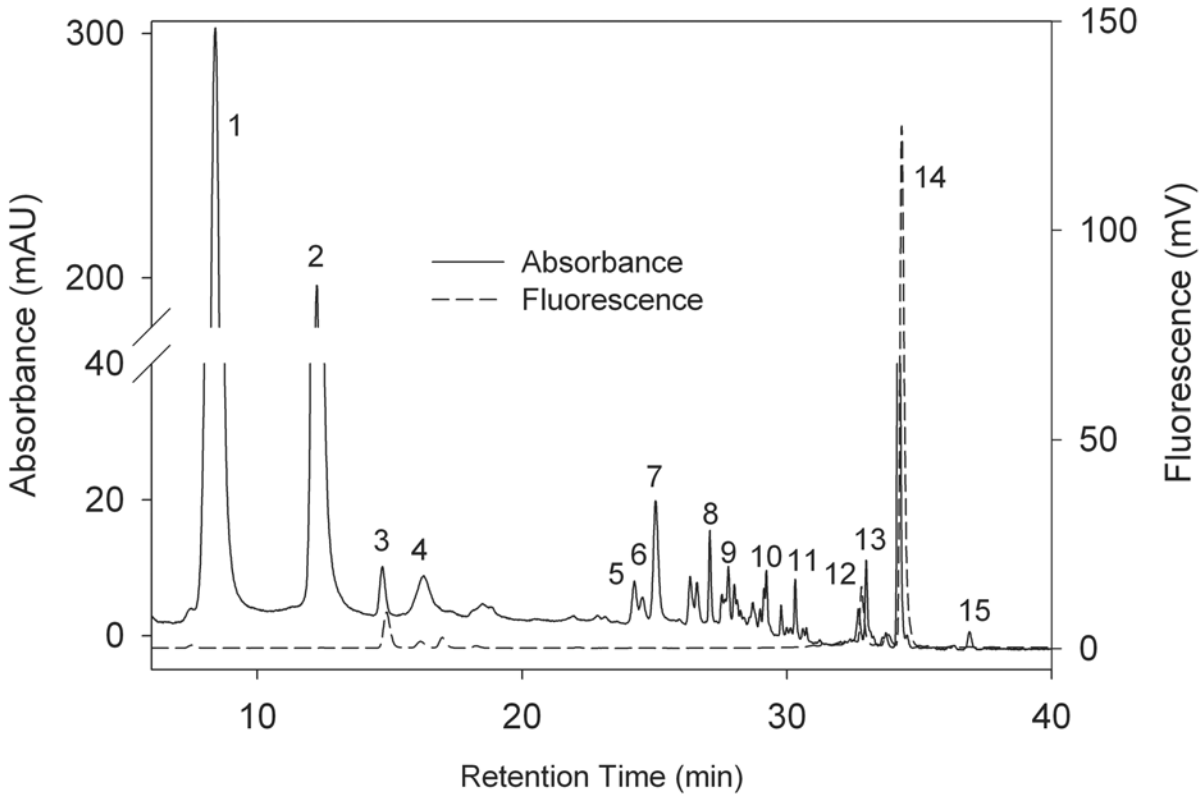

Figure 3.5 HPLC chromatogram of microbial mat pigments showing an absorbance channel (440 nm) and a fluorescence channel (Excitation 440 nm, Emission 650 nm).

Peaks are as follows: (1) red scytonemin, (2) scytonemin, (3) chlorophyllide-*a*-like, (4) scytonemin-related, (5) fucoxanthin, (6) oscillaxanthin-like, (7) 4-keto-myxol-2'-methylpentoside-like, (8) myxoxanthophyll, (9) unknown carotenoid (possibly okenone), (10) lutein (left shoulder) and zeaxanthin (main peak), (11) canthaxanthin, (12) chlorophyll *b*, (13) echinenone, (14) chlorophyll *a*, (15) β-carotene. Sample taken from Ward Hunt Ice Shelf Site B.

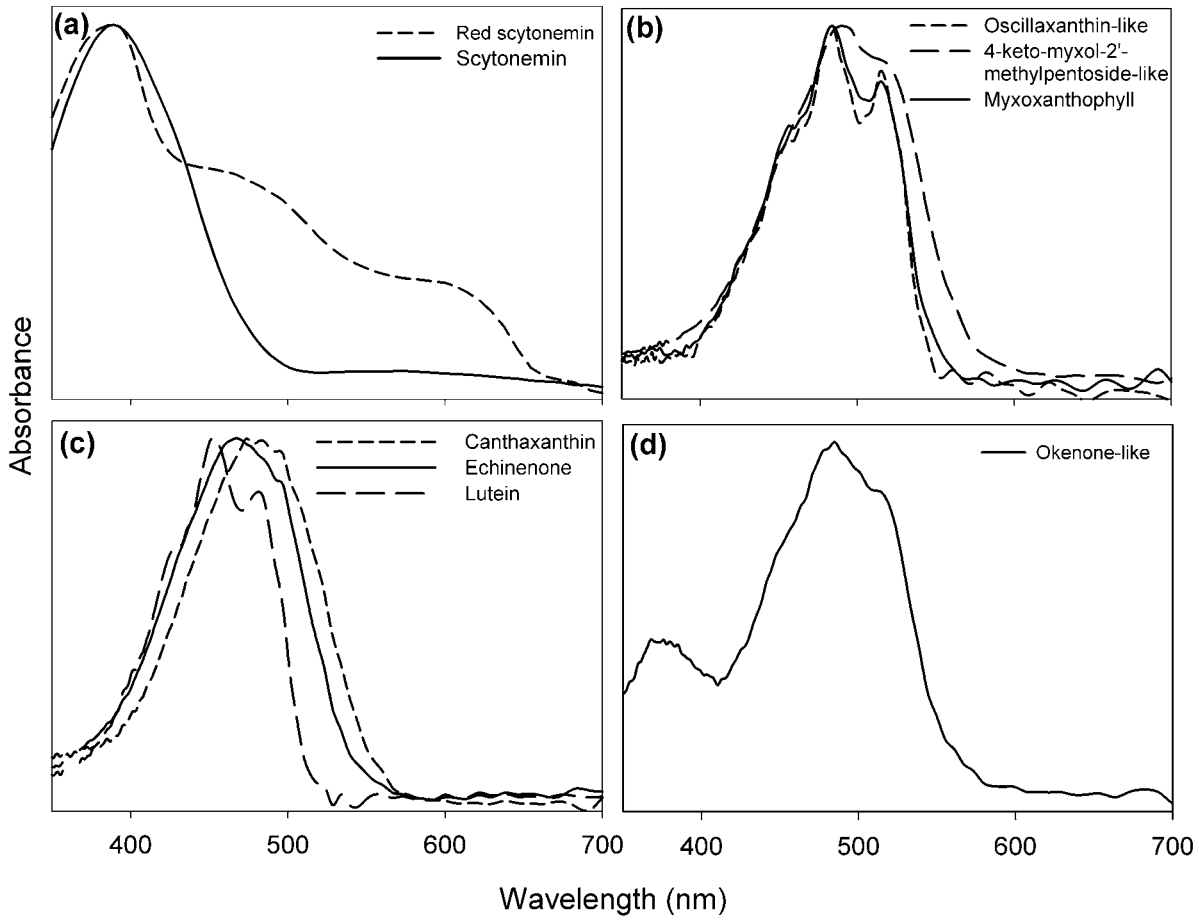

Figure 3.6 Spectra of pigments found in arctic ice shelf microbial mats.

A) The UV-A screening cyanobacterial sheath pigment scytonemin and its reduced form, red scytonemin. B) Cyanobacterial glycosides oscillaxanthin, myxoxanthophyll and a related pigment tentatively identified as 4-keto-myxol-2'-methylpentoside. C) Carotenoids lutein, canthaxanthin and echinone commonly found in the microbial mats. D) A bacterial carotenoid tentatively identified as okenone.

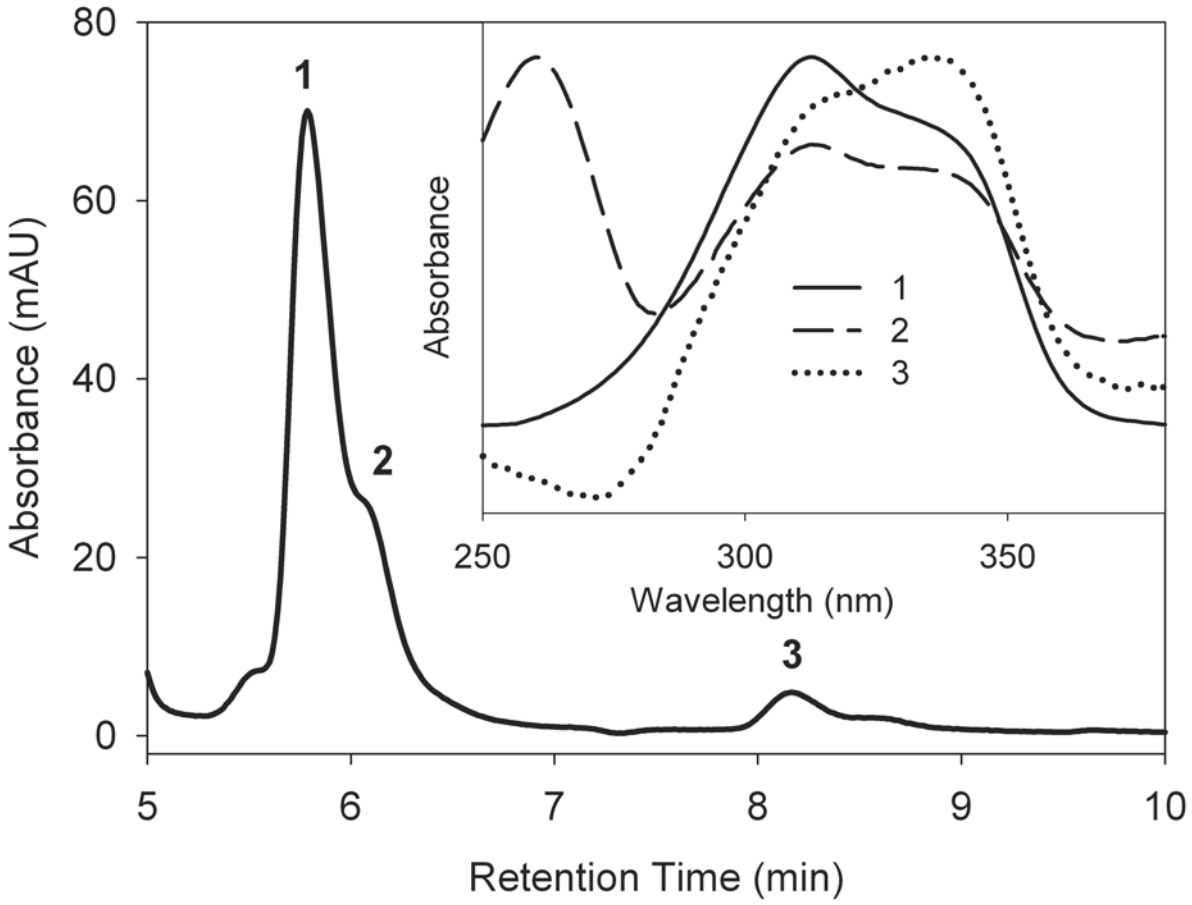

Figure 3.7 HPLC chromatogram of microbial mat oligosaccharide mycosporine-like amino acids showing the absorbance at 310 nm.

The inset shows the spectra of typical MAA fractions. Peaks are (1) the primary OS-MAA fraction, (2) an OS-MAA fraction with varying absorbance at 268 nm and (3) an OS-MAA whose 312 and 335 nm chromophores were found to be in different proportions relative to the previous peaks.

Chapitre 4 Microbial habitat dynamics and ablation control of the Ward Hunt Ice Shelf

4.1 Résumé

La plate-forme de glace Ward Hunt (83º02'N, 74º00'W) est un plateau formé de 40 m d'épaisseur de glace qui occupe une grande baie le long de la côte la plus septentrionale du Canada. Environ 10 % de sa surface est couverte par des sédiments qui fournissent un habitat à diverses communautés microbiennes composées principalement de cyanobactéries. Les assemblages forment une matrice organo-sédimentaire (tapis microbien) composée de cyanobactéries tolérantes au froid et de plusieurs autres organismes. Nous avons étudié les propriétés environnementales (la température, l'éclairement, la conductivité et la concentration en sels nutritifs) de l'habitat microbien et l'effet des tapis microbiens sur la morphologie de la plate-forme de glace. En comparaison à la neige et à la glace adjacentes, les tapis microbiens ont un faible albédo, ce qui entraîne la production d'eau de fonte et porte la saison de croissance à 61 jours, contrairement à seulement 52 jours lorsque les températures moyennes sont au-dessus de 0 ºC. De grands pics de salinité ont été observés près des tapis lors des épisodes de gel et de dégel. De plus, les colonnes d'eau de presque la moitié des étangs de fonte étaient stratifiée. Les concentrations en sels nutritifs dans les tapis microbiens étaient jusqu'à deux ordres de grandeur plus élevées que celles mesurées dans la colonne d'eau, ce qui souligne la différence entre le micro-environnement des tapis microbiens et les propriétés globales du cryo-écosystème. La perte moyenne de masse de la surface de la glace à notre site couvert de tapis microbiens était 1.22 m par an, ce qui est deux fois plus élevées que les valeurs mesurées sur le secteur voisin de la plate-forme de glace, où les tapis étaient moins répandus. La contribution des tapis microbiens à la diminution de la surface de la plate-forme de glace a montré que les agrégats microbiens cohésifs piègent et stabilisent le sédiment, ce qui réduit l'albédo et influencent la morphologie de la surface de la plate-forme de glace.

4.2 Abstract

The Ward Hunt Ice Shelf (83º02'N, 74º00'W) is a ~ 40 m thick ice feature that occupies a large embayment along Canada's northern-most coast. Sediments cover 10 % of its surface and provide a habitat for diverse microbial communities. These assemblages form an organo-sedimentary matrix (microbial mat) composed of cold-tolerant cyanobacteria and several other types of organisms. We investigated the environmental properties (temperature, irradiance, conductivity and nutrient concentration) of the microbial mat habitat and the effect of the microbial mats on the surface topography of the ice shelf. The low albedo of microbial mats relative to the surrounding snow and ice encouraged meltwater production, thereby extending the growth season to 61 days despite only 52 days with mean temperatures above 0 ºC. We found large excursions in salinity near the microbial mat during freeze-up and melt, and 54 % of all ponds sampled had conductivity profiles indicating stratification. Nutrient concentrations within the microbial mats were up to 2 orders of magnitude higher than those found in the water column which underscores the differences between the microbial mat microenvironment versus the overall bulk properties of the cryo-ecosystem. The average ice surface ablation in the microbial mat-rich study site was 1.22 m per year, two times higher than values measured in areas of the ice shelf where mats were less prevalent. We demonstrate with topographic surveys that the microbial mats promote differential ablation and conclude that the cohesive microbial aggregates trap and stabilize sediment, reduce albedo, and thereby influence the surface morphology of the ice shelf.

4.3 Introduction

Early explorers on the Greenland Ice Cap noted the presence of sediment and microbiota, and suggested that these communities could absorb heat and accelerate mass wasting. A. E. Nordenskjöld stated in 1870 that: "in the above-mentioned powder, a brown polycellular alga, which, small as it is, together with the powder and certain other microscopic organisms by which it is accompanied, is the most dangerous enemy to the mass of ice, so many thousand feet in height and hundreds of miles in extent" (Leslie, 1879). Since that time many studies have noted that microbiota on or within ice cause reduced albedo and could thereby accelerate the melting of sea ice (Blanck *et al.*, 1932), river ice (Brandt, 1931) and glaciers (Adams, 1966; McIntyre, 1984; Takeuchi *et al.*, 1998; Fountain *et al.*, 2004), although direct tests of this biotic control of the physical environment are generally lacking.

A related "inversion of relief hypothesis" was described anecdotally on ice islands (T-3 and ARLIS II) that calved from ice shelves along the northern coast of Ellesmere Island. Smith (1961) noted the dynamic nature of their surface topography and described a cyclical development of surface forms in which differences in surface-cover albedo lead to successional reversals in relative surface elevations. These and related observations (Smith, 1964; Schraeder, 1968) suggested that depressions fill with water or snow, freeze-up over winter and this ice remains resistant to ablation the following summer due to its relatively high albedo, with sediment acting as a driver of differential ablation. The underlying mechanism of ablation control has not, however, been tested.

The Ward Hunt and Markham Ice Shelves (Figure 4.1) are the easternmost of 5 major ice shelves in the Canadian High Arctic. They were formed by the *in situ* accretion of marine and meteoric ice between 4500 and 3000 years ago (Jeffries, 2002). The accumulation of sediments on the surface of these ice shelves has provided a habitat for diverse consortia of micro-organisms. These assemblages are dominated by filamentous oscillatorian cyanobacteria, but also contain diatoms, green algae and heterotrophic bacteria (Mueller *et al.*, 2005b) that together make up a loosely-cohesive microbial mat. These microbiota

tolerate the extreme conditions in their environment including the combined stresses of high salinities and low water activity during winter as well as high solar irradiance and near-freezing temperatures during the melt-season (Mueller *et al.*, 2005a). Over large scales, ice shelves appear to be immutably frozen in time and space, yet at the microhabitat scale the physico-chemical environment is potentially dynamic. Spatio-temporal variations in irradiance, temperature, salinity and nutrient concentrations at the scale of the microbial mats have implications for the productivity and survival of microbiota. To date, there is a paucity of information regarding the environmental characteristics of microhabitats on Northern Hemisphere ice shelves making it difficult to evaluate the limits to life in this extreme ecosystem. While environmental conditions may impinge on biological activity on these ice shelves it is also likely, as Nordenskjöld pointed out, that the microbiota have some capacity to influence the energy balance on the ice shelf and thereby alter the physical structure of their surroundings.

Our primary objectives in the present study were: (1) to quantify the physico-chemical environment of an ice shelf ecosystem at the scale of the microbial mats and to address the hypothesis that the microbiota exist in conditions that differ from those more generally found on the ice shelf, and (2) to test the 'inversion of relief' hypothesis put forward by Smith (1961) with quantitative survey and ablation data from two consecutive summers on the Ward Hunt Ice Shelf. We further developed this hypothesis by considering that the microbial mat exerts a stronger influence on the ice shelf ablation than abiotic, inorganic sediments.

4.4 Methods

4.4.1 Study site

Our study sites were established in a marine ice area on the Ward Hunt Ice Shelf and on the Markham Ice Shelf (Figure 4.1). These areas have a high coverage of surface sediment and have thick, luxuriant microbial mats, often with an orange-red surface layer. The mats are found both underwater (benthic) and above the water line (emergent). Less developed mats are also found in these locations and were often observed in cylindrical meltholes in the ice surface (cryoconite holes).

4.4.2 Micro-habitat climate

An automated climate station for micro-habitat environmental measurements was erected at the beginning of August 2001 at the Ward Hunt Ice Shelf study site (83º04.987'N, 74º25.277'W; Figure 4.2). Climatological data were averaged hourly by a CR10X datalogger, which was later augmented by an AMT25 multiplexer (Campbell Scientific, Logan Utah). Key variables were air temperature (Campbell Scientific, 107 thermistor shielded with a 6-plate Gill screen), downwelling photosynthetically active radiation (PAR), upwelling PAR (both LI-190SA Li-Cor, Inc., Lincoln, NE) and an underwater PAR sensor (Li-Cor, LI-192SA), that was placed just above the microbial mat surface. During the summer field seasons of 2002 and 2003, an anemometer (RM Young, 05103-10) was also installed. The station's 3 m-long supports were periodically re-installed to counteract ice ablation, therefore instrument (radiometers, air temperature and anemometer) heights varied between 1.50 and 2.60 m above the ice shelf surface. During the summer of 2002 and 2003, the anemometer shadowed the radiometers (Figure 4.2c) at certain times of the day necessitating the removal of affected data (< 1 hour per day).

To record dates of freeze-up and thaw plus temperature minima in microbial mats in areas adjacent to the climate station, thermistors (Omega 44033, Omega Engineering Inc., Stamford, CT) and self-contained temperature loggers (Stowaways, Onset Computer Corporation, Bourne, MA) were buried in microbial mats over winter. Microbial mat thermistor and Stowaway temperatures in a stirred ice bath agreed within ± 0.2 ºC which surpassed their rated accuracy of ± 0.1 ºC and ± 1.2 ºC, respectively.

In 2002, an XR-420 CTD datalogger (RBR Ltd., Ottawa) was installed 1-2 cm above the surface of microbial mat at the bottom of a meltwater pond at a depth of 42 cm and set to log temperature and specific conductivity (specific to 25 ºC) every 30 minutes. Two Stowaway temperature loggers were placed along a tether at depths of 20 and 30 cm between the CTD instrument and a post at the pond edge. These instruments were left in place over winter to record the progression of the freezing front and the change in pond water conductivity just above the microbial mat surface. The CTD temperature and conductivity accuracy was rated at ± 0.002 ºC and ± 0.003 mS cm^{-1}, respectively.

Spot measurements of albedo were taken at 50, 100 and 150 cm above representative surfaces on the Markham and Ward Hunt Ice Shelves using a Li-Cor, LI-1400 datalogger and 2 LI-190SA PAR sensors mounted on a leveled rod. This setup was also used to obtain albedo values from a helicopter that flew over representative ice surfaces at a constant altitude of 130 m.

4.4.3 Water column and microbial mat profiles

Water column profiles of conductivity and temperature were taken using a portable instrument (pH/Con 10 Series, Oakton Instruments, Vernon Hills, IL). If present, ice cover was carefully removed to allow access while minimizing water column disturbance. A variety of small cryoconite holes to medium sized meltponds on the Ward Hunt and Markham Ice Shelves were profiled at an interval of 5 to 10 cm. A stratification index was calculated by dividing the bottom water conductivity by the surface water conductivity to allow a direct comparison of the water column stratification between each profile.

Microbial mats were profiled using a DO-166-NP dissolved oxygen needle probe and a PHM-146 micro mono pH electrode as well as an ISM-146 chloride ion selective micro electrode, with a DJM-146 micro double junction reference electrode (Lazar Research Laboratories Inc., Los Angeles, CA). Profiles commenced at the microbial mat surface in 2 types of micro-habitats: a cryoconite hole with loosely-cohesive mats overlain by 8 cm of water and a thick emergent mat with an orange pigmented surface layer that was saturated with water. For dissolved oxygen concentration it was assumed that microbial mats overlain by water were at 1 ºC and mats not overlain by water were at 5 ºC. The vertical spatial resolution of the probes was up to 0.4, 0.3 and 1.5 mm for pH, chloride and dissolved oxygen, respectively. The electrodes were lowered into the mat with a micromanipulator at intervals of 0.62 mm.

4.4.4 Nutrient concentrations and isotopic ratios

The meltwaters from several small ice shelf ponds and cryoconite holes with benthic microbial mats were sampled for nutrient analysis. These ponds were then pumped dry, the microbial mats were lifted out of the holes and gently compressed between two clean

nesting plastic containers. Expressed microbial mat pore water was then collected for nutrient analysis (Vincent *et al.*, 1993a; Villeneuve *et al.*, 2001). Microbial mats that were not overlain by water (emergent mats) were also sampled in the same manner. Nutrients (NH_4^+-N, NO_3^--N, NO_2^--N, soluble reactive phosphorus (SRP), dissolved organic and inorganic carbon (DOC and DIC), total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) were determined from filtered (cellulose acetate, 0.2 μm) water samples by the National Laboratory for Environmental Testing (NLET), Burlington, ON, Canada. Methods included automatic colorimetry for total phosphorus (stannous chloride), SRP (ammonium molybdate/stannous chloride), total nitrogen and ammonium (indophenol) and nitrate/nitrite (cadmium reduction). DIC and DOC were determined by infrared gas analysis and by UV digestion followed by infrared gas analysis, respectively. Sample water was also filtered through GC-50 filters (GF/C equivalent, AMD Manufacturing, Mississauga, ON) to remove particulates, and the filtrate was preserved in amber glass bottles for chromophoric dissolved organic matter (CDOM) absorbance determinations at 320 nm by spectrophotometry on a Cary 300 Bio UV–Vis spectrophotometer (Varian, Mulgrave, Australia). The absorption coefficient of CDOM was calculated using the equation of Kirk (1983): $a_{CDOM} = 2.303\ (A_{320nm})/r$, where the a_{320nm} is the absorption coefficient at 320 nm (a_{CDOM}; in units of m^{-1}), A_{320nm} is the absorbance at 320 nm and r is the path length of the measurement cell. CDOM fluorescence data were obtained using a Cary Eclipse Spectrofluorometer with an excitation at 370 nm and emission wavelengths of 450 and 550 nm. Absorption at these wavelengths within the measurement cell was found to be negligible. The McKnight Ratio (fluorescence index) was calculated as the fluorescence at 450 nm divided by the fluorescence at 550 nm (McKnight *et al.*, 2001).

Microbial mats from a variety of small to medium sized cryoconite holes were sampled and frozen for transport to Quebec City. They were then acidified by fuming with 37 % HCl, to remove inorganic carbon, lyophilized and analyzed for carbon and nitrogen isotopes on an isotope ratio mass spectrometer (Fisons Instruments, model VG Prism Isotech) by Delta Lab, Geological Survey of Canada, Quebec City. Isotopic data were expressed in delta notation relative to standards of carbon (PeeDee Belemnite) and nitrogen (Atmospheric N). As an index of sample heterogeneity and analytical error, triplicate analysis of two samples yielded standard errors of 0.14 and 0.05 ‰ for carbon and nitrogen, respectively.

4.4.5 Ice ablation, snow cover and topographic surveys

In 2002, six ablation stakes were drilled into the ice surface surrounding the climate station. At each site visit, measurements were taken from the top of each pole to the ice surface, taking care to average out micro-topographic variations in the ice. Ice ablation was converted to water equivalent (w eq) ablation by multiplying ice ablation by 0.9 (Braun *et al.*, 2004). Two thermocouple arrays with 10 cm spacing between thermocouples were placed in contrasting locations (a plateau and a hollow) to assess differences in over-winter snow depth using thermal response to determine snow-cover presence or absence.

The 26 x 43 m area defined by the ablation stakes was surveyed, using a Wild-Heerbrugg T-1 optical theodolite and stadia rod, between August 4 and 6, 2002 and again on July 27 and 28, 2003. The tripod was re-leveled repeatedly due to its melting into the ice, creating closure errors that were on the order of 10 cm horizontal and 1 cm vertical. Topographic data (138 points in 2002, 291 points in 2003) were placed in the same Cartesian coordinate system, using one of the ablation stakes as an arbitrary datum. Both the surfaces were gridded by linear kriging to 108 x 65 grid nodes (Surfer 7.0, Golden Software, Golden, CO) and the modeled 2003 surface was subtracted from the modeled 2002 surface to identify regions of greatest ablation and to calculate the total volume of ice lost. The modeled surfaces in both years resembled the overall topographic pattern, however, due to kriging interpolation and some under surveyed areas, the surfaces do not accurately portray hydrological gradients. This was exacerbated by the ability of water to erode vertical slots into the ice. In this paper, we define surface lowering as the height difference between the 2003 ice surface and the 2002 ice surface. For the surveyed data, net ablation refers to the loss of water equivalent mass (assuming an ice density of 0.9 g cm^{-3}) between these two years and accounts for the presence of liquid water in the pond, even though advective gains and losses were not monitored.

The dominant surface cover types (ice, microbial mat, snow and water) were mapped using survey notes and photographs and were recreated in ArcMap 8.0 (ESRI Inc., Redlands, CA) by digitizing polygons referenced to survey points. Note that this characterization does not provide information on subjacent cover types. For example, the surface-cover-type water may refer to a pond with a benthic mat and/or a bare ice bottom. By ‘snow’ we mean a

highly reflective surface crystalline layer, that may be derived from snowfall or from the candling of pond ice. The change in cover type between 2002 and 2003 at each grid node was also determined and these data were used as levels in a one-way ANOVA on ranks (data were not normally distributed) of cover-type versus elevation at each grid node (SigmaStat, 3.0, SPSS Inc., Chicago).

In 2004, 30 ablation stakes were installed on the Ward Hunt Ice Shelf. The stakes were placed in clusters of six, 50-100 m apart at 5 locations (Figure 4.1). One of these clusters (B) was located near the climate station. Cluster A was located in a meteoric ice area (region where the surface exposed ice was derived from snow and/or rain) near stakes measured by Braun *et al.* (2004). Clusters C and D were located farther from land in meteoric ice areas whereas cluster E was located in a marine ice area in the southern portion of the Ward Hunt Ice Shelf. These stakes were re-measured in August 2005 following the methods described above. The interval between measurements was 362 days (clusters A and B) or 363 days (clusters C, D and E).

4.5 Results

4.5.1 Micro-habitat climate

A year-long (August 2001 to August 2002) comparison between air temperature and microbial mat temperatures indicated that all the microbial mats were encased in ice and/or snow through most of the year, since their temperatures were relatively constant and less extreme than air temperatures (Figure 4.3a). Over-winter mat temperatures were relatively stable, reaching an average minimum of -16.9 ºC (SE = 0.46) during April 2002, while mean daily air temperatures fell to -44.5 ºC in February, 2002 (Figure 4.3a). Dates of freeze-up and thaw for each instrumented microbial mat are given in Table 4.1 and the freeze-up and thaw of one microbial mat in 2001-2002 is shown in Figure 4.3b and c. Delays in mat freeze-up and thaw, relative to mean daily air temperatures, illustrate the thermal buffering effect of the high heat capacity and the latent heat of fusion for the water and snow/ice that envelop this ecosystem (Figure 4.3b and c). During summer months, this thermal buffering prevented mat temperatures from rising substantially above 0 ^{o}C. In 2001-2002, the microbial mats spent an average period of 300 (SE = 10.6, n = 3) days

frozen over winter, which compares to an average frozen period of 317 (SE = 4.0, n = 7) days in 2002-2003 (Table 4.1). From these observations we inferred growing seasons (365 minus the number of days below 0^{o} C) of 65 and 48 days. These inferences are reasonable given an observed melt period of 61 days in 2002.

The surface albedo at the climate station was monitored between August 2002 and 2003. Major increases and decreases in albedo indicated the onset of substantial snow covering the microbial mats in September and the onset of snowmelt in July (Figure 4.4). Spot measurements of albedo over various surface cover types and sky conditions are given in Table 4.2. The lowest albedos were measured over microbial mat and gravel, followed by water surfaces (especially those underlain by microbial mats or gravel), whereas snow consistently gave the highest albedos. Ice albedos were found to be variable depending on the amount and distribution of candling and sediment cover. The albedo of some surfaces doubled between 100 and 150 cm above the surface in clear sky conditions due to the inclusion of highly reflective snow and ice into the sensor's field of view. However, there were no differences between measurements at 50 and 100 cm.

The underwater PAR sensor at the microbial mat surface recorded relatively high irradiances until early September 2001 when snow likely covered the frozen pond surface (Figure 4.5). Microbial mats in this particular meltwater pond were covered by ice until at least early September when the PAR sensor wire was severed. Microbial mats were often observed to be covered by ice with a 5 to 10 cm air space directly above them, which reduced irradiances to 1.2 - 56 % of the incoming PAR (average = 15 %), based on the July and August 2002 data presented in Figure 4.5. This ice covering usually candled over the summer months and differences in PAR received under this covering may have been influenced by light piping through candled ice and solar zenith angles. The ice cover at nearby sites eventually collapsed often exposing the microbial mats to direct sunlight.

4.5.2 Conductivity

From the topographical survey data and water depth measurements, the meltwater pond that contained the conductivity and temperature datalogger was 55 m^2 in planar surface area and 9.4 m^3 in volume on August 11, 2002. At this point, the specific conductivity was 5.7 mS

cm^{-1}, which was typical of other measurements taken during the 2002 melt season (Figure 4.6). After 398 freezing degree-days, the first Stowaway froze into the ice on October 8, 2002 at -0.32 ºC and at this time the bottom water specific conductivity was 10.2 mS cm^{-1} and the volume of liquid water in the pond was estimated at 2.1 m^3. The water surrounding the second Stowaway froze on October 25, 2002 after an additional 242 freezing degree-days. The pond water was then an estimated 0.6 m^3 and the bottom water specific conductivity and temperature were 17.7 mS cm^{-1} and -0.65 ºC, respectively. The pond froze completely on October 30, 2002, after a further 106 freezing degree-days, at the elevated conductivity of 27.0 mS cm^{-1} and a temperature of -1.26 ºC (Figure 4.6). We assume that the rapid drop in conductivity after this maximum is an artifact associated with the presence of ice within the torus, which reduced the flow of electrons. Conductivity was therefore reduced to a constant over-winter value of -1000 when ice completely encased the instrument (see also Hawes *et al.*, 1999).

4.5.3 Water column and microbial mat profiles

Vertical stratification in conductivity (stratification index > 1.1) was observed in 54 % of water column profiles taken on the Ward Hunt and Markham Ice Shelves. There was a significant difference between the stratification indices of ice-covered ponds versus non-ice covered ponds (Mann-Whitney U = 204, $p < 0.001$). The depth of each pond was also a suitable predictor of water column stratification when the ice cover was taken into account (Figure 4.7: Multiple regression: Stratification Index = -2.192 + (0.101d) + (3.772i), where d is depth of water column in cm and i is the presence of an ice cover, 1 or 0, $R^2 = 0.35$, $p < 0.001$). Temperatures remained relatively constant throughout the water columns, with temperature rarely ~0.5 ºC higher in the bottom waters (but in one instance increasing by 1 ºC).

The microbial mat profiles of dissolved oxygen, pH and chloride typically showed little variation with depth and no evidence of discrete layering (Figure 4.8). There was a decrease in dissolved oxygen from the top of the mat to the bottom, consistent with the lack of photosynthesis and increased respiration in lower levels. pH increased abruptly by two units at the bottom of one of the cryoconite mats. Chloride concentrations were the same

with depth throughout the mats, however chloride levels contrasted between mat types. Using an empirical relationship between ice shelf meltwater chloride levels and conductivity (Cond = 0.02436 + 0.00374(Cl^-), R^2 = 0.98, n = 25, $p < 0.001$) where Cond = conductivity (mS cm^{-1}) and Cl^- = chloride (mg l^{-1}) we estimate that the conductivities in the cryoconite hole and emergent mats differed by three orders of magnitude from 0.05 ± 0.001 (cryoconite) to 64 ± 0.56 mS cm^{-1} (emergent).

4.5.4 Nutrient concentrations and isotopic ratios

The differences between nutrient concentration in microbial mat pore water and the overlying water column are given in Table 4.3. The mats had on average three orders of magnitude more DIC and NH_4^+-N than the water column. The remaining variables were two orders of magnitude more concentrated in the microbial mat than in the overlying water. However, there was a high degree of variability in mat pore water nutrient concentration, particularly in the emergent mat, relative to the water column nutrient concentration. Consequently, the differences in nutrient concentrations between emergent and benthic mat pore water were not significant (One-way ranked ANOVA, Dunn's post-hoc test, $P > 0.05$), while differences were significant between the benthic mat and the water column as well as between the emergent mat and the water column, with the exception of NH_4^+-N, NO_3^--N and SRP. Differences in nitrate and nitrite levels were not tested for significance due to data below detection limits.

The benthic mat pore water had a significantly higher CDOM content than the overlying water, as indicated by the analysis of a_{CDOM} values (Mann-Whitney test, $p = 0.008$). The McKnight Ratio derived from fluorescence analysis indicated that CDOM composition was similar between the benthic mat pore water and overlying water (averages = 1.27 (SE = 0.12) and 1.29 (SE = 0.12), respectively). This ratio differentiates between potential sources of organic matter and in this case suggests complex, typically terrestrially-derived, fulvic acids were present in the samples (McKnight *et al.*, 2001).

Microbial mats had $\delta^{13}C$ values ranging from -22.30 to -16.63 ‰ (mean = -18.95, SE = 0.50, n = 16) and $\delta^{15}N$ values ranging from -1.13 to 0.39 ‰ (mean = -0.61, SE = 0.35, n = 16).

4.5.5 Snow accumulation and ablation

Snow accumulation and ablation were compared in a hollow versus a plateau near the climate station. At the time of sensor installation, the hollow was exposed, with a microbial mat surface cover, whereas the plateau was composed of highly reflective ice that covered the mats. In the hollow, 0.30 ± 0.05 m of ice had ablated over the autumn (up to November 24) and a net accumulation of 0.60 ± 0.10 m of snow occurred by March 10, 2003. At this time, the station resumed measurements with the return of the sun to power the solar panels. Between mid-March and July 18, the surface lowered by 0.65 ± 0.05 m (average spring/early summer surface lowering = 0.5 cm d^{-1}). On the plateau, 0.10 ± 0.05 m of ablation occurred between August and November and there was no net accumulation of snow (0.00 ± 0.05 m) between November and March. However, over the four month period from mid March to mid July 1.35 ± 0.05 m of ice was lost (average spring/summer surface lowering = 1 cm d^{-1}).

4.5.6 Ice shelf ablation

Considerable ablation took place on the ice shelf during the study, in addition to morphological evolution and cover type changes (Figure 4.2). Over one year (364 days), an average loss of 1.22 m of ice was recorded, which is equivalent to 1.10 m water equivalent. Over a third (0.48 m) of this ablation occurred during the 2003 summer field season, 0.43 m was lost between the field seasons (at an average daily net loss of 0.13 cm d^{-1}) and the remainder was lost during the first 10 days of August 2002. During the 2002 field season, ice ablation was 2.9 cm d^{-1} (SE = 0.26) and the ablation rate was slightly higher (3.6 cm d^{-1}, SE = 0.15) during the 2003 field season (Figure 4.9). However, it should be noted that the 2003 measurements were taken earlier than in 2002.

The ice shelf ablation stake network installed in 2004 allowed the measurements at the climate station to be compared with sites elsewhere. Between 2004 and 2005, the climate station site (cluster B) experienced an average of 1.04 m (SE 0.17 m) of ablation (0.94 ± 0.15 m w eq). Ablation rates were significantly ($p \leq 0.05$) higher at the marine ice sites (B, E: mean = 0.75 m, SE = 0.19 m) versus the meteoric ice sites (A: mean = 0.42 m, SE =0.05 m; C: mean = 0.22 m, SE = 0.06 m, D: mean = 0.22 m, SE = 0.04 m) as indicated by a

Holm-Sidak pairwise test (with the exception of the comparison between site A and E, $p = 0.06$).

4.5.7 Ice shelf topographic surveys

The topographic surveys in 2002 (Figure 4.10a) and 2003 (Figure 4.10b) indicated that a volume of 1270 m^3 of ice was lost over the 1103 m^2 area of the survey (Figure 4.10c). However, this estimate was partly offset by the presence of liquid water in the pond in 2002 (13.1 m^3) and in 2003 (39.6 m^3) bringing the ablation (including net liquid water advection) estimate down to 1243 m^3 (or 1.13 m $\approx$ 1000 kg m^{-2}).

The elevation range in 2002 was between 9.11 and 10.67 m, while in 2003 this range narrowed to between 8.15 and 9.63 m. The amount of surface lowering between 2002 and 2003 was on average 1.15 m and varied substantially across the site, from 0.43 to 2.01 m (Figure 4.10c). It is this differential surface lowering that could either act to exaggerate the existing topography (derived from the previous summer), or conversely, could act towards inverting the relief between successive summers. If there were no variation in surface lowering between measurements then the existing relative topography would be maintained. According to the inversion of relief hypothesis, differential albedo ensures that by mid-summer, the high albedo cover types will remain at higher elevations (Table 4.2; Figure 4.10). The exception to this general observation is that water, under the influence of gravity, will typically occupy the lowest elevations, forming ponds (e.g., Figure 4.10a feature *1*). Two 4-level ranked ANOVAs confirmed that in both 2002 and in 2003 snow occupied the highest elevations, followed by ice, then mat, with water occupying the lowest elevations (all pairwise differences were significant, Dunn's post-hoc test, $p < 0.05$).

The principal driver of inversion of relief is the change in cover type from one summer to the next, which instigates differential ablation on the ice shelf. In areas covered with snow in 2002 that changed to mat cover (e.g., Figure 4.10a feature *2*), water cover (e.g., Figure 4.10a feature *3*), or ice (e.g., Figure 4.10a feature *4*) higher than average surface lowering was measured (see Figure 4.10c). The erosive nature of water was observed to also lower mat- and snow-covered surfaces substantially (e.g., Figure 4.10a features *5* and *6*), suggesting that the hydrologic regime can also drive the surface lowering pattern. One of

the changes in cover type associated with the least amount of surface lowering was water to snow cover (e.g., Figure 4.10a feature *7*), but low ablation also occurred in areas where cover type did not change (e.g., Figure 4.10a features *1* and *8*).

4.6 Discussion

Microbial mats were a significant component of overall cover at our study site on the Ward Hunt Ice Shelf. They were present over 23 % (2002) to 27 % (2003) of the survey site and, due to methodological differences, these figures were higher than the mat cover values of 13 to 17 % from a nearby point transect analysis (Mueller *et al.*, 2005b). The microbial mat environment contrasted markedly with bulk properties of the surrounding environment. This was observed both with regards to the climatology (irradiance and temperature) and the physical and chemical microenvironments (nutrient concentrations and conductivity). We observed an inversion of relief (Figure 4.2), and were able to quantify the extent of differential surface lowering (Figure 4.10).

4.6.1 Micro-habitat climate

The temperature of the microbial mats over time influences metabolic processes and can determine the overall microbial mat productivity. The high specific and latent heat of the meltwater combined with the low albedo of both the mat and the meltwater (Table 4.2) retard the freeze-up of the microbial mat relative to cumulative freezing degree days (Figure 4.3b). Over winter, snow and ice insulated the microbial mats thereby protecting them from extremely cold air temperatures, but also retarding melt out in the spring. Metabolic activity has been shown to occur at temperatures down to –20 ^{o}C, comparable to minimum temperatures we recorded in the ice shelf microbial mats (Rivkina *et al.*, 2000; Junge *et al.*, 2004), and it is likely that metabolic processes occur within the mats over winter, albeit at a minimal rate (Price and Sowers, 2004). The growth season, defined as the period of time when temperatures exceed ~0 ºC, is equal to 8.7 weeks or 16.7 % of the year. Given the moderately high rates of primary production within the microbial mats (64 mg C m^{-2} h^{-1}; Mueller *et al.*, 2005a), interannual variability in growth season is potentially important with regards to overall production over the entire ice shelf area that contains suitable microbial habitat (83 km^2; Mueller *et al.*, 2005b).

The snow accumulation and underwater (near-mat) PAR measurements suggest that microbial mats at the bottom of depressions can remain covered by iced firn or snow over an entire melt season, which supports the 'inversion of relief' hypothesis. The shading of the over-lying snow reduces PAR levels to 15 % of ambient, however this reduction in irradiance does not likely affect the productivity of microbial mats due to their demonstrated ability to acclimate to reduced irradiances both on the Ward Hunt Ice Shelf (Mueller *et al.*, 2005a) and the McMurdo Ice Shelf in Antarctica (Hawes *et al.*, 1999).

4.6.2 Conductivity

The high conductivity caused by brine exclusion during freezing (Figure 4.6) would probably have affected photosynthesis within the microbial mat since primary productivity in these mats was found to be 50 % lower at 29 mS cm^{-1} than at 0.1 and 2.9 mS cm^{-1} (Mueller *et al.*, 2005a). However, the heterotrophic bacterial productivity possibly suffered more from high conductivities, since experimental evidence shows a 3.4-fold reduction in heterotrophic bacterial production across this same range (Mueller *et al.*, 2005a). In contrast, Hawes *et al.* (1999) found that mat photoautotrophs on the McMurdo Ice Shelf readily acclimated to even higher salinities than we observed.

The relatively high conductivity measured here at the onset freezing and melt was also observed in Brack Pond on the McMurdo Ice Shelf (Hawes *et al.*, 1999). Freeze concentration was by a factor of 1.5 times relative to Brack Pond summer conductivity, 6 times for Fresh Pond (also on the McMurdo Ice Shelf) and 4.7 times for the pond in this experiment. The solute concentration at freezing depends greatly on the position of the conductivity sensor and the bathymetry of the pond, as well as the freezing rate, which determines the potential exclusion of salts from the growing ice cover. The heat capacity of this relatively large volume of water insured that the microbial mats in this microenvironment remained liquid long after other microbial mats in this study were frozen. Freezing of this particular pond was relatively slow, allowing for the rejection of a large proportion of the solutes within the water column. Thawing occurred far more rapidly in June (note the abrupt rise in temperature in Figure 4.6) and the specific conductivity was not as high (maximum = 20.6 mS cm^{-1}) relative to the conductivity during

freeze-up. This is probably due to the channeling of brine downwards away from the sensor at some point after October 30, or alternatively, it could be due to the percolation of low salinity meltwater from above prior to the complete thawing of the sensor.

4.6.3 Water column and microbial mat profiles

The observed water column stratification has implications for meltpond biology as it leads to a greater habitat differentiation between the water column and the benthic microbial mats. The stratification of small to medium meltponds on the Ward Hunt Ice Shelf likely occurs over time in the absence of wind mixing. The presence of ice covers and the depth of meltholes both act to reduce or prevent wind mixing and are therefore significant ($p < 0.01$) predictors of the stratification index (Figure 4.7). The wind speed over the period when measurements took place was under 5 m s^{-1}, except for the afternoon of August 4 (<10 m s^{-1}). All the ice-covered meltponds in lower right quadrant of Figure 4.7 (depth > 30 cm, stratification index < 8) were measured after this wind event. It is possible that these ice covers formed after wind induced mixing and the water columns had not completely re-stratified prior to measurement. The relative constancy of temperature throughout the water column suggests that solar heating of benthic material does not increase the temperature of bottom water, but rather melts ice. This is not the case in ponds on the McMurdo Ice Shelf, which have a very thick (~30 cm) sediment cover that insulate the subjacent ice (Issaac and Maslin, 1991). Bottom waters there regularly exceed 5 ºC and can be as warm as 11 ºC due to intense density stratification (Hawes *et al.*, 1999).

The electrode profiles of dissolved oxygen, pH and chloride of the mats on the Ward Hunt Ice Shelf highlight the differences between microhabitats. The high chloride concentration in the emergent orange mats is likely to reflect evaporative concentration of salts within the mat pore water. This high salinity within the emergent mats would reduce photosynthesis, relative to cryoconite holes, based on available bioassay data, yet it might favor photoautotrophs since photosynthesis may not decrease as much as heterotrophic productivity (Mueller *et al.*, 2005a). Furthermore, the emergent microbial mats are expected to be warmer than those in cryoconite holes, which has been noted to increase photosynthetic but not heterotrophic productivity (Mueller *et al.*, 2005a). Therefore, the

emergent mats may be a microhabitat that is conducive to the accumulation of organic matter due to minimal decomposition rates. Both types of microbial mats show a decrease in dissolved oxygen concentration, which suggests that the lower mat receives less light than the surface and is a zone where respiration is greater than photosynthesis. It was noted that the pH increased dramatically if the probe touched the ice at the bottom of the mat and it is possible that the bottom-most pH value in the cryoconite hole may be an artifact (Figure 4.8). Aside from this, the conductivity and pH profiles were featureless, which may reflect the loosely cohesive character of the mat. In this type of microbial mat, there were no macroscopic indications of defined strata with the exception of an orange surface layer up to 200 μm thick. This contrasts with a more layered mat type found in nearby Ward Hunt Lake on Ward Hunt Island (Villeneuve *et al.*, 2001; Bonilla *et al.*, 2005).

4.6.4 Nutrient concentrations and isotopic ratios

The relatively high concentration of nutrients within the microbial mats further illustrates how the microbial mat microenvironment is dissimilar from the rest of the ice shelf habitat. High microbial mat nutrient concentrations have been found in other locations including Ward Hunt Lake, adjacent to the Ward Hunt Ice Shelf (Villeneuve *et al.*, 2001) and the McMurdo Ice Shelf (Vincent *et al.*, 1993a). A comparison of the chloride concentrations in emergent (17000 mg l^{-1}) and benthic mats (7 mg l^{-1}; Figure 4.8) and the average water column chloride concentration on the Ward Hunt Ice Shelf (119 mg l^{-1}; Mueller *et al.*, 2005b) point to concentration of this conservative tracer in the emergent mats but not in the benthic mats. It is plausible that evapo-concentration may be partially responsible for elevated nutrient and chloride concentrations in emergent mats, in contrast with benthic mats where the process of nutrient concentration may be biologically mediated or influenced by the aeolian sediment flux.

It has been shown that benthic microbial mats can be effectively isolated from the water column nutrients due to a diffusion limited boundary layer and this may lead to deficiencies in DIC or other nutrients (Jørgensen, 1994), which would be exacerbated by water column stratification. The high nutrient and DIC concentration within microbial mat pore water on the Ward Hunt Ice Shelf, suggests that this microenvironment is carbon and nutrient-

replete. This view has been experimentally confirmed with microbial mat nutrient enrichment experiments in nearby Ward Hunt Lake (Bonilla *et al.*, 2005). Furthermore, there is no isotopic evidence of substantial carbon limitation on the Ward Hunt Ice Shelf as seen in benthic communities elsewhere (Turner *et al.*, 1994; Lawson *et al.*, 2004), although the water column and microbial mat pore water δ^{13}DIC remain unknown. The near-zero δ^{15}N signatures suggest that the nitrogen may be fixed by heterocystous cyanobacteria (Goericke *et al.*, 1994), which are known to exist within these mats (Mueller *et al.*, 2005b). It is also possible that the marine-derived ice in this locality contained sea water nitrate (+7.0 ‰; Wada *et al.*, 1981) and that the fractionation during uptake (Table 9.4 in Goericke *et al.*, 1994) led to an ultimate signature near 0 ‰ in the biomass.

The McKnight Ratio indicates that the CDOM within the microbial mats and in the pond water was either composed of complex molecules or is allochthonous (McKnight *et al.*, 2001). Terrestrial vegetation debris, such as *Salix arctica* leaves, has occasionally been observed within the ice shelf microbial mats but this input is unlikely to be large. The presence of other water-soluble compounds such as extracellular polymeric substances (EPS) and oligosaccharide mycosporine-like amino acids (OS-MAA), which are prevalent in the microbial mat and may mix into the water column, may be responsible for such low McKnight Ratios. Similarly, cellular contents such as DNA and amino acids, may be released into the water column due to cyanophage activity within these mats (Short and Suttle, 2005). An alternate hypothesis derived from observations of lake ice (Belzile *et al.*, 2002) is that complex fulvic acids may be differentially freeze-concentrated while less complex CDOM molecules would be incorporated within the ice and may be flushed out during spring melt.

4.6.5 Ice shelf surface mass balance

Past studies note the high interannual and spatial variability of snow cover on the Ward Hunt Ice Shelf (Hattersley-Smith and Serson, 1970; Serson, 1979). Using an assumed snow bulk density of 0.31 g cm^{-3} (Braun *et al.*, 2004) and our two snow depth measurements on the Ward Hunt Ice Shelf for the winter of 2002-3, we calculated a minimum accumulation of between 0.00 ± 0.015 and 0.186 ± 0.031 m w eq. This compares

with mean net winter surface accumulation values from previous Ward Hunt Ice Shelf data (mean = 0.10 to 0.17 m w eq, individual pole range 0.02 to 0.44 m w eq; Serson, 1979).

Our main study site was located in an area of exposed marine ice and was locally different from the main ice shelf where meteoric ice was observed at the surface. Marine ice covers 29 % of the surface of the Ward Hunt Ice Shelf, 86 % of Markham Ice Shelf and contains large amounts of sediment and microbial mats (Mueller *et al.*, 2005b). Braun *et al.* (2004) determined that the year 2002-3 had one of the largest negative mass balance on record for the Ward Hunt Ice Shelf (0.54 m w eq), from measurement of two ablation stakes in an area of meteoric ice to the east of Ward Hunt Island. The annual (net) surface mass balance recorded from our site for 2002-03 is 2 times higher than the ablation reported by Braun *et al.* (2004), and higher than past surface mass balance measurements on the Ward Hunt Ice Shelf. Previous measurements from individual poles ranged from 0.81 m of net accumulation to 1.04 m of net ablation (annual means ranged from +0.095 to –0.256 m w eq) between 1966 and 1976 (Serson, 1979). The difference in ablation between the meteoric and marine ice areas of the Ward Hunt Ice Shelf was also illustrated by data from 5 separate sites between 2004 and 2005. The original ablation network (positioned near site A in 1966) was not intended to be spatially representative of the entire ice shelf (Braun *et al.*, 2004). Nevertheless, our results indicate that ablation in marine ice areas can be twice as much as ablation at this original measurement site and over 4 times higher than in other meteoric ice areas (i.e., clusters C and D). We do not suggest that the microbial mats that are abundant in marine ice areas are solely responsible for the enhanced ablation that we observed, although they likely contribute to it. Rather, we suggest that marine ice areas on the Ward Hunt Ice Shelf may be partially instigated by local climatological differences from meteoric ice areas. For example, Walker Hill (450 m.a.s.l.) on Ward Hunt Island is a topographic barrier, which often disrupts layers of low-lying fog and stratus above our main study site, allowing direct solar radiation to penetrate to the ice surface (personal observation). The lack of net accumulation in marine ice areas keeps microbial mats at or near the ice surface, where they contribute to the overall surface lowering as well as to the cyclical inversion of relief via their relatively low albedo.

It is known that marine ice areas on the Ward Hunt Ice Shelf are replenished by the basal freeze-on of seawater (Crary, 1960). This is evidenced by the presence of marine invertebrates on the surface of the ice shelf that made their way through the ice via this ablation mechanism (Debenham, 1920). Using the 2002-3 ice ablation as a marine ice zone maximum rate and assuming an ice shelf thickness of 40 m, then marine sediments and invertebrates could be lifted to the surface of the ice shelf in as little as 33 years.

The Ward Hunt Ice Shelf is not glacially fed and its surface topography does not vary more than 7.5 m (Jeffries *et al.*, 1990). Therefore the concept of Equilibrium Line Altitude (ELA; defined as the altitude on a glacier where net surface ablation is zero) does not apply in the vertical sense to surface mass balance. Rather it exists horizontally, but on long time scales (> decadal), between regions of perennial surface mass loss (marine ice) and regions where surface accumulation takes place (meteoric ice). If the surface mass balance of the Ward Hunt Ice Shelf remains negative, this 'long-term horizontal equilibrium zone' will encroach on the meteoric ice regions, exposing more marine ice at the surface, as the overlying meteoric ice ablates. To compare with a characteristic glacial system in the High Arctic, the average (1960-2001) ELA for the White Glacier on Axel Heiberg Island (79 ºN) was 1100 m.a.s.l. and the elevation where the average net loss was equivalent to our 2002-3 measurement was at 500 m.a.s.l. (the terminus of the White Glacier is currently near 56 m.a.s.l.; Cogley, 2002).

4.6.6 Inversion of relief and the role of microbial mats

The observations obtained in this study allow an explicit test of the inversion of relief hypothesis. Two predictions follow from this hypothesis, and must be achieved to demonstrate that inversion of relief occurred on the ice shelf. Firstly, the hypothesis predicts a dynamic pattern of change over horizontal space, with a substantial shift in surface cover type between summers. Secondly, the hypothesis also predicts a consistency of vertical zonation that is associated with relative albedo and gravitational effects. Specifically, bright snow should be higher than less reflective ice, which in turn should be at a higher elevation than dark coloured mat, whereas water will drain downwards and will occupy the lowest elevations.

At our climate station site between surveys, the cover type changed at 42 % of the nodes. Although conditions were not conducive for a complete inversion of relief over this period (compare Figure 4.2b & c with Figure 4.2a & b), this change is substantial and is consistent with the first prediction of spatial dynamics. Using the data where cover class changed between surveys, the 2003 elevation data were grouped according to the cover type in 2003. The highest average elevation was for snow (9.1 m), followed by ice (8.9 m), then mat (8.8 m) and finally water (8.4 m). All pairwise comparisons between cover type elevations were significantly ($p < 0.05$) different with the exception of snow versus ice, which may reflect the low number of observations for snow in 2003. In addition, the same elevational zonation was identified in 2002 from the nodes where cover type changed. The highest average elevation for 2002 was snow (10.1 m), followed by ice (9.9 m), then mat (9.8 m) and finally water (9.6 m) consistent with the second prediction. All pairwise comparisons between cover type elevations were significantly ($p < 0.05$) different with the exception of ice versus mat. The only way that this elevational zonation can be preserved between two consecutive summers, despite the cover type change between measurements, is through the process of relief inversion as described by Smith (1961). We conclude that inversion of relief was occurring at our study site between the summers of 2002 and 2003, and influenced just under half of the icescape.

One factor that encourages the inversion of relief in this ice shelf environment is the tendency for microbial mats to slump downwards towards lower elevations, particularly when ice slopes become critically steep. The high salt content in emergent mats (Figure 4.8) will intensify ice melting, thereby lubricating the interface between microbial mat and ice. Slumping of microbial mats in a cohesive manner is likely enhanced by the biosynthesis of extracellular polymeric substances (EPS). This class of compounds acts to bind organisms to sediments as well as to each other and is an important component of microbial mats (Yallop *et al.*, 1994; Stal, 2003). Microbial mat EPS and the trichomes of filamentous cyanobacteria also act to trap and stabilize sediments thereby preventing their dispersion across the ice shelf environment by aeolian or hydrological processes. Ward Hunt Ice Shelf mats contain up to 24 % organic matter (D.R. Mueller, unpublished data) and are loosely cohesive, indicating the presence of EPS. Based on this evidence, we conclude that the EPS-stabilized microbial mats are likely to behave differently than purely

abiotic sediments and will thereby have a stronger influence the evolution of the ice shelf surface morphology than sediments alone.

The inversion of relief on ice appears to be sensitive to microbial mat cover and thickness. In the absence of mats or sediments there is no relief inversion and the existing topography is maintained or amplified. For example, old hummocks on a sediment-free multi year floe in the Arctic Ocean (81.5 to 84^{o} N), were shown to have 39 % less ablation than flat areas on the floe, suggesting that theses features are self perpetuating (Koerner, 1973). This is also the case for areas of meteoric ice on the Ward Hunt Ice Shelf, which are 7 % covered by microbial mats (Mueller *et al.*, 2005b). Ridges in these areas have slightly lower net ablation than the troughs (Serson, 1979). When a thin layer of sediment or microbial mat is present, conditions favour the inversion of relief. On the other hand, excessive inorganic debris can impede ice ablation due to insulation of the ice from both radiative and aeolian forcing (Schraeder, 1968). For example, in marine ice areas on the Ward Hunt and Markham Ice Shelves, microbial mats can accumulate to thicknesses in excess of 2 cm, which insulates the underlying ice and, consequently, the surface morphology includes features such as dirt cones (Sharp, 1949; Wilson, 1955). This provides an additional mechanism of biotic control of ice relief. Conversely, the inversion of relief is likely restricted to relatively thin mats that are less than the thickness required to fully insulate the underlying ice.

4.7 Conclusions

The temperature, radiation, conductivity and nutrient data reported here show that the microbial mat micro-habitat differs substantially from the bulk properties of the ice shelf ecosystem. In some respects, these microhabitats may be more clement for biological processes, with longer melt seasons, warmer over-winter temperatures and higher nutrient concentrations than the surroundings. However, depending on their location and time of year, microbial mats may experience sustained periods of low or high irradiance stress, and may be subjected to osmotic stress due to water column stratification, evaporation or freeze concentration.

Microbial mats can affect the physical ice shelf environment in such a way that favours their ongoing growth and ecological success. Mechanisms of physical-biotic coupling reduce mat albedo and include the trapping of sediments within the microbial mat matrix, the EPS stabilization of this matrix to prevent sediment redistribution, and mass-slumping of cohesive EPS-permeated mat towards water-filled depressions on the ice shelf surface, consistent with an inversion of relief. The accelerated ablation associated with the latter in marine ice areas of ice shelves benefit the microbial community by entraining more marine sediments and nutrients from below while also inhibiting surface mass balance gains and the accumulation of light-screening surface snow and ice.

4.8 Acknowledgements

We wish to acknowledge the financial and logistical support from the Polar Continental Shelf Project (this is PCSP/ÉPCP publication number 01005), a Discovery Grant and Scholarship from the Natural Sciences and Engineering Research Council, the Canada Research Chair in Aquatic Ecosystem Studies, ArcticNet, and the Northern Scientific Training Program. Field Assistance was provided by Katie Breen, Sébastien Roy, Jeffrey Kheraj, Denis Sarrazin, Alexandra Pontefract, Eric Bottos, Carsten Braun and Vicki Sahanatien. We thank Ladd Johnson and Wayne Pollard for the loan of equipment and Christine Martineau and Marie-Josée Martineau for laboratory assistance. We acknowledge the helpful comments of Carsten Braun, Dominic Hodgson and 2 anonymous reviewers.

Table 4.1 Freeze-up and thaw dates of microbial mats on the Ward Hunt Ice Shelf.

Year	Freeze-up date	Thaw date	Period below 0 °C (days)
2001-2002	August 31	July 18	321†
	September 7	June 23	289
	September 7	June 23	285
2002-2003	August 25	July 15	324
	August 26	July 24	332
	September 1	July 8	310
	September 1	July 11	313
	September 3	July 19	319
	September 7	July 6	302

Freeze-up and thaw was operationally defined as the date when the microbial mat temperature remained below 0 °C for the winter and when it rose above 0 °C for the summer, respectively. † denotes the microbial mat shown in Figures 4.3b and c.

Table 4.2 The albedo of various surface cover types on the Ward Hunt and Markham Ice Shelves.

Substrate	**Sky Conditions**			
	CLR	**FG**	**BKN AC**	**SCT AC**
Blue lake	0.31 (0.005)	0.33 (0.001)	-	0.60 (0.02)
Sediment on ice	-	0.26 (0.002)	-	0.37 (0.01)
Gravel	-	0.09 (0.001)	-	-
Marine ice	-	-	-	0.77 (0.03)
Mat	0.23 (0.03)	0.10 (0.001)	0.16 (0.004)	-
Climate station area	-	-	-	0.56 (0.01)
Pond underlain by mat	0.30 (0.04)	0.11 (0.001)	0.09 (0.002)	-
Snow	0.89 (0.04)	0.76 (0.003)	0.67 (0.02)	-

Measurement heights were at 100 cm for clear sky conditions (CLR), fog (FG) and broken altocumulus (BKN AC) and 130 m for scattered altocumulus (SCT AC). Averages of 5 to 55 measurements (± SE).

Table 4.3 Nutrient and CDOM concentrations of ice shelf meltwater and microbial mat pore water.

Nutrient/Constituent	Overlying Water	Benthic Mat	Emergent Mat
DIC (mg l^{-1})	0.76 (0.051)	108 (25)	203 (116)
DOC (mg l^{-1})	0.26 (0.024)	60 (13)	165 (84)
a_{CDOM} (m^{-1})	0.32 (0.027)	7.23 (0.080)	-
TDN (mg l^{-1})	0.13 (0.020)	23 (7)	47 (35)
NH_4^+ (mg N l^{-1})	0.064 (0.010)	10 (2)	12 (8)
NO_3^- (mg N l^{-1})	<0.006 (-)[1]	<0.19 (-)[4]	4.13 (2.6)
NO_2^- (mg N l^{-1})	<0.001 (-)[5]	<0.01 (-)[5]	0.05 (0.04)
TDP (mg l^{-1})	0.006 (0.001)	0.45 (0.15)	0.48 (0.1)
SRP (mg l^{-1})	0.004 (0.001)	0.41 (0.07)	<0.25 (-)[2]

Overlying water (n = 5), benthic mat (n = 5) and emergent mat (n = 4). Averages followed by standard error in parentheses. For mat pore waters, detection limits were variable and high due to the dilution of sample water with de-ionized water. If one or more samples in an average were not detected, the limit of detection for those samples were averaged averages are preceded by a less than symbol. The superscript indicates how many samples were below detection.

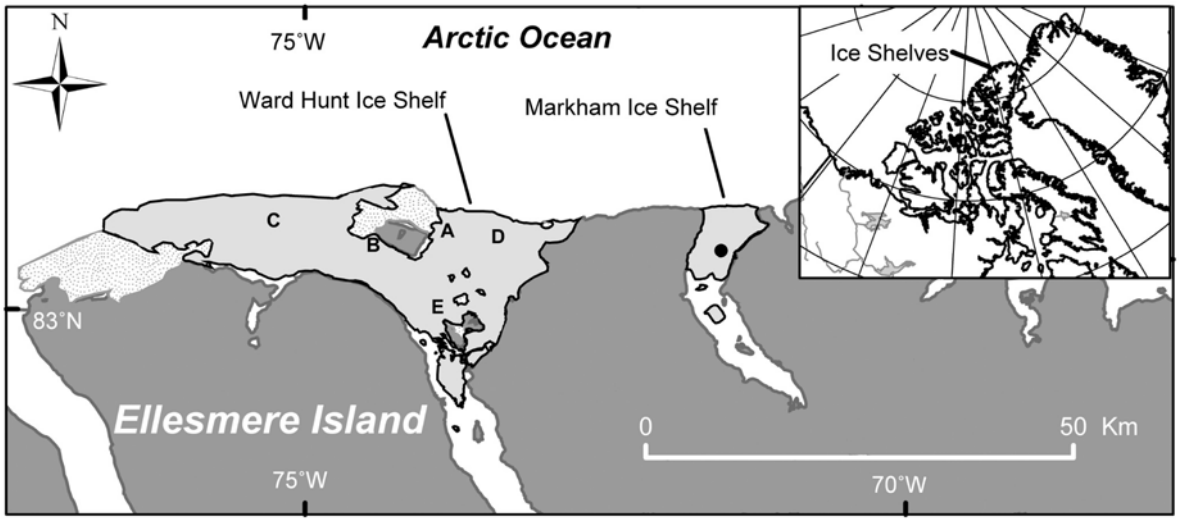

Figure 4.1 Location map of the Ward Hunt and Markham Ice Shelves.

Data were collected in areas adjacent to the climate station (B) and in the center of Markham Ice Shelf (black circle). The location of ablation stake clusters are shown (letters A through E). Cluster B and E were in marine ice areas, whereas clusters A, C and D were in meteoric ice areas.

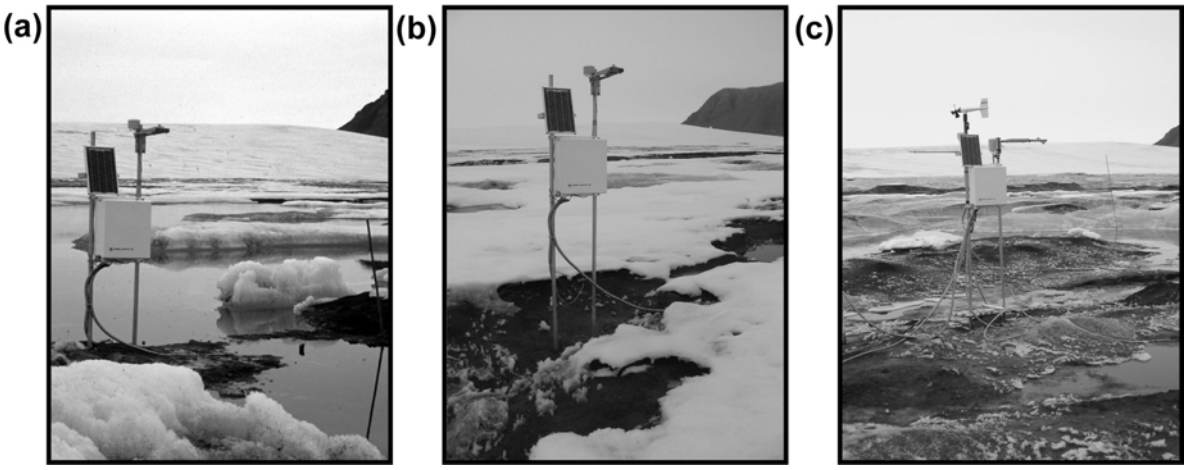

Figure 4.2 Photographs of the climate station in (a) August 2001, (b) July 2002 and (c) July 2003.

Changes in cover type (snow, mat, ice and water) and inversion in topography can be clearly seen between each successive year. Note that there was considerable melt between mid-July 2002 (Figure 4.2b) and when the topographic survey was completed in late July (Figure 4.10b).

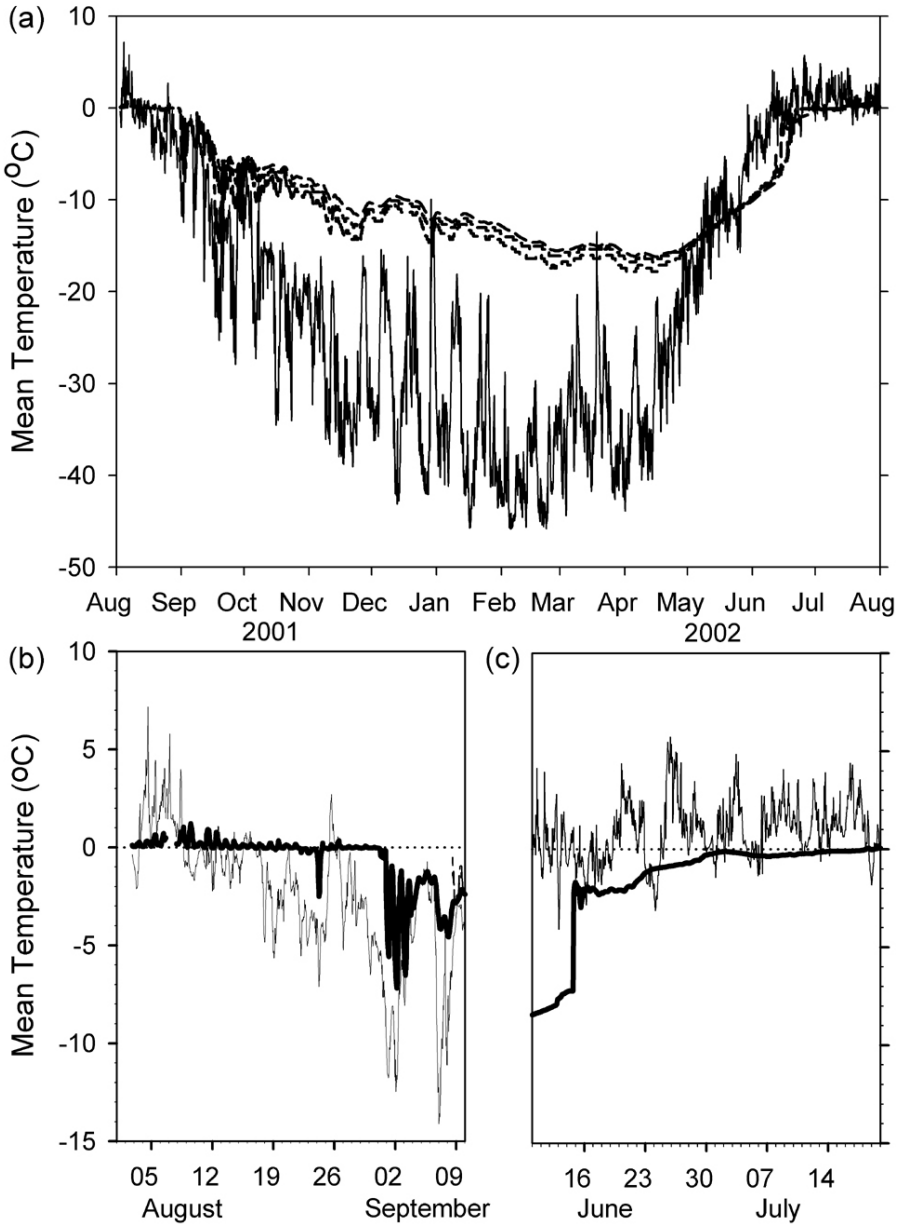

Figure 4.3 Mean surface air and microbial mat temperature.

(a) Air temperature (solid line) versus the temperature within three microbial mats (dashed lines) between August 2001 and August 2002. (b) Air temperature (thin line) and microbial mat (thick line) temperature during freeze-up in 2001. (c) Air temperature (thin line) and microbial mat (thick line) temperature during thaw in 2002. (b and c) dotted line indicates 0 ^{o}C. Other microbial mat temperatures during freeze-up and thaw were similar to the one depicted although timings varied (Table 4.1).

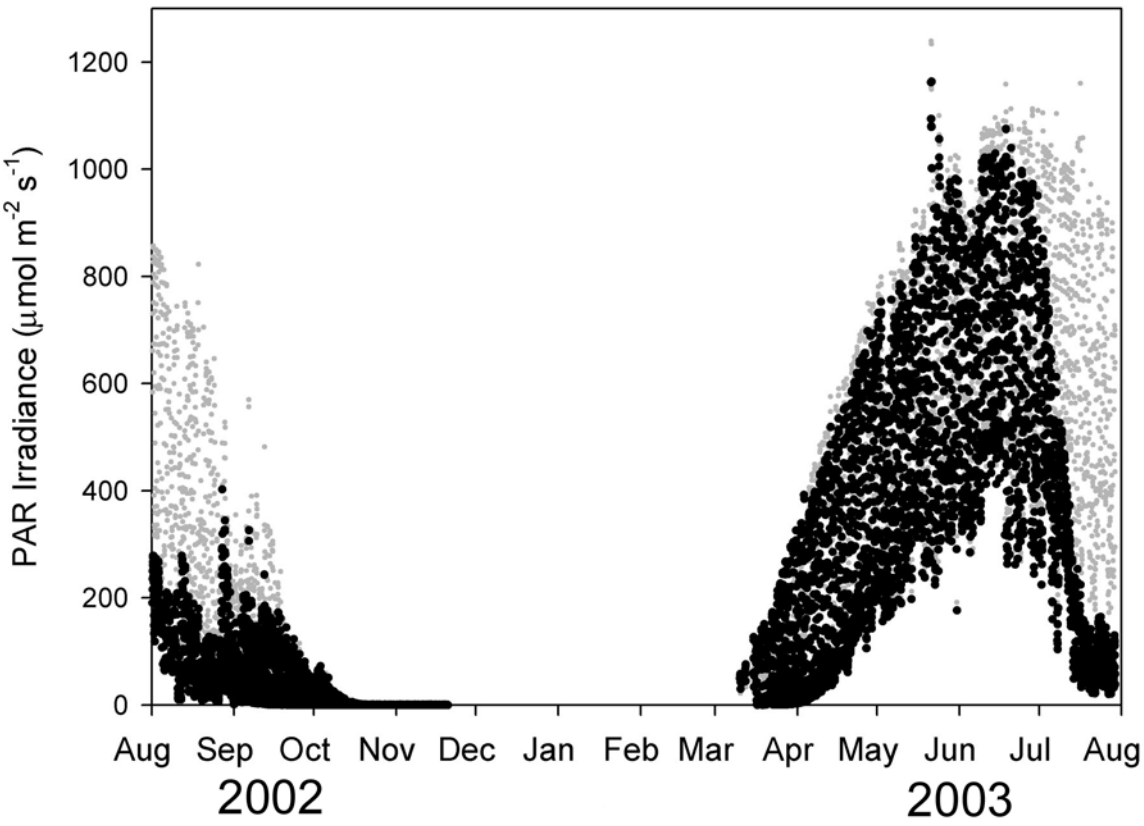

Figure 4.4 Downwelling (grey) and upwelling (black) PAR irradiance from August 2002 to August 2003.

The drop in albedo at the site due to snowmelt can be clearly seen in July 2003. Note that data are missing between November and March.

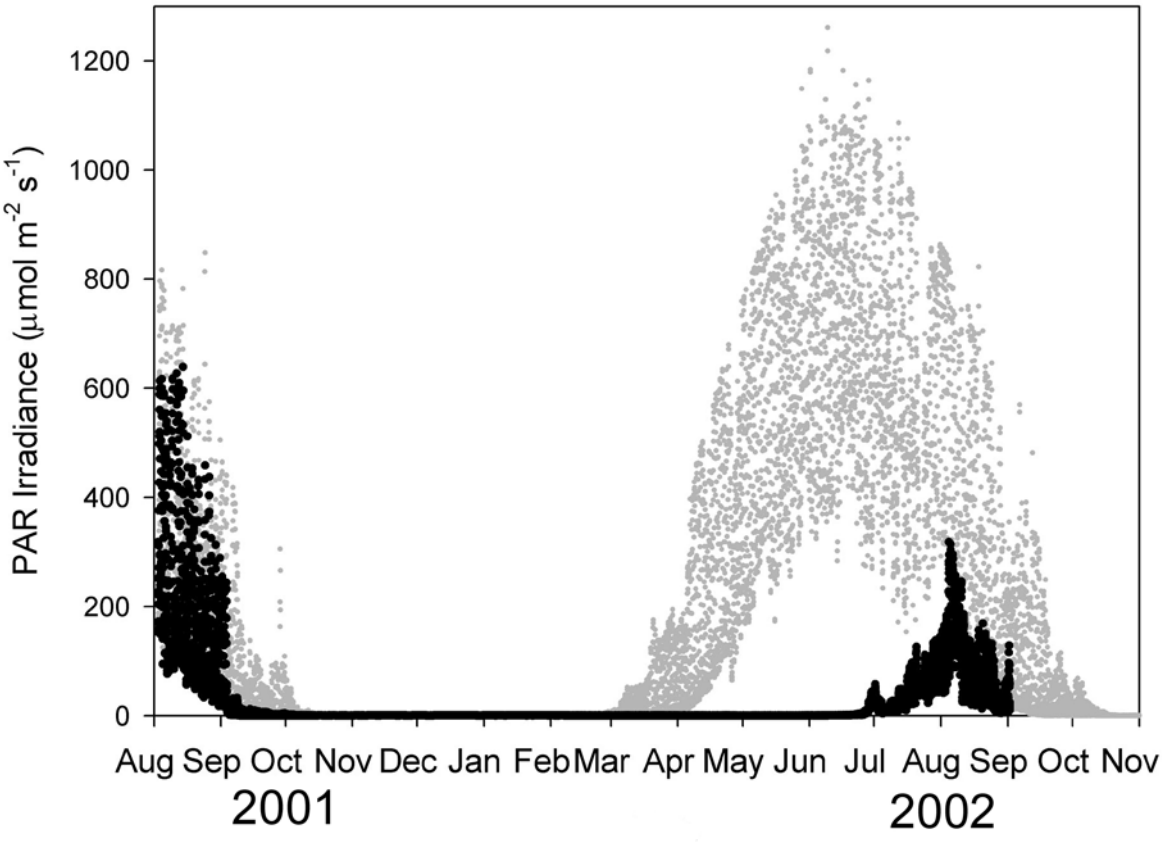

Figure 4.5 Downwelling (grey) PAR irradiance from August 2001 to August 2002 compared to irradiance 14 cm above the surface of a microbial mat (black).

Initially, the microbial mat sensor was at the bottom of a meltwater pond (under 20 cm water). A drop in mat-level irradiance in early September 2001, suggests a snowfall event covered the frozen pond. The snow cover over this sensor candled in late July/August and the sensor wire was severed in early September 2002.

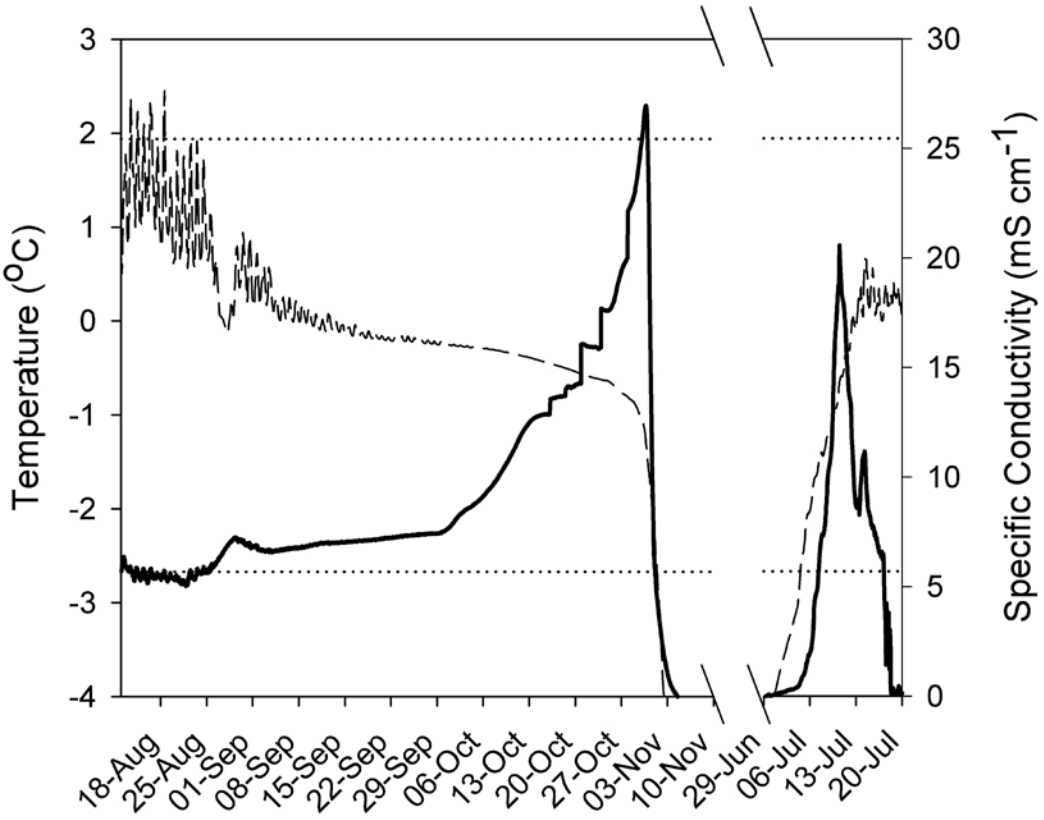

Figure 4.6 Freeze-up and thaw of a meltwater pond on the Ward Hunt Ice Shelf.

Specific conductivity (solid line) and temperature (dashed line) every 30 minutes by a CTD logger installed at the bottom of the 9.4 m^3 pond. Horizontal dotted lines indicate mean open water conditions (measured from July 23 to August 10, 2002) for temperature (upper line) and specific conductivity (lower line). Note that ice inside the induction coil (torus) of the sensor caused a reduction in specific conductivity to a subzero reading over winter, which accounts for rapid drop in conductivity at freeze-up and the rise in conductivity at thaw.

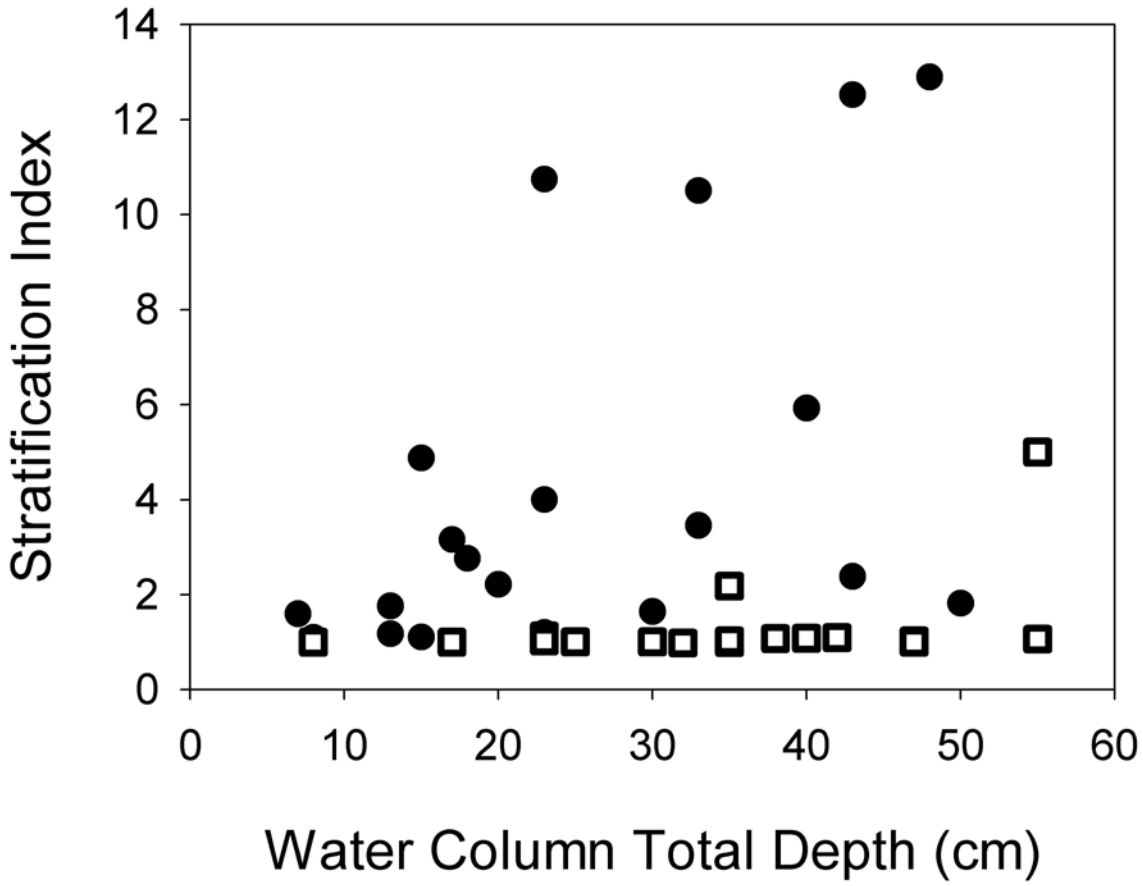

Figure 4.7 The relationship between stratification index (bottom water salinity divided by surface water salinity) and depth for ice shelf meltwater ponds covered with ice (solid circle) and ice free (open square).

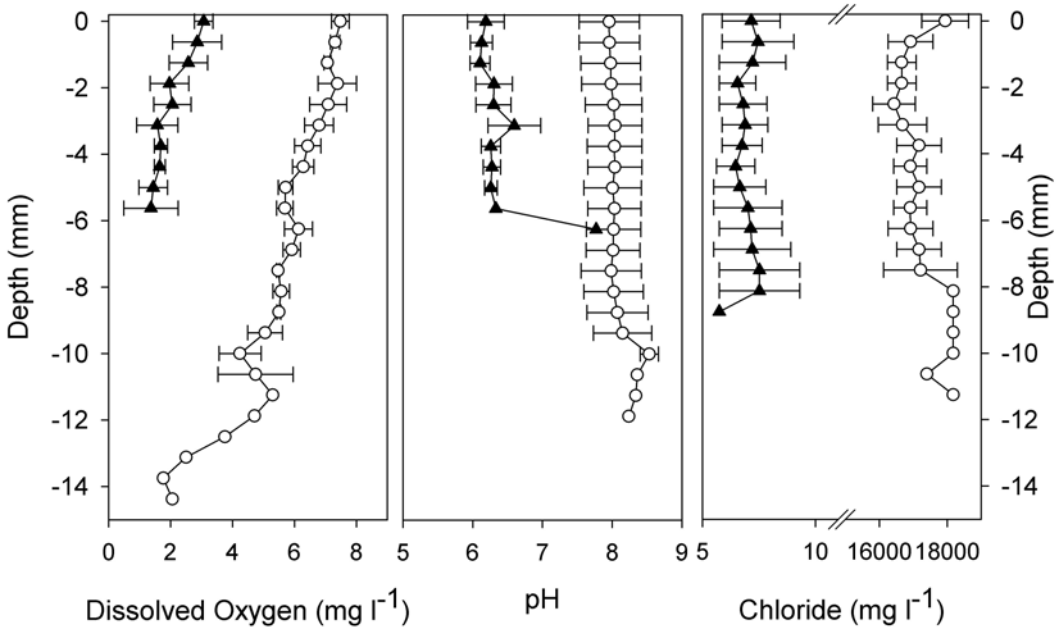

Figure 4.8 Microbial mat profiles of dissolved oxygen, pH and chloride for a 'matlet' type mat overlain by 8 cm of water in a cryoconite hole (closed triangles) and an 'orange' type mat not overlain by water (open circles). Averages with SE bars for 3 measurements.

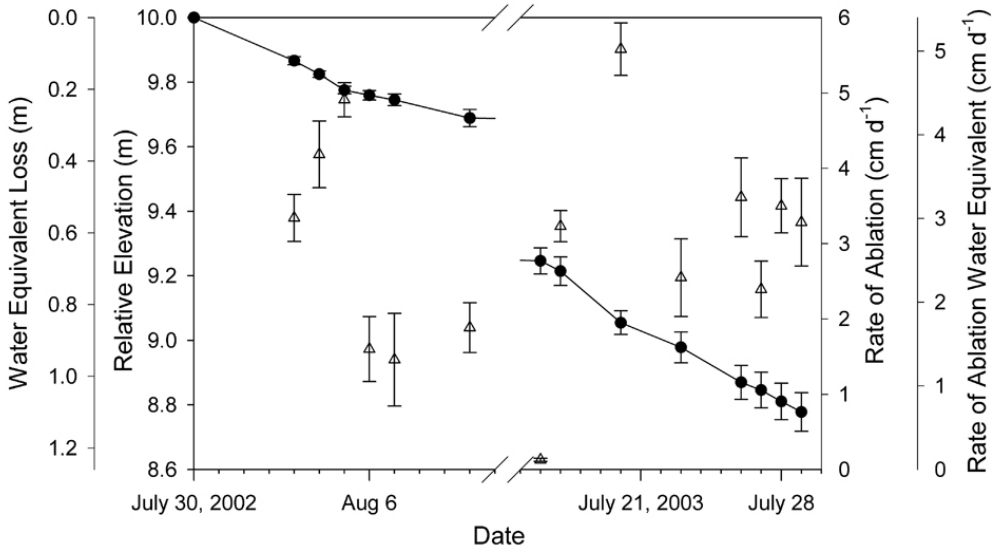

Figure 4.9 Ice ablation at the climate station site.

Cumulative elevation loss and water loss (solid circles) and rates of ice and water equivalent ablation between site visits (open triangles). Averages and standard errors were calculated from 6 stakes from an arbitrary datum (10 m). Total ablation was 1.222 m (1.10 m water equivalent) over 364 days. The average rate of melt was 2.9 cm d^{-1} (SE = 0.26) during field season 2002 and 3.6 cm d^{-1} (SE = 0.15) during field season 2003.

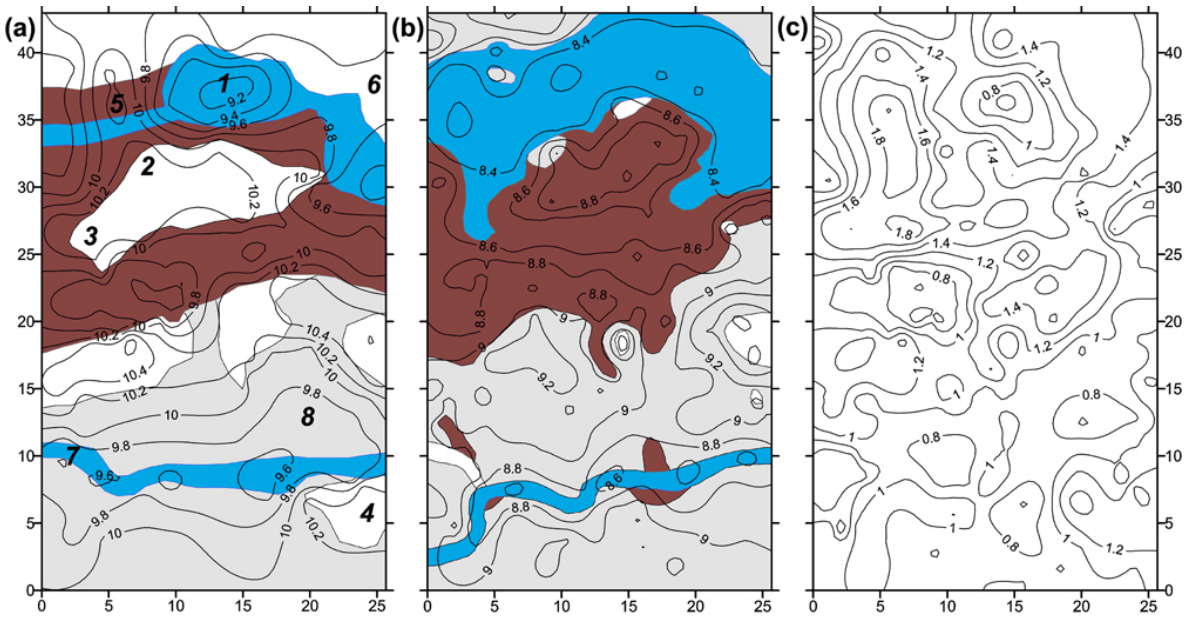

Figure 4.10 Ice shelf topography and ablation.

(a) Topography on August 4, 2002 (b) Topography on July 27, 2003 and (c) The difference between these surfaces (2002 - 2003) represents the ice surface lowering. Cover types were assigned based on survey notes and photographs of the site. For Figure 10 a & b, white: snow, light grey: ice (often with surface dirt), blue: water (often underlain by microbial mat), brown: microbial mat. The bold-italicized numbers in Figure 10a are features referred to in the text. Distances, elevations and surface lowering are given in metres.

Chapitre 5 Break-up of the largest Arctic ice shelf and associated loss of an epishelf lake

5.1 Résumé

Les observations de terrain et les images de télédétection RADARSAT indiquent qu'entre 2000 et 2002, la plate-forme de glace de Ward Hunt (Nunavut, Canada, 83ºN, 74ºW), s'est scindé en deux moitiés. Depuis lors, la plate-forme présente des fissures additionnelles et des détachements d'icebergs. Cette rupture a causé le drainage d'un lac épiplate-forme (le fjord Disraeli), un type d'écosystème rare. De 1967 jusqu'à maintenant, une hausse significative de la moyenne des températures de l'air a accompagné la réduction du volume d'eau douce du fjord Disraeli. L'effondrement récent des plates-formes de glace en Antarctique a été interprété comme une évidence du changement accéléré du climat de cette région. De la même manière, l'amincissement et la fragmentation de la plate-forme de glace ainsi que le drainage du lac épiplate-forme, sont des preuves additionnelles témoignant du changement de climat dans le Haut Arctique.

5.2 Abstract

Field observations and RADARSAT imagery of the Ward Hunt Ice Shelf (lat. 83ºN, long. 74ºW), Nunavut, Canada, show that it broke in two over the period 2000 to 2002, with additional fissuring and further ice island calving. The fracturing caused the drainage of an ice-dammed epishelf lake (Disraeli Fiord), a rare ecosystem type. Reductions in the freshwater volume of Disraeli Fiord occurred from 1967 to the present and accompanied a significant rise in mean annual air temperature over the same period in this far northern region. The recent collapse of ice shelves in West Antarctica has been interpreted as evidence of accelerated climate change in that region. Similarly, the inferred thinning and observed fragmentation of the ice shelf, plus the drainage of the epishelf lake, are additional evidence for climate change in the High Arctic.

5.3 Introduction

The abrupt collapse of glacially fed ice shelves in West Antarctica during the last two decades has been attributed to regional climate change (Vaughan and Doake, 1996). It is less widely known that ice shelves occur in the High Arctic, and that these are also undergoing substantial contraction (Vincent *et al.*, 2001; Jeffries, 2002). With a few exceptions, Arctic ice shelves are not glacially fed, relying instead on the basal accretion of sea ice and surface accumulation of precipitation to achieve a maximum thickness of a few tens of meters (Jeffries, 1992b). These northern systems may therefore be particularly responsive to climate warming and oceanographic change. Polar amplification of current global warming trends (Moritz *et al.*, 2002) may further threaten Arctic ice shelves. These ice shelves have undergone a marked decline in surface area during the past century (Vincent *et al.*, 2001) and, because of scant regional precipitation and the lack of significant glacial input, will not likely recover. Apart from their potential value as sentinels of climate change, Arctic ice shelves are also ecologically important. They provide cryo-habitats for well-developed communities of extremophilic microbes (Vincent and Howard-Williams, 2000). In some cases, they block the mouths of bays and fiords, partially impounding a body of low-salinity water which overlies the sea water below (epishelf lakes) which can contain unusual mixed communities of marine and freshwater biota (Laybourn-Parry *et al.*, 2001; Van Hove *et al.*, 2001).

The Ward Hunt Ice Shelf (latitude 83ºN, longitude 74ºW; Figure 5.1a), Nunavut, Canada, is a 443 km^2 remnant of a much larger feature that extended along the northern coast of Ellesmere Island at the beginning of the last century (Peary, 1907). The original ice shelf contracted 90 % during the period 1906-1982 by calving from its northern edge (Vincent *et al.*, 2001). Since then, the remnant ice shelves, including the ~3000 year old Ward Hunt Ice Shelf (Crary, 1960), have remained relatively stable.

The surface of the Ward Hunt Ice Shelf is characterized by a ridge and trough topography (observable by RADARSAT, Figure 5.1) with a wavelength of roughly 235 m, an amplitude of 3.5 m and an east-west trend (Holdsworth, 1987). Long melt pools (up to 20 km) form in the troughs each summer. The ice shelf dams the mouth of Disraeli Fiord,

where the topmost 43 m was, until recently, filled with freshwater derived from terrestrial snow and ice meltwater. Disraeli Fiord is 30 km long by approximately 5 km wide and has a drainage basin of 2100 km^2 (Keys, 1978). The low salinity water overlying ocean water in the 400 m deep fiord has a hydraulic residence time of decades (according to Keys (1978)) to centuries (according to Shpaikher (1969)). Lakes of this type are rare and are referred to as epishelf lakes in Antarctica (Laybourn-Parry *et al.*, 2001). Disraeli Fiord was the largest remaining such lake in the Northern Hemisphere (Jeffries, 2002).

In this paper we describe and evaluate recent changes that have taken place in the Ward Hunt Ice Shelf – Disraeli Fiord region. We undertook observations at this remote site, the northern limit of North America, by satellite-borne synthetic aperture radar, by helicopter overflight transects and by *in situ* profiling measurements. These show that the ice shelf has entered a period of accelerated break-up resulting in the complete drainage and loss of an epishelf lake ecosystem.

5.4 Results

RADARSAT observations show that in 1998 and 1999 the surface of the Ward Hunt Ice Shelf resembled aerial images acquired occasionally since 1954, with no evidence of fracturing other than peripheral tidecracks (Figure 5.1b). By contrast, observations made from a helicopter in 2001 revealed a north-south fracture that extended from the southern margin of Ward Hunt Island to Disraeli Fiord, not only cleaving the ice shelf in two, but destroying its overall integrity and consequently draining the epishelf lake in Disraeli Fiord. RADARSAT imagery in early April 2000 was the first to clearly show the beginning of this feature and subsequent images show evidence of its further extension (Figure 5.1c). By September 2002, the southern third of this fracture had a maximum width of 80 m and, near Disraeli Fiord, it had bifurcated several times, producing many small icebergs.

Our direct measurements on the ice shelf in July-August 2002 revealed extensive cracking with the separation of a 4 km^2 central portion into discrete, free-floating ice blocks. CTD profiling to depths of 37 to 58 m within these cracks confirmed that they extended right through the ice shelf to underlying seawater (Figure 5.1c). The resultant independent ice masses were retained within large expanses of intact shelf ice, and additional fissures

extended eastwards from the shore towards this central area. RADARSAT images revealed only some of these cracks, since many occur at the bottom of and parallel to the direction of the troughs, where they are masked by the signal from the undulating topography. In these cases, ponded water drained through the cracks, and considerable drainage also occurred when cracks ran perpendicular to the undulations. In addition to the fracturing south of Ward Hunt Island, a calving event occurred (Figure 5.1e) between August 6th and 11th, 2002 resulting in a loss of shelf ice (6 km^2 of ice islands) plus multiyear landfast sea ice (20 km^2). A comparison of RADARSAT images from 1998 and 2002 also showed recent calving from the southern edge of the ice shelf into Disraeli Fiord.

A number of authors reported on the strong density stratification in ice-dammed Disraeli Fiord and interpreted the depth of the freshwater layer as being equivalent to the draft of the ice shelf (Keys *et al.*, 1968; Hattersley-Smith, 1973; Jeffries and Krouse, 1984; Vincent *et al.*, 2001). A steady decrease in the thickness of the freshwater layer since the mid 1960s (Figure 5.2) suggests that there has been a general thinning of the Ward Hunt Ice Shelf or that freshwater has been preferentially draining via a localized conduit at the base of the ice shelf (Vincent *et al.*, 2001). Our observations between the summers of 1999 and 2002 (Table 5.1) reveal a catastrophic drainage of the freshwater layer, probably through the fractures described above (Figure 5.3). Estimates of the freeboard observed at the cracks in the central area imply an ice thickness of no greater than 25 m for this particular area. This differs appreciably from past estimates of ice shelf thicknesses of 43 to 54 m by seismic methods (Crary, 1958), a maximum of 60 m by survey methods (Crary, 1958) and 42 m by coring (Jeffries, 1991).

Several analyses point to atmospheric warming as a cause for ice shelf collapse on the Antarctic Peninsula (Mercer, 1978; Vaughan and Doake, 1996; Scambos *et al.*, 2000). In that region, a warming rate of 3.7 ± 1.6 ºC century^{-1} has been documented (Vaughan *et al.*, 2003), which is several time the 'global' warming rate of 0.6 ± 0.2 ºC century^{-1} (IPCC, 2001). The longest meteorological record for Northern Ellesmere Island is at Alert, 175 km east of the Ward Hunt Ice Shelf (Figure 5.1a). A relatively small air temperature increase of 0.01 ºC yr^{-1}, p = 0.1396 (p is the probability that the slope of the regression line is zero, assuming a linear association between the variables) has been observed at Alert since 1951.

However, during the period of epishelf lake contraction and drainage (1967 to present), the air temperature increase (0.04 °C yr^{-1}, $p = 0.0045$) has been of a similar order to that observed on the Antarctic Peninsula. For the period August 2001 to July 2002, surface air temperature was measured at an automated meteorological station on the ice shelf. The mean monthly temperature at this site was highly correlated with air temperature values at Alert ($R^2 = 0.985$, $p < 0.0001$, RMSE = 1.8, $n = 12$), and this relationship was employed to generate historical proxy data for the Ward Hunt Ice Shelf. This yielded a mean July surface air temperature (1967-2002) of 1.3 °C, well above the 0 °C isotherm that has been identified as the critical threshold for ice shelf break-up in Antarctica by Robin and Adie(1964) as cited in Vaughan and Doake (1996).

No significant trend was observed in proxy summer air temperatures yet spring and fall warming trends were both significant (Table 5.1), as has been observed elsewhere in the Arctic (Rigor *et al.*, 2000). The first observation of the ice crack (April 2000) and past ice island calving (Hattersley-Smith, 1963) from the Ward Hunt Ice Shelf show that major break-up events can occur in the spring and fall, indicating that warming trends in these seasons may play a significant role in ice shelf disintegration. The cumulative effects of a long-term warming trend since the Little Ice Age (Overpeck *et al.*, 1997) likely caused the ongoing changes in the Ward Hunt Ice Shelf. This includes the 20th century disintegration of the Ellesmere Ice Shelf (Vincent *et al.*, 2001) and the abrupt break-up and loss of integrity of the Ward Hunt Ice Shelf that we observed over the period 2000-2002. The precise timing and pattern of fracturing may involve a variety of mechanical stressors such as freeze-thaw, wind and tidal events that act on the ice shelf already weakened by climatic warming.

5.5 Discussion

Arctic ice shelf mass balance includes gains and losses at both the surface and underside and changes in geographical extent. On the Ward Hunt Ice Shelf, the surface mass balance was negative (-0.96 m water equivalent) between 1965 and 1975 (Serson, 1979) plus there was no net accumulation between 1906 and 1954 (Hattersley-Smith *et al.*, 1955). Surface ablation has been offset, at least in part, by the accretion of freshwater that flowed north-

eastward under the ice shelf from Disraeli Fiord (Keys, 1978; Jeffries and Krouse, 1984). The new fractures in the ice shelf now provide a direct conduit for freshwater transport from Disraeli Fiord to the open ocean (Figure 5.3). This will discontinue the sub-ice freshwater transport previously available for bottom accretion and may consequently amplify the thinning rate of the Ward Hunt Ice Shelf. However, the bottom mass balance of the ice shelf has not been quantified and therefore its role in recent events and relative importance remain unknown.

A complete understanding of the observed and future changes requires the systematic study of ocean, atmosphere, ice shelf and epishelf lake interactions. Apart from an increase in air temperature, other possible reasons for the recent events observed on the Ward Hunt Ice Shelf include changes in Arctic Ocean temperature, salinity and flow patterns (Newton and Sotirin, 1997; Morison *et al.*, 2000), changes in Disraeli Fiord hydrology and hydrography, or changes in the ice shelf surface heat budget. General or local thinning may have reduced the mechanical strength of the ice shelf, leaving it prone to the fracturing we observed.

The pattern of disintegration of the Ward Hunt Ice Shelf differs radically from that observed in Antarctica. Antarctic ice shelves are glacially fed and extend northwards from the cold landmass of the Antarctic continent. In contrast, Arctic ice shelves extend poleward from land and may be warmed on their landward side and bottom by hydrological input from the entire drainage basin (Figure 5.3). Epishelf lakes trapped behind these ice shelves provide a second front where calving may occur, as well as a reservoir for sub-ice flow.

Recent fracturing on the Ward Hunt Ice Shelf may not only lead to additional shrinkage of the largest Arctic ice shelf, but is also a precursor to ice island production, which is of concern for ship operations and drilling platforms in the Arctic Ocean (Jeffries, 1992b). Furthermore, the fracturing of the Ward Hunt Ice Shelf has ecological implications since the observed change in the salinity profile of Disraeli Fiord shows a 96 % loss (Table 5.1) of the fresh and brackish water habitats that were known to support a unique biological community (Van Hove *et al.*, 2001). The ongoing loss of ice and drainage of surface meltwater lakes has also reduced the available habitat for ice shelf biota (Vincent *et al.*, 2000; Vincent and Howard-Williams, 2000). These observations draw attention to the

vulnerability of ice-dependent polar ecosystems to environmental change, and the accelerating loss of unique cryo-ecosystems in the Northern Hemisphere.

5.6 Acknowledgements

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Table 5.1 Disraeli Fiord epishelf lake loss and Ward Hunt Ice Shelf mean seasonal air temperature trends (1967-2002).

Year or Season	Depth of 3 ppt isohaline (m)[a]	Volume of low salinity water (km^3)[b]
1967	43	6.1
1983	30	4.3
1999	28	4.0
2002	3	0.5
	Months	Temperature trend (ºC/decade)[c]
Winter	DJM	+0.18
Spring	MAM	+0.68[d]
Summer	JJA	+0.21
Fall	SON	+0.63[d]

[a] calculated using the data presented in Fig. 2. [b] we consider water < 3 ppt to be low salinity, the fiord walls were assumed to be vertical and the surface area of Disraeli Fiord (143 km^2) was obtained from recent RADARSAT imagery. Also, note that Disraeli Fiord is perennially covered with 2 m of ice (Keys, 1978), thereby further reducing the available low salinity habitat by approximately 0.25 km^3. [c] Ward Hunt proxy temperatures were transformed from the Alert, Nunavut meteorological record (Meteorological Service of Canada). [d] significant ($p<0.05$) trend.

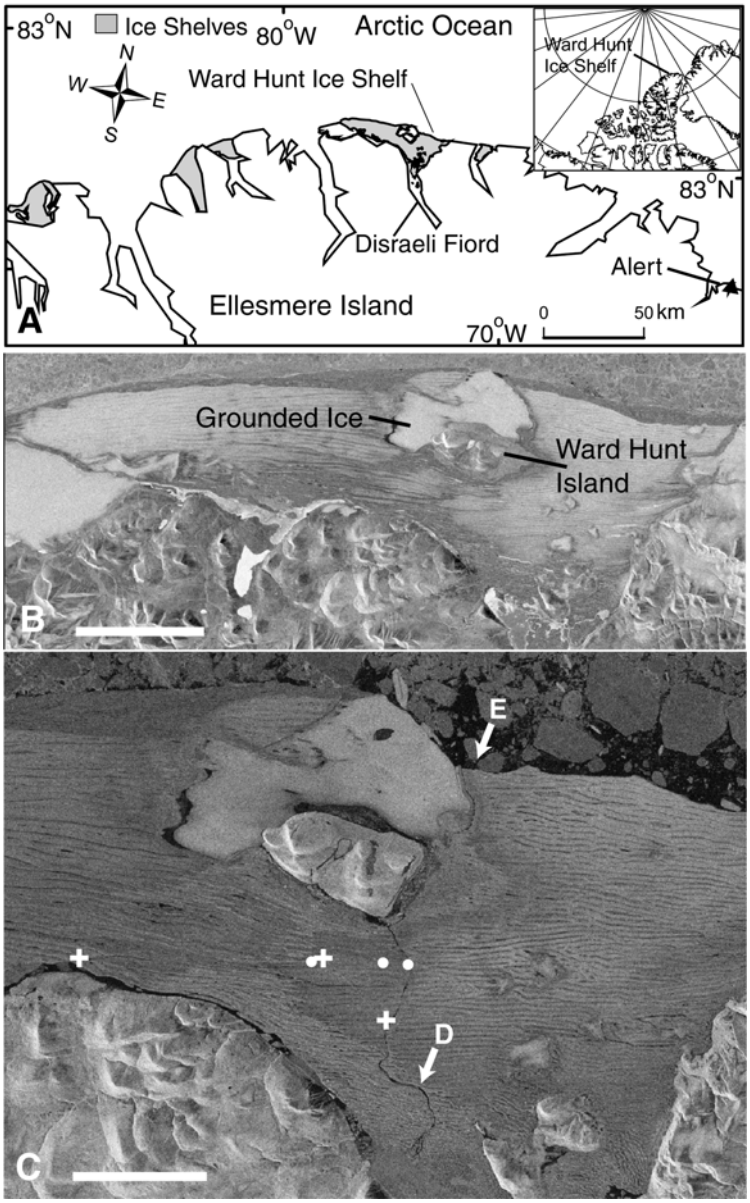

Figure 5.1 The development of cracks and calving on the Ward Hunt Ice Shelf.

A, Location map of the Ward Hunt Ice Shelf. B, The ice shelf prior to crack development - October 29, 1999, RADARSAT-1, orbit 20756, standard beam mode 5, resolution 12.5 m, scale bar indicates 10 km. C, The ice shelf after crack development - August 30, 2002, RADARSAT-1, orbit 35605, fine beam mode 1, resolution 6.5 m, scale bar indicates 5 km. D, The main north-south crack is apparent in the center of the image. E, Indentation resulting from the loss of 6 km^2 of ice shelf and 20 km^2 of multi year landfast ice from the northern end of the ice shelf can be seen following the calving event in August 2002. The profile locations confirming complete fracturing through the ice shelf are indicated by white crosses. The triangular region of free-floating ice blocks is outlined by GPS waypoints (white dots) and the southern-most ice crack profile. Both images were spatially and radiometrically corrected.

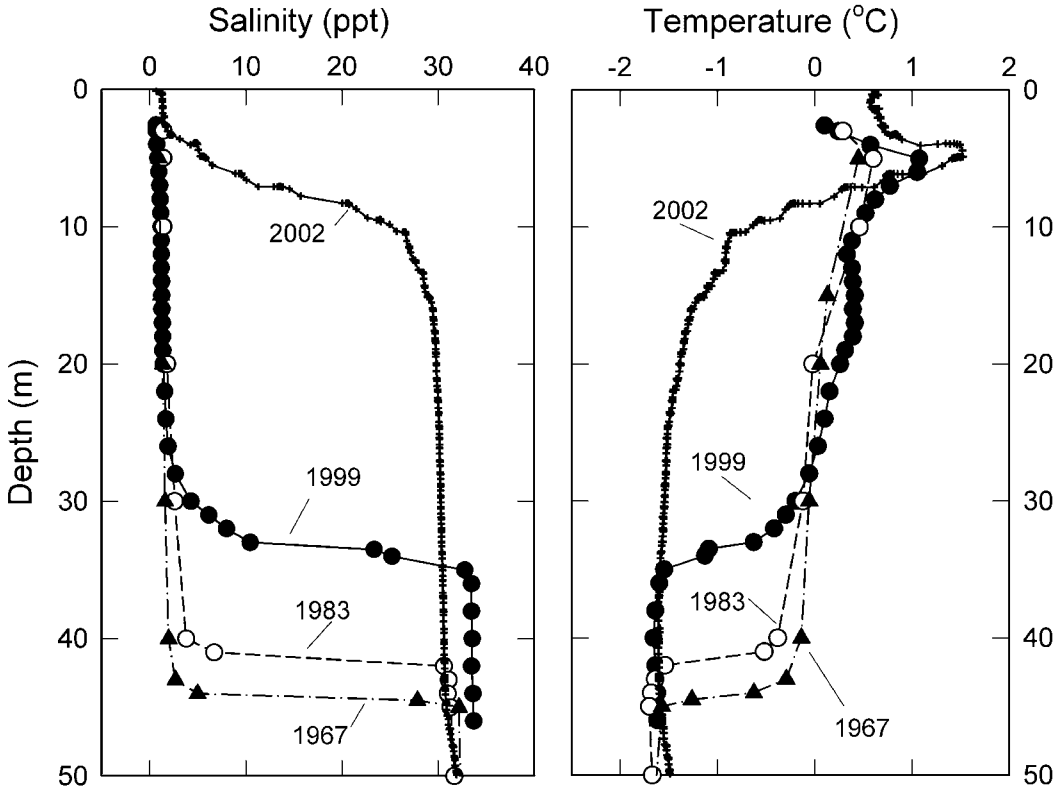

Figure 5.2 CTD profiles in Disraeli Fiord.

Profile data are from June 1967 (Keys *et al.*, 1968), May 1983 (Jeffries and Krouse, 1984), June 1999 (Vincent *et al.*, 2001) and August 2002 (present study). Temperature data from 1999 were post-calibrated by adding 0.35 °C to adjust bottom water (45 m) temperatures to the mean for 1967-2002. Slightly higher salinity at depth in the 1999 profile was likely due to a calibration offset. The 2002 profile was logged at 1 second intervals with a Brancker XR-420 CTD, which was lowered from an ice island into the fiord by hand.

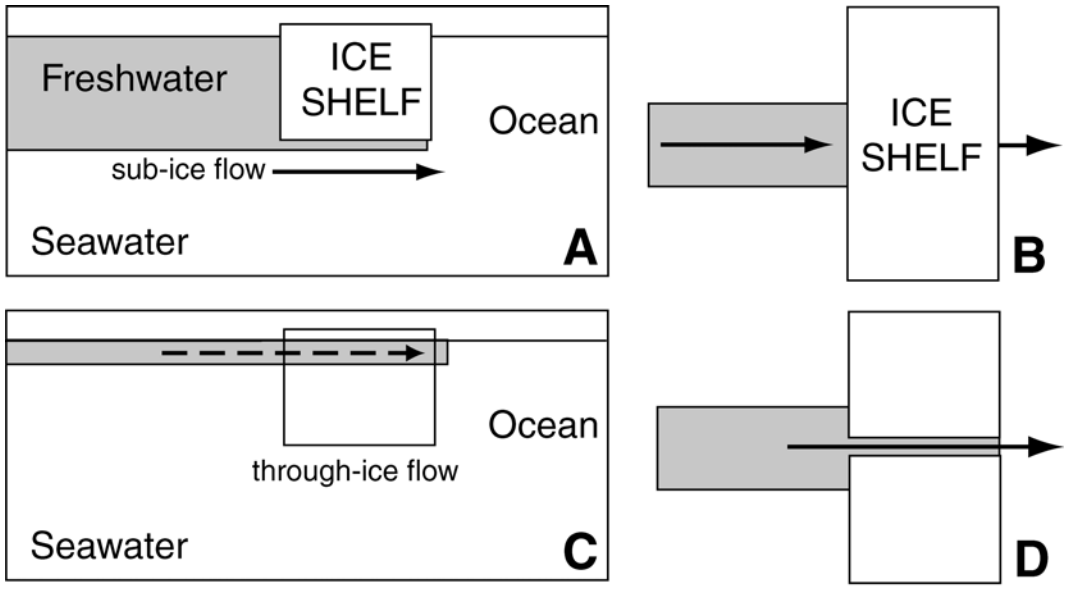

Figure 5.3 Schematic diagram showing the epishelf freshwater lake of Disraeli Fiord dammed behind the Ward Hunt Ice Shelf (A, side view; B, plan view).

Current draining at the surface via the fissure that now separates the two halves of the ice shelf (C, side view; D, plan view).

Chapitre 6 Conclusion générale

Les cryo-écosystèmes situés sur les plates-formes de glace nordiques dans l'Arctique canadien ont été découverts très récemment et n'ont donc pas été étudiés systématiquement. Les consortiums spécifiques de tapis microbiens, qui existent dans cet habitat unique, ne se retrouvent nulle part ailleurs sur la Terre. Ils représentent en soit une ressource scientifique de valeur et une archive importante de la biodiversité qui, comme d'autres habitats polaires (cf. Taton *et al.*, 2003 ; cf. Tindall, 2004), contient probablement des espèces endémiques. De plus, ces cryo-écosystèmes sont à bien des égards des analogues modernes aux conditions qui devaient exister sur la Terre il y a des milliards d'années, et pourrait donc fournir des indices sur l'origine et l'évolution de la vie (Vincent *et al.*, 2004c).

Les plates-formes de glace nordiques ont des similarités avec plusieurs plates-formes de glace antarctiques, ce qui donne l'occasion d'entreprendre des comparaisons biogéographiques et bipolaires de ces deux biomes. Les organismes trouvés dans les tapis microbiens tolèrent les conditions extrêmes de ces plates-formes de glace puisqu'ils contiennent pigments, enzymes et autres produits biochimiques spécialisés, produits pouvant être d'un grand intérêt pour des applications industrielles ou scientifiques. D'autre part, comme ils font partie d'un écosystème dépendant de la glace, ces tapis microbiens sont sous la menace des changements climatiques. Par conséquent, ils représentent une opportunité d'évaluer les impacts d'un réchauffement du climat sur la fragmentation et la perte d'habitat dans le grand Nord. Un tel travail pourrait aussi fournir un aperçu des impacts éventuels sur des écosystèmes plus méridionaux.

Le but de cette étude était d'accroître nos connaissances sur la structure et la dynamique des cryo-écosystèmes des plates-formes de glace nordiques. Elle représente le premier effort systématique de compréhension des interactions entre les aspects physiques et biologiques de ce « nouvel » écosystème. Cette étude a considéré plusieurs échelles spatiales : l'échelle de la plate-forme de glace d'Ellesmere, qui fournit une vue d'ensemble de toutes les plates-formes de glace contemporaines ; l'échelle du micro-environnement, qui se concentre sur les propriétés physico-chimiques et la physiologie des tapis microbiens ; et finalement, une échelle intermédiaire qui prend en considération les types

de glace et la distribution des tapis microbiens. Ainsi, les méthodologies utilisées dans mon étude vont de la microscopie jusqu'à l'interprétation d'images de télédétection .

La présente étude a révélé que le cryo-écosystème des plates-formes de glace nordiques est plus étendu et répandu que l'on ne croyait. La variété de micro-environnements des plates-formes de glace amène les communautés de tapis microbiens à se diversifier. De plus, ce type de cryo-écosystème semble être dynamique à plusieurs échelles, à la fois spatiales et temporelles. L'étude a montré que l'environnement des plates-formes de glace peut influencer les communautés des tapis microbiens, mais que dans certains cas, l'inverse peut aussi se produire. Finalement, cette thèse a illustré le lien entre les écosystèmes qui dépendent des plates-formes de glace et le climat. Les principaux résultats et réalisations de chacun des chapitres de cette thèse sont résumés ci-dessous.

6.1 Synthèse des chapitres

Cette étude a examiné les effets de la fragmentation d'un habitat et les effets des gradients environnementaux sur la structure des consortiums de tapis microbiens. Une stratégie éco-physiologique d'extrêmotrophie a été répertoriée chez les photoautotrophes des tapis microbiens des plates-formes de glace. Cette stratégie leur permettrait de tolérer des environnements extrêmes. Les relations entre la couverture des tapis microbiens et l'ablation de la surface des plates-formes de glace ont été étudiées. La période d'étude comprend également un événement de désintégration de la plate-forme de glace qui été décrit et analysé, ainsi que le drainage d'un lac d'épiplate-forme. Ces événements soulignent la vulnérabilité des habitats qui sont dépendants des plates-formes de glace au réchauffement climatique.

Le chapitre 2 traite l'hypothèse selon laquelle la fragmentation de l'habitat de la plate-forme de glace d'Ellesmere en cinq plates-formes de glace inégales serait reflétée dans des mesures de biodiversité selon la théorie de la biogéographie insulaire. Il s'est avéré que l'analyse quantitative n'a pas confirmé cette hypothèse, suggérant que la capacité élevée de dispersion des organismes des tapis microbiens, ou encore que les gradients environnementaux, avaient plus d'influence sur la structure de la communauté. Cette dernière hypothèse était soutenue par l'association significative entre la structure de la

communauté des tapis microbiens et les gradients de quatre variables environnementales (la concentration en nitrate, en ammonium et en phosphore réactif soluble et la conductivité). L'hétérogénéité chimique et physique des cryo-habitats dans l'ensemble de l'écosystème a été démontrée et l'abondance relative des micro-organismes des consortiums de tapis microbien de chaque plate-forme de glace restante a été documentée. L'ampleur de l'habitat microbien et la masse de matière organique microbienne de toutes les plates-formes de glace ont été estimés afin de déterminer les limites de la distribution de ce cryo-écosystème et de permettre des comparaisons aussi bien entre les plates-formes qu'avec d'autres écosystèmes. Le deuxième chapitre se termine avec une description du patron général du type de glace et de la distribution des sédiments à travers les plates-formes de glace. Le patron semble être lié à la présence d'épais tapis microbien bien développés, ce qui renforce l'hypothèse d'un contrôle environnemental des processus biologiques.

Au chapitre 3, la productivité des tapis microbiens pour les communautés phototrophes et hétérotrophes a été mesurée en microcosmes recréant les conditions estivales arctiques. Lors d'une série d'expériences, l'hypothèse selon laquelle les organismes des tapis microbiens des plates-formes de glace subsistent en conditions sub-optimales a été évaluée en examinant leurs réponses métaboliques aux changements de température, de salinité, d'éclairement et d'hydratation. Un assemblage de pigments à large spectre a été identifié et mesuré à l'aide de la chromatographie liquide de haute performance (HPLC, pour *High Performance Liquid Chromatography*). L'hypothèse selon laquelle ces pigments permettent à la communauté phototrophe de tolérer une gamme plus étendue de conditions environnementales que la communauté hétérotrophe a été testée. La communauté des phototrophes a été identifiée comme étant extrêmotrophe. Cette stratégie éco-physiologique, formulée pour la première fois dans la présente étude, est définie comme étant une grande tolérance à une variété de conditions environnementales extrêmes. Ceci contraste avec la réponse extrêmophile de la communauté hétérotrophe qui ne produit pas de séries de pigments semblables à ceux retrouvés chez la communauté des extrêmotrophes.

Au chapitre 4, l'ablation de la surface de la plate-forme de glace a été suivie durant une année. L'hypothèse centrale de ce chapitre supposait que les tapis microbiens affectent

l'ablation de la plate-forme de glace via la rétroaction positive de l'albédo, c'est à dire que le faible albédo des tapis microbiens (dû à leur couleur foncée) contribue à capter davantage de chaleur ce qui accentuerait la fonte de la plate-forme de glace. La relation qui existe entre les tapis microbiens et l'ablation de la plate-forme de glace montre que l'activité biologique peut affecter les propriétés physiques des cryo-écosystèmes. Des instruments ont été installés pour mesurer la température, la salinité et l'éclairement à l'échelle du tapis microbien en vue de documenter la variabilité des conditions sur une période de deux ans. La durée de la saison de fonte, estimée à partir des données de température, a montré que les tapis microbiens passent la majeure partie de leur existence figés dans la neige et la glace. La concentration en nutriments plus élevée indique que les micro-environnements des tapis microbiens diffèrent considérablement des propriétés globales de l'écosystème. Ceci suggère que, contrairement aux attentes, les tapis microbiens ne sont pas limités en nutriments, même si l'eau de fonte qui les entourent est oligotrophe.

Le chapitre 5 décrit la découverte d'un événement de désintégration sur la plate-forme de glace Ward Hunt et en analyse la principale conséquence, soit le drainage d'un lac épiplate-forme dans le fjord Disraeli. Il est suggéré qu'une hausse significative de la température de 0,47 ºC par décennie durant les 30 dernières années ait été un facteur important qui aurait contribué à cet événement. Ces observations renforcent le lien entre le réchauffement climatique et la désintégration des plates-formes de glace dans le Haut Arctique. Cette étude souligne également la vulnérabilité des habitats qui dépendent des plates-formes de glace au changement climatique. D'autre part, l'étude démontre comment l'intégrité de l'environnement physique est liée à l'écologie microbienne de la plate-forme de glace.

6.2 Des voies de recherche futures

Les observations et expérimentations de cette thèse doctorale fournissent de solides bases à partir desquelles pourront émerger de nouveaux axes de recherche concernant l'écologie microbienne des plates-formes de glace nordiques. Cet environnement unique offre de nombreuses opportunités d'investigation, dont plusieurs volets de ce potentiel inexploité qui sont identifiés ci-dessous.

L'application de techniques moléculaires telles que l'électrophorèse sur gel de gradient dénaturant (DGGE), le séquençage et clonage du rARN 16S et l'hybridation *in situ* (Abed *et al.*, 2002 ; Taton *et al.*, 2003) seraient très pertinentes pour l'étude des tapis microbiens des plates-formes de glace nordiques. Dans un premier temps, ces outils peuvent être utilisés pour évaluer la biodiversité et pour reconnaître des espèces endémiques dans les consortiums des tapis microbiens. Ils pourront également révéler les rapports biogéographiques et écologiques avec d'autres communautés du Haut Arctique et de l'Antarctique, et permettre de tester les hypothèses concernant la dispersion et la répartition de micro-organismes à travers le monde. Les nouveaux outils moléculaires, tels que les micro-réseaux, peuvent aussi fournir des informations en ce qui concerne la diversité phylogénétique et fonctionnelle des tapis microbiens (Greer *et al.*, 2001). L'approche des micro-réseaux, présentement en cours de développement, pourrait fournir un moyen pour surveiller de façon continue les changements écologiques dans les tapis microbiens sur les plates-formes de glace. Ceci devrait être intéressant pour Parcs Canada qui est mandaté de maintenir l'intégrité écologique des écosystèmes dans leurs territoires.

L'architecture des tapis microbiens et les relations entre les diverses communautés pourront être comprises en employant des techniques avancées de microscopie telles que la microscopie électronique à balayage environnementale et la microscopie à balayage laser confocal (de los Rios *et al.*, 2004). L'utilisation de micro-capteurs pourrait permettre de déterminer les taux de recyclage biogéochimique en plus de préciser l'endroit et le moment où les processus-clés, tels que la photosynthèse et la respiration, se produisent (Brotas *et al.*, 2003). La combinaison de ces techniques pourrait fournir l'information sur les régions actives dans le tapis et les communautés responsables de cette activité.

Les températures hivernales minimales dans les tapis microbiens des plates-formes de glace nordiques atteignent -18 ºC. Malgré tout, il est raisonnable de supposer qu'une certaine activité métabolique ait lieu dans ces conditions. Pour vérifier l'hypothèse qu'une activité métabolique hivernale existe dans les tapis microbiens des plates-formes de glace nordiques, elle pourrait être mesurée en utilisant les techniques de bioéssais décrites par Rivkina *et al.* (2000). Il est possible que la production des EPS (substances polymériques extracellulaires) aide les tapis microbiens à être productif malgré les basses températures.

Par conséquent, la quantification et la caractérisation des EPS pourraient révéler d'autres stratégies adaptatives des extrêmotrophes et des extrêmophiles des plates-formes de glace.

Le chapitre 5 mentionne que le drainage du lac épiplate-forme dans le fjord Disraeli aurait pu avoir détruit l'habitat d'eau douce des invertébrés indigènes, tels que *Limnocalanus macrurus*. Cependant, peu a été fait pour vérifier cette hypothèse ou pour répondre aux questions concernant le rétablissement de cet écosystème. Un échantillonnage préliminaire indique que les copépodes d'eau douce qui étaient abondants dans les 30 premiers mètres du fjord Disraeli ne sont plus présents (M. Rautio, données non publiées). Un effort de surveillance plus complet est vivement recommandé.

Les plates-formes de glace restantes long de la côte de l'île Ellesmere risquent de se dégrader davantage dans un avenir rapproché à cause des changements du climat. Cependant, il y a un manque de données concernant l'épaisseur des plates-formes de glace et un manque d'information fiable et représentative sur leur bilan de masse. Actuellement, une collaboration entre Parcs Canada et ArcticNet a mis en place un réseau de mesure de bilan de masse de surface pour remédier à cette lacune pour la plate-forme de glace Ward Hunt. De plus, un de mes objectifs de recherche post-doctoraux concerne le développement d'outils de télédétection pour mesurer l'épaisseur des plates-formes de glace nordiques en utilisant l'altimétrie radar par satellite (cf. Corr *et al.*, 2002).

Finalement, il est clair que le climat de cette région polaire s'est réchauffé significativement et continuera à le faire au cours du prochain siècle (ACIA, 2004). Il est indéniable que les impacts du réchauffement sur les écosystèmes qui dépendent des plates-formes de glace seront importants (Mueller *et al.*, 2003a ; Vincent *et al.*, 2004b). Par conséquent, la surveillance du climat régional est une priorité, et c'est ce qui a mené à l'installation d'une station climatique stratégiquement localisée sur l'île Ward Hunt. Cette station climatique a vu le jour grâce au partenariat entre Parcs Canada, ArcticNet et le réseau SILA du Centre d'études nordiques.

Le changement anthropique du climat est un défi primordial pour l'humanité et le restera pour les générations à venir. Les scientifiques ont fourni l'information aux décisionnaires concernant les impacts potentiels du réchauffement climatique, mais les solutions possibles

pour contrer les problèmes éventuels et les investissements nécessaires sont en compétition avec les réalités géopolitiques et économiques. Ceci a engendré une discussion fortement politisée et a ralenti l'avancement des solutions au problème. Cependant, un argument éthique fondamental est absent des discussions - les humains ont-ils le droit de changer la planète sur une échelle sans précédent, et cela indépendamment des résultats? Les études sur les cryo-écosystèmes peuvent fournir des réponses aux questions liées aux limites de la vie, aussi bien qu'à la tolérance de la vie aux extrêmes et aux changements environnementaux. Cependant, mon expérience de vulgarisation objective d'un évènement lié au changement climatique m'a fait réaliser que l'exploration et la poursuite de la connaissance scientifique ne sont pas isolées des autres efforts humains. Il est donc important de comprendre le lien entre la philosophie morale et naturelle et de contribuer aux débats de société par des faits et des opinions pertinentes.

Références bibliographiques

Abed, R.M.M., Schonhuber, W., Amann, R., and Garcia-Pichel, F. (2002) Picobenthic cyanobacterial populations revealed by 16S rRNA-targeted *in situ* hybridization. *Environmental Microbiology* 4: 375-382.

ACIA (2004) *Impacts of a Warming Arctic*, Arctic Climate Impact Assessment: Cambridge.

Adams, W.P. (1966) Studies of ablation and run-off on an Arctic glacier. PhD Thesis, Department of Geography, McGill University, Montreal. 158 pp.

Aizenshtat, Z., Lipiner, G., and Cohen, Y. (1984) Biogeochemistry of carbon and sulfur cycle in the microbial mats of Solar Lake (Sinai). In: *Microbial Mats: Stromatolites*. Cohen, Y., Castenholz, R., and Halvorson, H. O. (eds.), Alan R Liss Inc: New York, 281-312.

Behrenfeld, M.J., Prasil, O., Babin, M., and Bruyant, F. (2004) In search of a physiological basis for covariations in light-limited and light-saturated photosynthesis. *Journal of Phycology* 40: 4-25.

Bell, R.T. (1993) Estimating production of heterotrophic bacterioplankton via incorporation of tritiated thymidine. In: *Handbook of Methods in Aquatic Microbial Ecology*. Kemp, P. F., Sherr, B. F., Sherr, E. B., and Cole, J. J. (eds.), Lewis Publishers: Boca Raton, 495-504.

Belzile, C., Gibson, J.A.E., and Vincent, W.F. (2002) Colored dissolved organic matter and dissolved organic carbon exclusion from lake ice: Implications for irradiance transmission and carbon cycling. *Limnology and Oceanography* 47: 1283-1293.

Bentley, M.J., Hodgson, D.A., Sugden, D.E., Roberts, S.J., Smith, J.A., Leng, M.J., and Bryant, C. (2005) Early Holocene retreat of the George VI Ice Shelf, Antarctic Peninsula. *Geology* 33: 173-176, doi:10.1130/G2103.1.

Bhaya, D., Schwarz, R., and Grossman, A.R. (2000) Molecular responses to environmental stress. In: *The Ecology of Cyanobacteria: Their Diversity in Time and Space*. Whitton, B. A. and Potts, M. (eds.), Kluwer Academic Publishers: Boston, 397-442.

Bissonette, J.A. and Storch, I. (2002) Fragmentation: Is the message clear? *Conservation Ecology* 6: 14.

Blanck, E., Poser, H., and Oldershausen, E. (1932) Über Kryokonitvorkommnisse im ostgrönländischen Packeis und ihre chemische Zusammensetzung. *Chemie der Erde* 7: 434-440.

Böhm, G.A., Pfeiderer, W., Böger, P., and Scherer, S. (1995) Structure of a novel oligosaccharide-mycosporine-amino acid ultraviolet A/B sunscreen pigment from the terrestrial cyanobacterium *Nostoc commune*. *The Journal of Biological Chemistry* 270: 8536-8539.

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*: In Press.

Bradley, R.S. (1990) Holocene paleoclimatology of the Queen Elizabeth Islands, Canadian High Arctic. *Quaternary Science Reviews* 9: 365-384.

Brandt, B. (1931) Kryokonit auf Flußeis in Mitteleuropa. *Zeitschrift für Gletscherkunde* 19: 317-320.

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, doi:10.1029/2004JD004560.

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

Broady, P.A. (1982) Taxonomy and ecology of algae in a freshwater stream in Taylor Valley, Victoria Land Antarctica. *Archiv für Hydrobiologie/Algological Studies* 32: 331-349.

Brotas, V., Risgaard-Petersen, N., Serodio, J., Ottosen, L., Dalsgaard, T., and Ribeiro, L. (2003) *In situ* measurements of photosynthetic activity and respiration of intertidal benthic microalgal communities undergoing vertical migration. *Ophelia* 57: 13-26.

Canfield, D.E. and Des Marais, D.J. (1994) Cycling of carbon, sulfur, oxygen and nutrients in a microbial mat. In: *Microbial Mats: Structure, Development and Environmental Significance*. Stal, L. J. and Caumette, P. (eds.), Springer-Verlag: Berlin, 255-263.

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

Castenholz, R.W. (1994) Microbial mat research: The recent past and new perspectives. In: *Microbial Mats: Structure, Development and Environmental Significance*. Stal, L. J. and Caumette, P. (eds.), Springer-Verlag: Berlin, 3-18.

Chen, P.C. and Lai, C.L. (1996) Physiological adaptation during cell dehydration and rewetting of a newly-isolated *Chlorella* species. *Physiologia Plantarum* 96: 453-457.

Christie, R.L. (1957) *Geological Reconnaissance of the North Coast of Ellesmere Island, District of Franklin, Northwest Territories*. Paper 56-9, Geological Survey of Canada: Ottawa.

Christner, B.C. (2000) Recovery and identification of viable bacteria immured in glacial ice. *Icarus* 144: 479-485, doi:10.1006/1999.6288.

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 Knowland, J. (1999) Ultraviolet radiation screening compounds. *Biological Reviews of the Cambridge Philosophical Society* 74: 311-345.

Cockell, C.S. and Stokes, M.D. (2004) Widespread colonization by polar hypoliths. *Nature* 431: 414, doi:10.1038/431414a.

Cogley, J.G. (2002) *Mass Balance of Axel Heiberg Island Glaciers*. wwvv.trentu.ca/geography/glaciology.2003/glaciology.htm, Trent University: Peterborough, ON.

Comiso, J. (2002) A rapidly declining perennial sea ice cover in the Arctic. *Geophysical Research Letters* 29: 1956, doi:10.1029/2002GL015650.

Corr, H.F.J., Jenkins, A., Nicholls, K.W., and Doake, C.S.M. (2002) Precise measurement of changes in ice-shelf thickness by phase-sensitive radar to determine basal melt rates. *Geophysical Research Letters* 29: 1232, doi:10.1029/2001GL014618.

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, doi:10.1034/j.1600-0587.2000.d01-1638.x.

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

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.

Davison, I. (1991) Environmental effects on algal photosynthesis: temperature. *Journal of Phycology* 27: 2-8.

de los Rios, A., Ascaso, C., Wierzchos, J., Fernandez-Valiente, E., and Quesada, A. (2004) Microstructural characterization of cyanobacterial mats from the McMurdo Ice Shelf, Antarctica. *Applied and Environmental Microbiology* 70: 569-580, doi:10.1128/AEM.70.1.569–580.2004.

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.

Debinski, D.M. and Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14: 342-355.

Decho, A.W. (1994) Exopolymers in microbial mats: Assessing their adaptive role. In: *Microbial Mats: Structure, Development and Environmental Significance*. Stal, L. J. and Caumette, P. (eds.), Springer-Verlag: Berlin, 215-219.

Deming, J.W. (2002) Psychrophiles and polar regions. *Current Opinion in Microbiology* 5: 301-309.

Des Marais, D.J., Cohen, Y., Nguyen, H., Cheatham, M., Cheatham, T., and Munoz, E. (1989) Carbon isotopic trends in the hypersaline ponds and microbial mats at Guerrero Negro, Baja California Sur, Mexico: Implications for Precambrian stromatolites. In: *Microbial Mats: Physiological Ecology of Benthic Microbial Communities*. Cohen, Y. and Rosenberg, E. (eds.), American Society for Microbiology: Washington, D.C., 191-203.

Des Marais, D.J. (2003) Biogeochemistry of hypersaline microbial mats illustrates the dynamics of modern microbial ecosystems and the early evolution of the biosphere. *Biological Bulletin* 204: 160-167.

Doake, C.S.M., Corr, H.F.J., Rott, H., Skvarca, P., and Young, N.W. (1998) Breakup and conditions for stability of the northern Larsen Ice Shelf, Antarctica. *Nature* 391: 778-780, doi:10.1038/35832.

Dorrer, E. (1971) Movement of the Ward Hunt Ice Shelf, Ellesmere Island, N.W.T., Canada. *Journal of Glaciology* 10: 211-225.

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.

Dunlap, W.C. and Yamamoto, Y. (1995) Small-molecule antioxidants in marine organisms: antioxidant activity of mycosporine-glycine. *Comparative Biochemistry and Physiology* 112B: 105-114.

Edge, R., McGarvey, D.J., and Truscott, T.G. (1997) The carotenoids as anti-oxidants - a review. *Journal of Photochemistry and Photobiology B: Biology* 41: 189-200.

Ehling-Schulz, M., Bilger, W., and Scherer, S. (1997) UV-B-induced synthesis of photoprotective pigments and extracellular polysaccharides in the terrestrial cyanobacterium *Nostoc commune*. *Journal of Bacteriology* 179: 1940-1945.

Ehling-Schulz, M. and Scherer, S. (1999) UV protection in Cyanobacteria. *European Journal of Phycology* 34: 329-338.

Elster, J. (1999) Algal versatility in various extreme environments. In: *Enigmatic Microorganisms and Life in Extreme Environments*. Seckbach, J. (ed.), Kluwer Academic Publishers: Dordrecht, The Netherlands, 155-162.

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.

Estep, M.L.F. (1984) Carbon and hydrogen isotopic compositions of algae and bacteria from hydrothermal environments, Yellowstone National Park. *Geochimica et Cosmochimica Acta* 48: 591-599.

Evans, D.J.A. and England, J. (1992) Geomorphological evidence of Holocene climatic change from northwest Ellesmere Island, Canadian High Arctic. *The Holocence* 2: 148-158.

Fairchild, I.J. (1991) Origins of carbonate in neoproterozoic stromatolites and the identification of modern analogues. *Precambrian Research* 53: 281-300.

Falkowski, P.G. and Raven, J.A. (1997) *Aquatic photosynthesis*. Blackwell Science: Malden, Mass., 375 pp.

Farmer, J. (1992) Grazing and bioturbation in modern microbial mats. In: *The Proterozoic Biosphere*. Schopf, J. W. and Klein, C. (eds.), Cambridge University Press: New York, 295-297.

Fauque, G.D. (1995) Ecology of sulfate-reducing bacteria. In: *Sulfate-Reducing Bacteria*. Barton, L. L. (ed.), Plenum Press: New York, 217-241.

Fischer, H. and Pusch, M. (1999) Use of the [^{14}C]leucine incorporation technique to measure bacterial production in river sediments and the epiphyton. *Applied and Environmental Microbiology* 65: 4411-4418.

Fong, N.J., Burgess, M.L., Barrow, K.D., and Glenn, D.R. (2001) Carotenoid accumulation in the psychrotrophic bacterium *Arthrobacter agilis* in response to thermal and salt stress. *Applied Microbiology and Biotechnology* 56: 750-756, doi:10.1007/s002530100739.

Forbes, V.E. and Calow, P. (1997) Responses of aquatic organisms to pollutant stress: Theoretical and practical implications. In: *Environmental Stress, Adaptation, and Evolution*. Bijlsma, R. and Loeschcke, V. (eds.), Birkhäuser: Boston, 25-41.

Fountain, A.G., Tranter, M., Nylen, T.H., Lewis, K.J., and Mueller, D.R. (2004) Evolution of cryoconite holes and their contribution to melt-water runoff from glaciers in the McMurdo Dry Valleys, Antarctica. *Journal of Glaciology* 50: 35-45.

Francis, G.W., Hertzberg, S., Andersen, K., and Liaan-Jensen, S. (1970) New carotenoid glycosides from *Oscillatoria limosa*. *Phytochemistry* 9: 629-635.

Franks (1985) *Biophysics and Biochemistry at Low Temperatures*. Cambridge University Press: Cambridge, 210 pp.

Franks, F. (2000) *Water: A Matrix of Life*. 2nd ed. Royal Society of Chemistry: Cambridge, 225 pp.

Fujii, R., Chen, C.-H., Mizoguchi, T., and Koyama, Y. (1998) ^{1}H NMR, electronic-absorption and resonance-Raman spectra of isomeric okenone as compared with those of isomeric β-carotene, canathaxanthin, β-apo-8'-carotenal and spheroidene. *Spectrochimica Acta Part A* 54: 727-743.

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

Garcia-Pichel, F., Sherry, N.D., and Castenholz, R.W. (1992) Evidence for an ultraviolet sunscreen role of the extracellular pigment scytonemin in the terrestrial cyanobacterium *Chlorogloeopsis* sp. *Photochemistry and Photobiology* 56: 17-23.

Garcia-Pichel, F. and Castenholz, R. (1993a) Occurrence of UV-absorbing mycosporine-like compounds among cyanobacterial isolates and an estimate of their screening ability. *Applied and Environmental Microbiology* 59: 163-169.

Garcia-Pichel, F. and Castenholz, R. (1993b) Evidence regarding the UV sunscreen role of a mycosporine-like compound in the cyanobacterium *Gloeocapsa* sp. *Applied and Environmental Microbiology* 59: 170-176.

Gibson, J.A.E. and Andersen, D.T. (2002) Physical structure of epishelf lakes of the southern Bunger Hills, East Antarctica. *Antarctic Science* 14: 253-261.

Goericke, R., Montoya, J.P., and Fry, B. (1994) Physiology of isotopic fractionation in algae and cyanobacteria. In: *Stable Isotopes in Ecology and Environmental Science*. Lajtha, K. and Michener, R. H. (eds.), Blackwell Scientific: Boston, 187-221.

Golldack, D., Dietz, K.J., and Gimmler, H. (1995) The effects of sudden salt stress on protein synthesis in the green alga *Dunaliella parva*. *Journal of Plant Physiology* 146: 508-514.

Goodwin, T.W. (1980) *The Biochemistry of the Carotenoids*. 2nd ed. Chapman and Hall: New York, 377 pp.

Gow, A.J. and Epstein, S. (1972) On the use of stable isotopes to trace the origins of ice in a floating ice tongue. *Journal of Geophysical Research* 77: 6552-6557.

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

Greer, C.W., Whyte, L.G., Lawrence, J.R., Masson, L., and Brousseau, R. (2001) Current and future impact of genomics-based technologies on environmental science. *Environmental Science and Technology* 35: 360A-366A.

Guerrero, R., Urmeneta, J., and Rampone, G. (1993) Distribution of types of microbial mats at the Ebro Delta, Spain. *Biosystems* 31: 135-144.

Gunde-Cimerman, N., Sonjak, S., Zalar, P., Frisvad, J., Diderichsen, B., and Plemenitas, A. (2003) Extremophilic fungi in arctic ice: a relationship between adaptation to low temperature and water activity. *Physics and Chemistry of the Earth* 28: 1273-1278, doi:10.1016/j.pce.2003.08.056.

Habicht, K.S. and Canfield, D.E. (1996) Sulphur isotope fractionation in modern microbial mats and the evolution of the sulphur cycle. *Nature* 382: 342-343, doi:10.1038/382342a0.

Handfield, M., Jones, H.G., Letarte, R., and Simard, P. (1992) Seasonal fluctuation patterns of microflora on the Agassiz Ice Cap, Ellesmere Island, Canadian Arctic. *Musk-Ox* 39: 119-123.

Hattersley-Smith, G., Crary, A.P., and Christie, R.L. (1955) Northern Ellesmere Island, 1953-1954. *Arctic* 8: 3-36.

Hattersley-Smith, G. (1967) Note on ice shelves off the north coast of Ellesmere Island. *Arctic Circular* 17: 13-14.

Hattersley-Smith, G. and Serson, H. (1970) Mass balance of the Ward Hunt Ice Rise and Ice Shelf: a 10 year record. *Journal of Glaciology* 9: 247-252.

Hattersley-Smith, G. (1973) *Ice shelf and Fiord Ice Problems in Disraeli Fiord Northern Ellesmere Island, NWT.* Report Number 7234, Defence Research Establishment Ottawa: Ottawa.

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 Vincent, W.F. (1992) Desiccation and recovery of cyanobacterial mats. *Polar Biology* 12: 587-594.

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.

Hawes, I. and Howard-Williams, C. (1998) Primary production processes in streams of the McMurdo Dry Valleys, Antarctica. In: *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*. Priscu, J. C. (ed.), American Geophysical Union: Washington, 129-140.

Hawes, I. and Schwarz, A.M. (1999) Photosynthesis in an extreme shade environment: Benthic microbial mats from Lake Hoare, a permanently ice-covered Antarctic lake. *Journal of Phycology* 35: 448-459.

Hawes, I., Smith, R., Howard-Williams, C., and Schwarz, A.M. (1999) Environmental conditions during freezing, and response of microbial mats in ponds of the McMurdo Ice Shelf, Antarctica. *Antarctic Science* 11: 198-208.

Hertzberg, S. and Liaan-Jensen, S. (1969) The structure of oscillaxanthin. *Phytochemistry* 8: 1281-1292.

Heywood, R.B. (1977) A limnological survey of the Ablation Point area, Alexander Island, Antarctica. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 279: 39-54.

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

Hill, D.R., Hladun, S.L., Scherer, S., and Potts, M. (1994a) Water stress proteins of *Nostoc commune* (Cyanobacteria) are secreted with UV-A/B-absorbing pigments and associate with 1,4-β-D-xylanxylanohydrolase activity. *The Journal of Biological Chemistry* 269: 7726-7734.

Hill, D.R., Peat, A., and Potts, M. (1994b) Biochemistry and structure of the glycan secreted by desiccation-tolerant *Nostoc commune* (Cyanobacteria). *Protoplasma* 182: 126-148.

Hirschberg, J. and Chamovitz, D. (1994) Carotenoids in cyanobacteria. In: *The Molecular Biology of Cyanobacteria*. Bryant, D. A. (ed.), Kluwer Academic Publishers: Dordrecht, 559-579.

Hodgson, D., Vyverman, W., Verleyen, E., Sabbe, K., Leavitt, P., Taton, A., Squier, A., and Keely, B. (2004) Environmental factors influencing the pigment composition of in situ benthic microbial communities in east Antarctic lakes. *Aquatic Microbial Ecology* 37: 247-263.

Hoehler, T.M., Bebout, B.M., and Des Marais, D.J. (2001) The role of microbial mats in the production of reduced gases on the early Earth. *Nature* 412: 324-327, doi:10.1038/35085554.

Hoffman, P.F., Kaufman, A.J., Halverson, G.P., and Schrag, D.P. (1998) A Neoproterozoic snowball earth. *Science* 281: 1342-1346.

Holdsworth, G. (1971) Calving from Ward-Hunt Ice Shelf, 1961-1962. *Canadian Journal of Earth Sciences* 8: 299-305.

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.

Horikoshi, K. and Grant, W.D. (1998) *Extremophiles: Microbial Life in Extreme Environments*. Wiley-Liss, Inc.: New York, 322 pp.

Howard-Williams, C., Vincent, C.L., Broady, P.A., and Vincent, W.F. (1986) Antarctic stream ecosystems: Variability in environmental properties and algal community structure. *Internationale Revue der gesamten Hydrobiologie* 71: 511-544.

Howard-Williams, C., Pridmore, R.D., Downes, M.T., and Vincent, W.F. (1989) Microbial biomass, photosynthesis and chlorophyll *a* related pigments in the ponds of the McMurdo Ice Shelf, Antarctica. *Antarctic Science* 1: 125-131.

Howard-Williams, C. and Vincent, W.F. (1989) Microbial communities in southern Victoria Land streams (Antarctica). 1. Photosynthesis. *Hydrobiologia* 172: 27-38.

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: *Antarctic Ecosystems: Ecological Change and Conservation*. Kerry, K. R. and Hempel, G. (eds.), Springer-Verlag: Berlin, 23-31.

IPCC (2001) *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press: Cambridge, 881 pp.

Issaac, P. and Maslin, D. (1991) *Physical Hydrology of the McMurdo Ice Shelf*. Immediate Science Report K162, New Zealand Antarctic Research Programme: Christchurch.

Ito, S. and Hirata, Y. (1977) Isolation and structure of a mycosporine from the zoanthid. *Tetrahedron Letters* 18: 2429-2430.

Jackson, B.E. and McInerney, M.J. (2002) Anaerobic microbial metabolism can proceed close to thermodynamic limits. *Nature* 415: 454-456, doi:10.1038/415454a.

James, M.R., Hall, J.A., and Laybourn-Parry, J. (1998) Protozooplankton and microzooplankton ecology in lakes of the Dry Valleys, Southern Victoria Land. In: *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*. Priscu, J. C. (ed.), American Geophysical Union: Washington, 255-268.

Jeanjean, R., Matthijs, H.C.P., Onana, B., Havaux, M., and Joset, F. (1993) Exposure of the cyanobacterium *Synechocystis* PCC6803 to salt stress induces concerted changes in respiration and photosynthesis. *Plant & Cell Physiology* 34: 1073-1079.

Jeffrey, S.W., Mantoura, R.F.C., and Wright, S.W. (1997) *Phytoplankton Pigments in Oceanography*. SCOR UNESCO: Paris, 661 pp.

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. and Krouse, H.R. (1984) Arctic ice shelf growth, fiord oceanography and climate. *Zeitschrift für Gletscherkunde und Glazialgeologie* 20: 147-153.

Jeffries, M.O. (1986a) 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. (1986b) 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. (1987) Structure and growth of Arctic ice shelves and ice islands. *Workshop on Extreme Ice Features, Technical Memoir 141 (NRCC 28003)*: 39-51.

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: *Canada's Missing Dimension: Science and History in the Canadian Arctic Islands*. Harington, C. R. (ed.), Canadian Museum of Nature: Ottawa, 229-254.

Jeffries, M.O. (1991) Massive, ancient sea-ice strata and preserved physical-structural characteristics in the Ward Hunt Ice Shelf. *Annals of Glaciology* 15: 125-131.

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: *Satellite Image Atlas of Glaciers of the World: North America*. Williams, R. S. and Ferrigno, J. G. (eds.), United States Geological Survey: Washington, J147-J164.

JGOFS (1996) *Protocols for Joint Global Ocean Flux Study Core Measurements*. Joint Global Ocean Flux Study Report No 19, International Ocean Commission: Bergen, Norway.

Jørgensen, B.B. (1989) Light penetration, absorption, and action spectra in cyanobacterial mats. In: *Microbial Mats: Physiological Ecology of Benthic Microbial Communities*. Cohen, Y. and Rosenberg, E. (eds.), American Society of Microbiology: Washington, 123-137.

Jørgensen, B.B. (1994) Diffusion processes and boundary layers in microbial mats. In: *Microbial Mats: Structure, Development and Environmental Significance*. Stal, L. J. and Caumette, P. (eds.), Springer-Verlag: Berlin, 243-254.

Joye, S.B. and Paerl, H.W. (1994) Nitrogen cycling in microbial mats: rates and patterns of denitrification and nitrogen fixation. *Marine Biology* 119: 285-295.

Junge, K., Eicken, H., and Deming, J.W. (2004) Bacterial activity at -2 to -20 degrees C in Arctic wintertime sea ice. *Applied and Environmental Microbiology* 70: 550-557, doi:10.1128/AEM.70.1.550–557.2004.

Karentz, D., McEuen, F.S., Land, M.C., and Dunlap, W.C. (1991) Survey of mycosporine-like amino acid compounds in Antarctic marine organisms: potential protection from ultraviolet exposure. *Marine Biology* 108: 157-166.

Keys, J., Johannessen, O.M., and Long, A. (1968) *On the Oceanography of Disraeli Fjord on Northern Ellesmere Island*. Report Number 6, Marine Sciences Centre, McGill University: Montreal.

Keys, J.E. (1978) *Water Regime of Disraeli Fiord, Ellesmere Island*. Report Number 792, Defence Research Establishment Ottawa: Ottawa, Canada.

Kirchman, D.L. (1993a) Estimating conversion factors for the thymidine and leucine methods for measuring bacterial production. In: *Handbook of Methods in Aquatic Microbial Ecology*. Kemp, P. F., Sherr, B. F., Sherr, E. B., and Cole, J. J. (eds.), Lewis Publishers: Boca Raton, 513-517.

Kirchman, D.L. (1993b) Leucine incorporation as a measure of biomass production by heterotrophic bacteria. In: *Handbook of Methods in Aquatic Microbial Ecology*. Kemp, P. F., Sherr, B. F., Sherr, E. B., and Cole, J. J. (eds.), Lewis Publishers: Boca Raton, 509-512.

Kirk, J.T.O. (1983) *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press: Cambridge, 401 pp.

Kirschvink, J.L. (2002) Quand tous les océans étaient gelées. *La Recherche* 355: 26-30.

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

Koerner, R.M. (1973) The mass balance of the sea ice of the Arctic Ocean. *Journal of Glaciology* 12: 173-185.

Kohshima, S. (1984) A novel cold-tolerant insect found in a Himalayan glacier. *Nature* 310: 225-227, doi:10.1038/310225a0.

Krebs, C.J. (1994) *Ecology: The Experimental Analysis of Distribution and Abundance*. Fourth ed. Harper Collins College Publishers: New York, 801 pp.

Krembs, C., Gradinger, R., and Spindler, M. (2000) Implications of brine channel geometry and surface area for the interaction of sympagic organisms in Arctic sea ice. *Journal of Experimental Marine Biology and Ecology* 243: 55-80.

Krembs, C., Eicken, H., Junge, K., and Deming, J.W. (2003) High concentrations of exopolymeric substances in Arctic winter sea ice: Implications for the polar ocean carbon cycle and cryoprotection of diatoms. *Deep Sea Research Part I* 49: 2163-5181.

Ladas, N.P. and Papageorgiou, G.C. (2000) Cell turgor: A critical factor for the proliferation of cyanobacteria at unfavorable salinity. *Photosynthesis Research* 65: 155-164, doi:10.1023/A:1006423221150.

Lawson, J., Doran, P.T., Kenig, F., Des Marais, D.J., and Priscu, J.C. (2004) Stable carbon and nitrogen isotopic composition of benthic and pelagic organic matter in lakes of the McMurdo Dry Valleys, Antarctica. *Aquatic Geochemistry* 10: 269-301.

Laybourn-Parry, J., Quayle, W.C., Henshaw, T., Ruddell, A., and Marchant, H.J. (2001) Life on the edge: the plankton and chemistry of Beaver Lake, an ultra-oligotrophic epishelf lake, Antarctica. *Freshwater Biology* 46: 1205-1217.

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

Leslie, A. (1879) *The Arctic Voyages of A.E. Nordenskjöld*. MacMillan and Co.: London, 440 pp.

Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.

Lister, H. (1962) *Heat and Mass Balance at the Surface of the Ward Hunt Ice Shelf, 1960*. Research Report Number 19, Arctic Institute of North America: Washington, D.C.

Liu, H. and Buskey, E.J. (2000) Hypersalinity enhances the production of extracellular polymeric substance (EPS) in the Texas brown tide alga, *Aureoumbra lagunensis* (Pelagophyceae). *Journal of Phycology* 36: 71-77.

Lock, G.S.H. (1990) *The Growth and Decay of Ice*. Cambridge University Press: Cambridge, 434 pp.

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.

Lyons, J.B. and Mielke, J.E. (1973) Holocene history of a portion of northernmost Ellesmere Island. *Arctic* 26: 314-323.

Lyons, W.B., Hines, M.E., and Gaudette, H.E. (1984) Major and minor element pore water geochemistry of modern marine sabkhas: The influence of cyanobacterial mats. In: *Microbial Mats: Stromatolites*. Cohen, Y., Castenholz, R., and Halvorson, H. O. (eds.), Allan R Liss Inc: New York, 411-423.

MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press: Princeton, NJ, 203 pp.

MacAyeal, D., Scambos, T., Hulbe, C., and Fahnestock, M. (2003) Catastrophic ice-shelf break-up by an ice-shelf-fragment-capsize mechanism. *Journal of Glaciology* 49: 22-36.

Machalek, K.M., Davison, I.R., and Falkowski, P.G. (1996) Thermal acclimation and photoacclimation of photosynthesis in the brown alga *Laminaria saccharina*. *Plant Cell and Environment* 19: 1005-1016.

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

McIntyre, N.F. (1984) Cryoconite hole thermodynamics. *Canadian Journal of Earth Sciences* 21: 152-156.

McKnight, D.M., Alger, A., Tate, C.M., Shupe, G., and Spaulding, S. (1998) Longitudinal patterns in algal abundance and species distribution in meltwater streams in Taylor Valley, Southern Victoria Land, Antartctica. In: *Ecosystem Dynamics in a Polar Desert: The McMurdo Dry Valleys, Antarctica*. Priscu, J. C. (ed.), American Geophysical Union: Washington, 109-128.

McKnight, D.M., Boyer, E.W., Westerhoff, P.K., Doran, P.T., Kulbe, T., and Andersen, D.T. (2001) Spectrofluorometric characterization of dissolved organic matter for

indication of precursor organic material and aromaticity. *Limnology and Oceanography* 46: 38-48.

McLachlan, J.L., Curtis, J.M., Boutilier, K., Keusgen, M., and Seguel, M.R. (1999) *Tetreutreptia pomquetensis* (Euglenophyta), a psychrophilic species: Growth and fatty acid composition. *Journal of Phycology* 35: 280-286.

Mercer, J.H. (1978) West Antarctic ice sheet and CO_2 greenhouse effect: a threat of disaster. *Nature* 271: 321-325.

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.

Molitor, V., Kuntner, O., Sleytr, U.B., and Peschek, G.A. (1990) The ultrastructure of plasma and thylakoid membrane vesicles from the fresh water cyanobacterium *Anacystis nidulans* adapted to salinity. *Protoplasma* 157: 112-119.

Moorhead, D.L., Davis, W.S., and Wharton, R.A. (1997) Carbon dynamics of aquatic microbial mats in the Antarctic dry valleys: a modelling synthesis. In: *Ecosystem Processes in Antarctic Ice-Free Landscapes*. Lyons, W. B., Howard-Williams, C., and Hawes, I. (eds.), A.A. Balkema: Rotterdam, Netherlands, 181-196.

Morison, J., Aagaard, K., and Steele, M. (2000) Recent environmental changes in the Arctic: A review. *Arctic* 53: 359-371.

Morita, R.Y. (1975) Psychrophilic bacteria. *Bacteriological Reviews* 39: 144-167.

Moritz, R., E, Bitz, C.M., and Steig, E.J. (2002) Dynamics of recent climate change in the Arctic. *Science* 297: 1497-1502.

Morris, G.J. and Clarke, A. (1987) Cells at low temperature. In: *The Effects of Low Temperatures on Biological Systems*. Grout, B. W. W. and Morris, G. J. (eds.), Edward Arnold Ltd.: London, 72-119.

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., 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., Jeffries, M.O., and Vincent, W.F. (2003a) Ice shelf break-up and ecosystem loss in the Canadian High Arctic. *Eos, Transactions of the American Geophysical Union* 84: 548,552.

Mueller, D.R., Vincent, W.F., and Jeffries, M.O. (2003b) Break-up of the largest Arctic ice shelf and associated loss of an epishelf lake. *Geophysical Research Letters* 30: 2031, doi:10.1029/2003GL017931.

Mueller, D.R. and Vincent, W.F. (2005) Microbial habitat dynamics and ablation control on the Ward Hunt Ice Shelf. *Hydrological Processes*: In Press.

Mueller, D.R., Vincent, W.F., Bonilla, S., and Laurion, I. (2005a) Extremotrophs, extremophiles and broadband pigmentation strategies in a high arctic ice shelf ecosystem. *FEMS Microbiology Ecology* 53: 73-87, doi:10.1016/j.femsec.2004.11.001.

Mueller, D.R., Vincent, W.F., and Jeffries, M.O. (2005b) Fragmented habitats, environmental gradients and microbiota of a northern ice shelf cryo-ecosystem. *Arctic, Antarctic, and Alpine Research* Submitted.

Nadeau, T., Howard-Williams, C., and Castenholz, R. (1999) Effects of solar UV and visible irradiance on photosynthesis and vertical migration of *Oscillatoria* sp. in microbial mats. *Aquatic Microbial Ecology* 20: 231-243.

Nadeau, T.L. and Castenholz, R.W. (2000) Characterization of psychrophilic oscillatorians (Cyanobacteria) from Antarctic meltwater ponds. *Journal of Phycology* 36: 914-923.

Neale, P.J., Banaszak, A.T., and Jarriel, C.R. (1998) Ultraviolet sunscreens in *Gymnodinium sanguineum* (Dinophyceae): mycosporine-like amino acids protect against inhibition of photosynthesis. *Journal of Phycology* 34: 928-938.

Newton, J.L. and Sotirin, B.J. (1997) Boundary undercurrent and water mass changes in the Lincoln Sea. *Journal of Geophysical Research-Oceans* 102: 3393-3403.

Nisbet, E.G. and Fowler, C.M.R. (1999) Archaean metabolic evolution of microbial mats. *Proceedings of the Royal Society Biological Sciences Series B* 266: 2375-2382.

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

Oremland, R.S. and King, G.M. (1989) Methanogenisis in hypersaline environments. In: *Microbial Mats: Physiological Ecology of Benthic Microbial Communities*. Cohen, Y. and Rosenberg, E. (eds.), American Society for Microbiology: Washington, 180-190.

Overpeck, J., Hughen, K., Hardy, D., Bradley, R., Case, R., Douglas, M., Finney, B., Gajewski, K., Jacoby, G., Jennings, A., Lamoureux, S., Lasca, A., MacDonald, G., Moore, J., Retelle, M., Smith, S., Wolfe, A., and Zielinski, G. (1997) Arctic environmental change of the last four centuries. *Science* 278: 1251-1256.

Paerl, H.W. and Pinckney, J.L. (1996) A mini-review of microbial consortia: Their roles in aquatic production and biogeochemical cycling. *Microbial Ecology* 31: 225-247.

Parker, B.C., Simmons, G.M., Love, F.G., Wharton, R.A., and Seaburg, K.G. (1981) Modern stromatolites in Antarctic Dry Valley Lakes. *BioScience* 31: 656-660.

Parker, B.C. and Wharton, R.A. (1985) Physiological ecology of bluegreen algal mats (modern stromatolites) in Antarctic oasis lakes. *Archiv für Hydrobiologie/Algological Studies* 38/39: 331-348.

Peary, R.E. (1907) *Nearest the Pole*. Hutchinson: London, 411 pp.

Platt, T., Gallegos, C.L., and Harrison, W.G. (1980) Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *Journal of Marine Research* 38: 687-701.

Podgorny, I.A. and Grenfell, T.C. (1996) Absorption of solar energy in a cryoconite hole. *Geophysical Research Letters* 23: 2465-2468.

Price, P.B. (2000) A habitat for psychrophiles in deep Antarctic ice. *Proceedings of the National Academy of Sciences* 97: 1247-1251.

Price, P.B. and Sowers, T. (2004) Temperature dependance of metabolic rates for microbial growth, maintenance, and survival. *Proceedings of the National Academy of Sciences* 101: 4631-4636, doi:10.1073/pnas.0400522101.

Priscu, J.C. and Christner, B.C. (2004) Earth's icy biosphere. In: *Microbial Diversity and Bioprospecting*. Bull, A. (ed.), American Society for Microbiology: Washington, D.C., 130-145.

Priscu, J.C., Adams, E.E., Paerl, H.W., Fritsen, C.H., Dore, J.E., Lisle, J.T., Wolf, C.F., and Mikucki, J.A. (2005) Perennial Antarctic lake ice: A refuge for cyanobacteria in an extreme environment. In: *Life in Ancient Ice*. Rogers, S. and Castello, J. (eds.), Princeton Press: Princeton, 22-49.

Psenner, R. and Sattler, B. (1998) Life at the freezing point. *Science* 280: 2073-2074.

Quesada, A., Mouget, J.-L., and Vincent, W.F. (1995) Growth of antarctic cyanobacteria under ultraviolet radiation: UVA counteracts UVB inhibition. *Journal of Phycology* 31: 242-248.

Quesada, A., Vincent, W.F., and Lean, D.R.S. (1999) Community and pigment structure of Arctic cyanobacterial assemblages: the occurrence and distribution of UV-absorbing compounds. *FEMS Microbiology Ecology* 28: 315-323.

Rae, R., Howard-Williams, C., Hawes, I., and Vincent, W.F. (2000) Temperature dependence of photosynthetic recovery from solar damage in Antarctic phytoplankton. In: *Antarctic Ecosystems: Models for wider ecological understanding*. Davison, W., Howard-Willams, C., and Broady, P. A. (eds.), New Zealand Natural Sciences: Christchurch, New Zealand, 183-189.

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, doi:10.1016/j.soilbio.2004.05.017.

Raymond, J.A. and Fritsen, C.H. (2000) Ice-active substances associated with Antarctic freshwater and terrestrial photosynthetic organisms. *Antarctic Science* 12: 418-424.

Rigor, I.G., Colony, R.L., and Martin, S. (2000) Variations in surface air temperature observations in the Arctic, 1979-97. *Journal of Climate* 13: 896-914.

Rivkina, E.M., Friedmann, E.I., McKay, C.P., and Gilichinsky, D.A. (2000) Metabolic activity of permafrost bacteria below the freezing point. *Applied and Environmental Microbiology* 66: 3230-3233.

Robin, G. and Adie, R.J. (1964) The ice cover. In: *Antarctic Research*. Priestley, R., Adie, R. J., and Robin, G. (eds.), Butterworths: London, 100-118.

Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M.L., Fitch, H.S., and Martinko, E.A. (1992) Diverse and contrasting effects of habitat fragmentation. *Science* 257: 524-527.

Roos, J.C. and Vincent, W.F. (1998) Temperature dependence of UV radiation effects on Antarctic cyanobacteria. *Journal of Phycology* 34: 118-125.

Rosing, M.T. and Frei, R. (2004) U-rich Archaean sea-floor sediments from Greenland - indications of > 3700 Ma oxygenic photosynthesis. *Earth and Planetary Science Letters* 217: 237-244, doi:10.1016/S0012-821X(03)00609-5.

Russell, N.C. (1990) Cold adaptation of microorganisms. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 326: 595-611.

Russell, N.J. and Hamamoto, T. (1998) Psychrophiles. In: *Extremophiles: Microbial Life in Extreme Environments*. Horikoshi, K. and Grant, W. D. (eds.), Wiley-Liss, Inc.: New York, 25-45.

Sabbe, K., Hodgson, D., Verleyen, E., Taton, A., Wilmotte, A., Vanhoutte, K., and Vyverman, W. (2004) Salinity, depth and the structure and composition of microbial mats in continental Antarctic lakes. *Freshwater Biology* 49: 296-319.

Sakshaug, E., Bricaud, A., Dandonneau, Y., Falkowski, P.G., Kiefer, D.A., Legendre, L., Morel, A., Parslow, J., and Takahashi, M. (1997) Parameters of photosynthesis: definitions, theory and interpretation of results. *Journal of Plankton Research* 19: 1637-1670.

Sattler, B., Puxbaum, H., and Psenner, R. (2001) Bacterial growth in supercooled cloud droplets. *Geophysical Research Letters* 28: 239-242.

Scambos, T.A., Hulbe, C., Fahnestock, M., and Bohlander, J. (2000) The link between climate warming and break-up of ice shelves in the Antarctic Peninsula. *Journal of Glaciology* 46: 516-530.

Scherer, S., Chen, T.W., and Böger, P. (1988) A new UV-A/B protecting pigment in the terrestrial cyanobacterium *Nostoc commune*. *Plant Physiology* 88: 1055-1057.

Schidlowski, M., Matzigkeit, U., and Krumbein, W.E. (1984) Superheavy organic carbon from hypersaline microbial mats: Assimilatory pathway and geochemical implications. *Naturwissenschaften* 71: 303-308.

Schraeder, R.L. (1968) Ablation of Ice Island ARLIS II, 1961. MSc Thesis, Department of Geology, University of Alaska, College, AK. 59 pp.

Schubert, H., Fulda, S., and Hagemann, M. (1993) Effects of adaptation to different salt concentrations on photosynthesis and pigmentation of the cyanobacterium *Synechocystis* sp. PCC 6803. *Journal of Plant Physiology* 142: 291-295.

Schülter, L., Garde, K., and Kaas, H. (2004) Detection of the toxic cyanobacteria *Nodularia spumigena* by means of a 4-keto-myxoxanthophyll-like pigment in the Baltic Sea. *Marine Ecology Progress Series* 275: 69-78.

Serson, H.V. (1979) *Mass Balance of the Ward Hunt Ice Rise and Ice Shelf: An 18-Year Record*. Report Number 79-4, Defence Establishment Pacific, Victoria: Victoria, B.C.

Sharp, R.P. (1949) Studies of superglacial debris on valley glaciers. *American Journal of Science* 247: 289-315.

Sheath, R.G., Vis, M.L., Hambrook, J.A., and Cole, K.M. (1996) Tundra stream macroalgae of North America: composition, distribution and physiological adaptations. *Hydrobiologia* 336: 67-82.

Sheath, R.G. and Müller, K.M. (1997) Distribution of stream macroalgae in four High Arctic drainage basins. *Arctic* 50: 335-364.

Shepherd, A., Wingham, D., Payne, T., and Skvarca, P. (2003) Larsen ice shelf has progressively thinned. *Science* 302: 856-859.

Shick, J.M., Romaine-Lioud, S., Ferrier-Pagès, C., and Gattuso, J.P. (1999) Ultraviolet-B radiation stimulates shikimate pathway-dependent accumulation of mycosporine-like amino acids in the coral *Stylophora pistillata* despite decreases in its population of symbiotic dinoflagellates. *Limnology and Oceanography* 44: 1667-1682.

Short, C. and Suttle, C. (2005) Nearly identical bacteriophage structural gene sequences are widely distributed in both marine and freshwater environments. *Applied and Environmental Microbiology* 71: 480-486, doi:10.1128/AEM.71.1.480–486.2005.

Shpaikher, A.O. (1969) Oceanographic characterization of Disraeli Fiord (Ellesmere Island). *Problemy Arktiki i Antarktiki* 32: 511-518.

Smith, B.N. (1997) The origin and evolution of C_4 photosynthesis. In: *Handbook of Photosynthesis*. Pessarakli, M. (ed.), Marcel Dekker Inc.: New York, 977-986.

Smith, D.D. (1961) Sequential development of surface morphology on Fletcher's Ice Island, T-3. In: *Geology of the Arctic*. Raasch, G. O. (ed.), University of Toronto Press: Toronto, 896-914.

Smith, D.D. (1964) Ice lithologies and structure of Ice Island ARLIS II. *Journal of Glaciology* 5: 17-38.

Sommaruga, R. and Garcia-Pichel, F. (1999) UV-absorbing mycosporine-like compounds in planktonic and benthic organisms from a high-mountain lake. *Archiv für Hydrobiologie* 144: 255-269.

Sorensen, K., Canfield, D., and Oren, A. (2004) Salinity responses of benthic microbial communities in a solar saltern (Eilat, Israel). *Applied and Environmental Microbiology* 70: 1608-1616, doi:10.1128/AEM.70.3.1608–1616.2004.

Spindler, M. (1994) Notes on the biology of sea ice in the Arctic and Antarctic. *Polar Biology* 14: 319-324.

Squier, A.H., Airs, R.L., Hodgson, D.A., and Keely, B.J. (2004a) Atmospheric pressure chemical ionisation liquid chromatography/mass spectrometry of the ultraviolet screening pigment scytonemin: characteristic fragmentations. *Rapid Communications in Mass Spectrometry* 18: 2934–2938, doi:10.1002/rcm.1714.

Squier, A.H., Hodgson, D.A., and Keely, B.J. (2004b) A critical assessment of the analysis and distributions of scytonemin and related UV screening pigments in sediments. *Organic Geochemistry* 35: 1221–1228, doi:10.1016/j.orggeochem.2004.07.005.

Stal, L. (2003) Microphytobenthos, their extracellular polymeric substances, and the morphogenesis of intertidal sediments. *Geomicrobiology Journal* 20: 463-478, doi:10.1080/01490450390237157.

Stal, L.J. (1994) Microbial mats in coastal environments. In: *Microbial Mats: Structure, Development and Environmental Significance*. Stal, L. J. and Caumette, P. (eds.), Springer-Verlag: Berlin, 21-32.

Stal, L.J. (1995) Physiological ecology of cyanobacteria in microbial mats and other communities. *New Phytologist* 131: 1-32.

Staley, J.T. and Gosink, J.J. (1999) Poles apart: Biodiversity and biogeography of sea ice bacteria. *Annual Review of Microbiology* 53: 189-215.

Stefels, J. (2000) Physiological aspects of the production and conversion of DMSP in marine algae and higher plants. *Journal of Sea Research* 43: 183-197.

Strickland, J.D.H. and Parsons, T.R. (1972) *A Practical Handbook of Seawater Analysis*. Bulletin of the Fisheries Research Board of Canada 167, Fisheries Research Board, Canada: Ottawa.

Sumner, D.Y. (2001) Microbial influences on local carbon isotopic ratios and their preservation in carbonate. *Astrobiology* 1: 57-70.

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

Takeuchi, N., Kohshima, S., and Fujita, K. (1998) Snow algae community on a Himalayan glacier, Glacier AX010 East Nepal: Relationship with glacier summer mass balance. *Bulletin of Glacier Research* 16: 43-50.

Takeuchi, N., Kohshima, S., and Seko, K. (2001) Structure, formation, and darkening process of albedo-reducting material (cryoconite) on a Himalayan glacier: A granular algal mat growing on the glacier. *Arctic, Antarctic, and Alpine Research* 33: 115-122.

Tang, E.P.Y., Tremblay, R., and Vincent, W.F. (1997) Cyanobacteria dominance of polar freshwater ecosystems: are high-latitude mat-formers adapted to low temperature? *Journal of Phycology* 33: 171-181.

Tang, E.P.Y. and Vincent, W.F. (1999) Strategies of thermal adaptation by high-latitude cyanobacteria. *New Phytologist* 142: 315-323.

Taton, A., Grubisic, S., Brambilla, E., De Wit, R., and Wilmotte, A. (2003) Cyanobacterial diversity in natural and artificial microbial mats of Lake Fryxell (McMurdo dry valleys, Antarctica): A morphological and molecular approach. *Applied and Environmental Microbiology* 69: 5157-5169, doi:10.1128/AEM.69.9.5157–5169.2003.

Taylor, M.J. (1987) Physico-chemical principles in low temperature biology. In: *The Effects of Low Temperatures on Biological Systems*. Grout, B. W. W. and Morris, G. J. (eds.), Edward Arnold Ltd.: London, 3-71.

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.* Microcomputer Power: Ithaca, New York, 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.

Thomas, D.N. and Dieckmann, G.S. (2002) Antarctic sea ice - a habitat for extremophiles. *Science* 295: 641-644.

Tilman, D.R., May, R.M., Lehman, C.L., and Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature* 371: 66, doi:10.1038/371065a0.

Tindall, B. (2004) Prokaryotic diversity in the Antarctic: The tip of the iceberg. *Microbial Ecology* 47: 271 - 283, doi:10.1007/s00248-003-1050-7.

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

Tuominen, L. (1995) Comparison of leucine uptake methods and a thymidine incorporation method for measuring bacterial activity in sediment. *Journal of Microbiological Methods* 24: 125-134.

Turner, M.A., Howell, E.T., Robinson, G.G.C., Campbell, P., Hecky, R.E., and Schindler, E.U. (1994) Roles of nutrients in controlling growth of epilithon in oligotrophic lakes of low alkalinity. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 2784-2793.

van den Ende, F.P. and van Gemerden, H. (1994) Relationships between functional groups of organisms in microbial mats. In: *Microbial Mats: Structure, Development and Environmental Significance*. Stal, L. J. and Caumette, P. (eds.), Springer-Verlag: Berlin, 339-352.

Van Hove, P., Swadling, K., Gibson, J.A.E., Belzile, C., and Vincent, W.F. (2001) Farthest north lake and fiord populations of calanoid copepods *Limnocalanus macrurus* and *Drepanopus bungei* in the Canadian high Arctic. *Polar Biology* 24: 303-307, doi:10.1007/s003000000207.

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. 148 pp.

Vaughan, D.G. and Doake, C.S.M. (1996) Recent atmospheric warming and retreat of ice shelves on the Antarctic Peninsula. *Nature* 379: 328-331, doi:10.1038/379328a0.

Vaughan, D.G., Marshall, G.J., Connolley, W.M., Parkinson, C., Mulvaney, R., Hodgson, D.A., King, J.C., Pudsey, C.J., and Turner, J. (2003) Recent rapid regional climate warming on the Antarctic Peninsula. *Climatic Change* 60: 243-274.

Vézina, S. and Vincent, W.F. (1997) Arctic cyanobacteria and limnological properties of their environment: Bylot Island, Northwest Territories, Canada (73°N, 80°W). *Polar Biology* 17: 523-534.

Villeneuve, V. (2000) Algues benthiques du haut Arctique canadien: microhabitat et évaluation des facteurs de contrôle chimiques. MSc Thesis, Department of Biology, Laval University, Quebec, QC. 125 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. and Howard-Williams, C. (1986) Antarctic stream ecosystems: physiological ecology of a blue-green algal epilithon. *Freshwater Biology* 16: 219-233.

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

Vincent, W.F. and Howard-Williams, C. (1989) Microbial communities in southern Victoria Land streams (Antarctica). 2. The effects of low temperature. *Hydrobiologia* 172: 39-49.

Vincent, W.F. (1990) The dynamic coupling between photosynthesis and light in the phytoplankton environment. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 24: 25-37.

Vincent, W.F., Castenholz, R.W., Downes, M.T., and Howard-Williams, C. (1993a) Antarctic cyanobacteria: Light, nutrients, and photosynthesis in the microbial mat environment. *Journal of Phycology* 29: 745-755.

Vincent, W.F., Downes, M.T., Castenholz, R.W., and Howard-Williams, C. (1993b) Community structure and pigment organisation of cyanobacteria-dominated microbial mats in Antarctica. *European Journal of Phycology* 28: 213-221.

Vincent, W.F., Howard-Williams, C., and Broady, P.A. (1993c) Microbial communities and processes in Antarctic flowing waters. In: *Antarctic Microbiology*. Friedmann, E. I. (ed.), Wiley-Liss Inc.: New York, 543-569.

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. (1997) Polar desert ecosystems in a changing climate: A north-south perspective. In: *Ecosystem Processes in Antarctic Ice-Free Landscapes*. Lyons, W. B., Howard-Willams, C., and Hawes, I. (eds.), A.A. Balkema: Rotterdam, 3-14.

Vincent, W.F. and Quesada, A. (1997) Microbial niches in the polar environment and the escape from UV radiation in non-marine habitats. In: *Antarctic Communities: Species, Structure and Survival*. Battaglia, B., Valencia, J., and Walton, D. (eds.), Cambridge University Press: Cambridge, 388-395.

Vincent, W.F. (2000) Cyanobacterial dominance in the polar regions. In: *The Ecology of Cyanobacteria: Their Diversity in Time and Space*. Whitton, B. A. and Potts, M. (eds.), Kluwer Academic Press: The Netherlands, 321-340.

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. and Howard-Williams, C. (2000) Life on snowball Earth. *Science* 287: 2421.

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. (2004a) Ecosystems on ice: the microbial ecology of Markham Ice Shelf in the high Arctic. *Cryobiology* 48: 103-112, doi:10.1016/j.cryobiol.2004.01.006.

Vincent, W.F., Mueller, D.R., and Van Hove, P. (2004b) Break-up and climate change at Canada's northern coast, Quttinirpaaq National Park. *Meridian* Spring/Summer 2004: 1-6.

Vincent, W.F., Mueller, D.R., Van Hove, P., and Howard-Williams, C. (2004c) Glacial periods on early Earth and implications for the evolution of life. In: *Origins: Genesis, Evolution and Diversity of Life*. Seckbach, J. (ed.), Kluwer Academic Publishers: Dortrecht, 481-501.

Wada, E., Shibata, R., and Torii, T. (1981) ^{15}N abundance in Antarctica: origin of soil nitrogen and ecological implications. *Nature* 292: 327-329, doi:10.1038/292327a0.

Ward, D.M., Weller, R., Shiea, J., Castenholz, R.W., and Cohen, Y. (1989) Hot spring microbial mats: Anoxygenic and oxygenic mats of possible evolutionary

significance. In: *Microbial Mats: Physiological Ecology of Benthic Microbial Communities*. Cohen, Y. and Rosenberg, E. (eds.), American Society for Microbiology: Washington, D.C., 3-15.

Ward, D.M., Ferris, M.J., Nold, S.C., Bateson, M.M., Kopczynski, E.D., and Ruff-Roberts, A.L. (1994) Species diversity in hot spring microbial mats as revealed by both molecular and enrichment culture approaches - relationship between biodiversity and community structure. In: *Microbial Mats: Structure, Development and Environmental Significance*. Stal, L. J. and Caumette, P. (eds.), Springer-Verlag: Berlin, 33-44.

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

Wharton, R.A., Parker, B.C., and Simmons, G.M. (1983) Distribution, species composition and morphology of algal mats in Antarctic dry valley lakes. *Phycologia* 22: 355-365.

Wieland, A. and Kuhl, M. (2000) Irradiance and temperature regulation of oxygenic photosynthesis and O_2 consumption in a hypersaline cyanobacterial mat (Solar Lake, Egypt). *Marine Biology* 137: 71-85.

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.

Wilson, J.W. (1955) The initiation of dirt cones on snow. *Journal of Glaciology*: 281-287.

With, K.A. and Crist, T.O. (1995) Critical thresholds in species' responses to landscape structure. *Ecology* 76: 2446-2459.

Wolff, J.O., Schauber, E.M., and Edge, W.D. (1997) Effects of habitat loss and fragmentation on the behaviour and demography of gray-tailed voles. *Conservation* Biology 11: 945-956.

Wynn-Williams, D.D., Russell, N.C., and Edwards, H.G.M. (1997) Moisture and habitat structure as regulators for microalgal colonists in diverse Antarctic terrestrial habitats. In: Ecosystem Processes in Antarctic Ice-Free Landscapes. Lyons, W. B., Howard-Willams, C., and Hawes, I. (eds.), Balkema: Rotterdam, 77-88.

Wynn-Williams, D.D. (2000) Cyanobacteria in deserts - Life at the limit? In: The Ecology of Cyanobacteria: Their Diversity in Time and Space. Whitton, B. A. and Potts, M. (eds.), Kluwer Academic Press: The Netherlands, 341-366.

Yallop, M.L., Dewinder, B., Paterson, D.M., and Stal, L.J. (1994) Comparative structure, primary production and biogenic stabilization of cohesive and noncohesive marine-

sediments inhabited by microphytobenthos. Estuarine Coastal and Shelf Science 39: 565-582.

Zapata, M., Rodriguez, F., and Garrido, J.L. (2000) Separation of chlorophylls and carotenoids from marine phytoplankton: a new HPLC method using a reversed phase C8 column and pyridine containing mobile phases. Marine Ecology Progress Series 195: 29-45.

Zinger, E.M. and Koryakin, V.S. (1965) Are there ice shelves on Severnaya Zemlya? Data of Glaciological Studies 11: 250-253.

Annexe 1. Photographies du cryo-écosystème des plates-formes de glace nordiques

Figure A1.1 La plate-forme de glace Ward Hunt, juillet 2004 (D. Sarrazin).

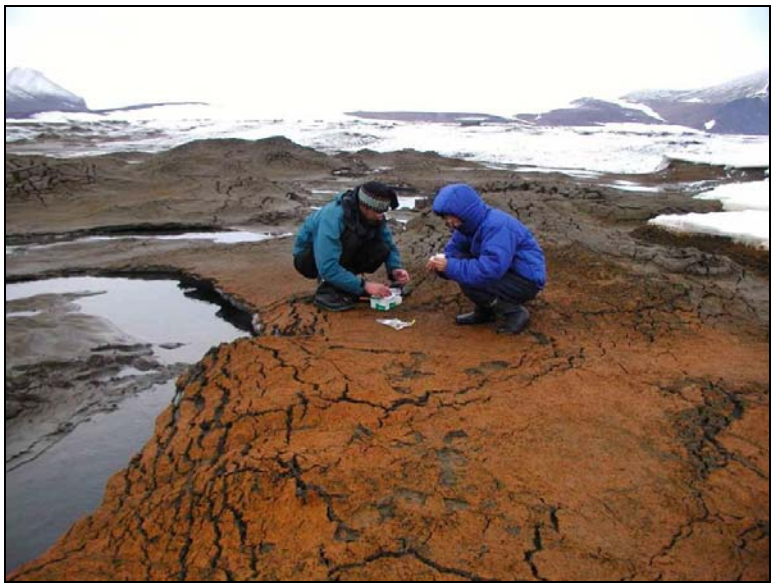

Figure A1.2. Échantillonnage du tapis microbien sur la plate-forme de glace Markham, juillet 2003 (W.F. Vincent).

Figure A1.3. Fissures dans la plate-forme de glace Ward Hunt, juillet 2002 (V.Sahanatien).

Figure A1.4. Profilage du fjord Disraeli, juillet 2004 (D. Sarrazin).