Université du Québec
à Rimouski

STRUCTURE ET FONCTIONNEMENT DES COMMUNAUTÉS MICROBIENNES DANS LA GLACE ANNUELLE ET PLURIANNUELLE DE LA MER DE LINCOLN AU PRINTEMPS

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AVANT-PROPOS

Ce mémoire traite de la structure et du fonctionnement des communautés microbiennes dans la glace annuelle et pluriannuelle de la mer de Lincoln au printemps. Il est constitué d'un résumé en français et en anglais, d'une introduction générale, d'un chapitre central rédigé sous la forme d'un article scientifique et d'une conclusion générale. Les résultats de cette étude ont été présentés au cours de divers ateliers et congrès scientifiques.

Duffaud C, Gosselin M, Charette J, Campbell K, Lange B, Galindo V, Coupel P, Duerksen S, Tremblay P, Belzile C, Michel C. **(**2020) Structure and function of the microbial loop in spring first-year ice and multiyear ice of the Lincoln Sea. Multidisciplinary Arctic Program (MAP) – Last Ice Workshop, Winnipeg, Canada, 28 – 29 janvier (Présentation orale).

Duffaud C. **(**2019) Répartition verticale des bactéries et des virus dans la glace annuelle et pluriannuelle de la mer de Lincoln au cours du printemps. Présentation des résultats de maîtrise, Institut des sciences de la mer de Rimouski, Rimouski, Canada, 16 décembre (Présentation orale).

Duffaud C, Gosselin M, Charette J, Campbell K, Lange B, Galindo V, Coupel P, Duerksen S, Tremblay P, Belzile C, Michel C. (2019) Influence of environmental factors on the spatial distribution of microbial communities in first-year ice and multiyear ice of the Lincoln Sea during spring. Multidisciplinary Arctic Program (MAP) – Last Ice Workshop, Winnipeg, Canada, 22 – 23 janvier (Présentation orale).

Duffaud C, Gosselin M, Charette J, Galindo V, Campbell K, Lange B, Coupel P, Duerksen S, Tremblay P, Belzile C, Michel C. (2019) Spring distribution of bacteria and viruses

in first-year and multiyear sea ice of the Lincoln Sea. International Glaciological Society – Sea Ice Symposium 2019, Winnipeg, Canada, 19 – 23 août (Affiche).

Duffaud C, Gosselin M, Charette J, Campbell K, Lange B, Galindo V, Coupel P, Duerksen S, Tremblay P, Belzile C, Michel C. **(**2018) Répartition verticale des bactéries et des virus dans la glace annuelle et pluriannuelle de la mer de Lincoln au cours du printemps. Assemblée générale annuelle de Québec-Océan, Rivière-du-Loup, Canada, 5 – 6 novembre (Affiche).

RÉSUMÉ

La glace de mer est un écosystème unique au sein des régions polaires qui constitue un habitat pour une communauté de microorganismes diversifiée, active et spécialisée associée à la glace. La diminution de l'étendue et de l'épaisseur de glace de mer dans l'océan Arctique et le remplacement progressif de la glace pluriannuelle par la glace annuelle modifient l'habitat des communautés microbiennes présentes dans la glace de mer. Dans ce contexte de changement climatique et en raison de leur rôle central dans les cycles biogéochimiques des milieux marins, il est essentiel de caractériser la dynamique microbienne dans la glace de mer. Dans cette étude, nous évaluons la structure et le fonctionnement des communautés microbiennes dans la glace de mer annuelle et pluriannuelle de la mer de Lincoln en déterminant la répartition des bactéries et des virus ainsi que leur relation avec les facteurs biotiques et abiotiques. Nos résultats révèlent de forts gradients verticaux dans la répartition verticale des bactéries et des virus dans la glace de mer où les abondances sont plus élevées à la base de la glace. De plus, la répartition verticale des bactéries et des virus est similaire à celle des nutriments, du carbone organique dissous (COD) et de la chlorophylle *a* (chl *a*). Des relations significatives et positives entre l'abondance des bactéries et des virus et le phosphate, le COD, la chl *a* et le volume de saumure (un indice de la perméabilité de la glace) ont été mises en évidence pour la glace de mer annuelle et pluriannuelle en période printanière. Un modèle écologique basé sur l'analyse des coefficients de direction a révélé un réseau trophique microbien dans la glace de mer du Haut-Arctique canadien et un couplage étroit entre les bactéries et les algues via le COD et le phosphate. La même analyse souligne que les virus dans la glace de mer sont essentiellement bactériophages. Ce projet fournit de nouvelles connaissances sur la structure et le fonctionnement des microorganismes dans la glace annuelle et pluriannuelle de la mer de Lincoln, une région unique où la glace pluriannuelle devrait persister au cours des prochaines décennies.

Mots clés : Glace de mer, bactéries, virus, répartition verticale, réseau microbien, mer de Lincoln, zone séculaire de glace, Haut-Arctique canadien

ABSTRACT

Sea ice is a unique ecosystem within the polar regions and constitutes a habitat for a diverse, active and specialized ice-associated community of microorganisms. The decline in sea ice extent and thickness in the Arctic Ocean and the gradual replacement of multiyear ice by first-year ice significantly alters the habitat of sea-ice microbial communities. In this context of climate change and due to their central role in biogeochemical cycles in marine systems, it is essential to characterize the dynamics of sea-ice microbes. In this study, we assess the structure and function of microbial communities in first-year and multiyear ice in the Lincoln Sea by determining the distribution of bacteria and viruses and their relationships with biotic and abiotic variables. Our results show strong vertical gradients in the distribution of bacteria and viruses in the ice, with higher bacterial and viral abundances at the bottom ice horizon. The vertical distribution of bacteria and viruses in the ice was closely related to that of nutrients, dissolved organic carbon (DOC) and chlorophyll *a* (chl *a*). Significant and positive relationships were found between bacterial and viral abundances and phosphate, DOC, chl *a* and brine volume (a proxy of sea ice permeability) in first-year and multiyear ice during spring. Ecological modelling through path analysis reveals an active microbial food web in the sea ice of the Canadian High Arctic and a tight coupling between bacteria and sea ice algae via DOC and phosphate. The same analysis highlights that viruses in sea ice are likely bacteriophages. This study provides new knowledge on the structure and functioning of microorganisms in first-year and multiyear ice in the Lincoln Sea, a unique region where multiyear ice is predicted to persist over the next decades.

Keywords: Sea ice, bacteria, viruses, vertical distribution, microbial food web, Lincoln Sea, Last Ice, Canadian High Arctic

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LISTE DES ACRONYMES

ANOVA	Analysis of variance
BV	Brine volume
CFS	Canadian Forces Station
chl *a*	chlorophylle *a* (chlorophyll *a*)
CTD	Conductivity – Temperature - Depth
DOC	Dissolved organic carbon
DOM	Dissolved organic matter
FYI	First-year ice
GF/F	Glass microfiber filter
MOD	Matière organique dissoute
MYI	Multiyear ice
nd	no data
ns	not significant
NO_2	Nitrite
NO_3	Nitrate
PO_4	Phosphate
S	Salinity

SD	Standard deviation
$Si(OH)_4$	Silicic acid
T°C	Temperature

INTRODUCTION GÉNÉRALE

LA GLACE DE MER

La glace de mer est un des plus grands biomes sur Terre et l'habitat marin le plus froid, couvrant jusqu'à 4% de la surface de la Terre (Dieckmann & Hellmer 2010, Arrigo 2014). C'est un environnement dynamique au sein des régions polaires dont l'étendue fluctue de plus du double entre la couverture minimale en été et la couverture maximale en hiver (Comiso 2010). Au cours des 40 dernières années, l'étendue minimale de la glace de mer arctique a diminué de 7×10^6 km² en septembre 1979 à $4{,}2 \times 10^6$ km² en septembre 2019 tandis que l'étendue minimale de la glace de mer antarctique a varié de $3{,}1 \times 10^6$ km² en février 1979 à $2{,}5 \times 10^6$ km² en février 2019 (NSIDC 2020).

La glace de mer constitue un environnement unique au sein de l'écosystème marin polaire (Figure 1). Elle est utilisée par les mammifères marins (p. ex., ours polaires, phoques et morses) pour leur alimentation et leur reproduction et par les communautés autochtones pour la chasse et le transport. Elle constitue également un substrat pour les producteurs primaires et secondaires. En effet, on retrouve une communauté diversifiée, active et spécialisée de microorganismes qui colonisent les interstices de la glace. Les principaux groupes qu'on y retrouve sont les algues unicellulaires et les bactéries hétérotrophes qui constituent une source de nourriture pour les petits brouteurs vivant dans la glace tels que les flagellés, dinoflagellés et ciliés hétérotrophes. D'autres brouteurs de plus grande taille sont également associés à la glace de mer, par exemple la méiofaune de glace, les amphipodes sous la glace et le copépode pélagique *Calanus glacialis* (Mock & Thomas 2005, Becquevort et al. 2009, Arrigo 2014). Lorsqu'elles sont libérées dans la colonne d'eau, les algues de glace sont également consommées par les herbivores pélagiques et les organismes benthiques (Michel et al. 2002, Morata et al. 2011, Bluhm et al. 2018).

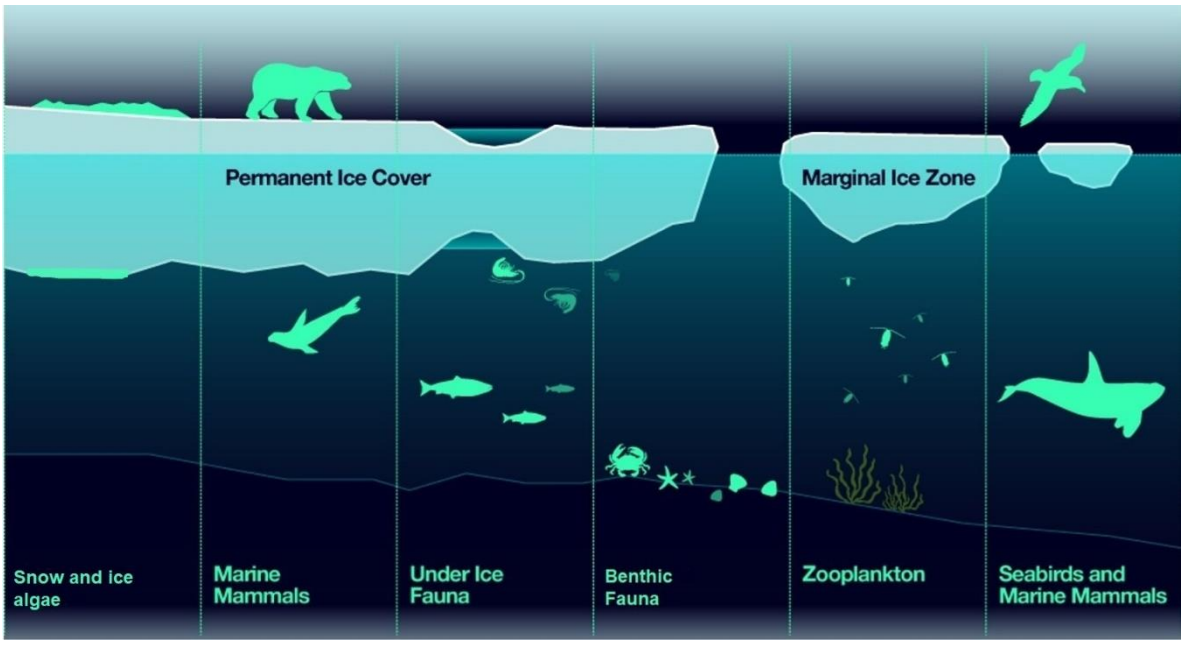

Figure 1. Représentation schématique de l'écosystème marin polaire associée à la glace de mer. Modifiée de CAFF (2010)

La glace de mer arctique se caractérise par la glace annuelle qui se retrouve surtout sur les plateaux continentaux de l'océan Arctique et la glace pluriannuelle qui couvre en grande partie les bassins océaniques (Wadhams 2000, Polyakov et al. 2012). La glace annuelle se forme à l'automne, et fond l'été suivant tandis que la glace pluriannuelle subsiste à la fonte estivale et s'épaissit d'une année à l'autre, à mesure que de la nouvelle glace se forme en dessous de celle de l'année précédente (Wadhams 2000, AMAP 2011). Ainsi, la glace pluriannuelle se compose d'au moins deux couches dont une, plus âgée, qui a survécu à la fonte estivale ainsi que d'une couche de glace annuelle qui se développe à la base de la couche de glace plus âgée. La glace de mer pluriannuelle au nord de l'île d'Ellesmere a une épaisseur moyenne comprise entre 2 et 3,4 m (Haas et al. 2017). L'épaisseur de glace et la salinité sont les principaux facteurs physiques qui accentuent les différences entre la glace annuelle et la glace pluriannuelle. Ces deux types de glace présentent également de forts gradients verticaux de température, de volume de saumure, de lumière et de concentrations de nutriments (Eicken 2003). Lors de la formation de la glace de mer, la saumure contenue dans l'eau est rejetée dans la colonne d'eau par le biais de canaux de saumure qui se

développent à mesure que la glace s'épaissit alors que la salinité élevée dans ces canaux maintient la saumure à l'état liquide (Figure 2). Les canaux de saumure forment un système semi-fermé où les conditions physico-chimiques sont très variables (Thomas & Dieckmann 2010). En effet, la température et la salinité influencent le volume de saumure. À basse température, les canaux de saumure sont étroits et la saumure plus concentrée tandis qu'à des températures plus élevées, les canaux de saumure s'élargissent, se connectent et la glace de mer devient perméable (Petrich & Eicken 2017). À des températures supérieures à -5°C et une salinité de 5 ou un volume de saumure de 5%, la glace de mer devient perméable et permet le transport de fluides et des nutriments (Golden et al. 1998). La petite taille des canaux de saumure peut limiter la taille des organismes qui colonisent la glace, favorisant ainsi le développement de communautés microbiennes.

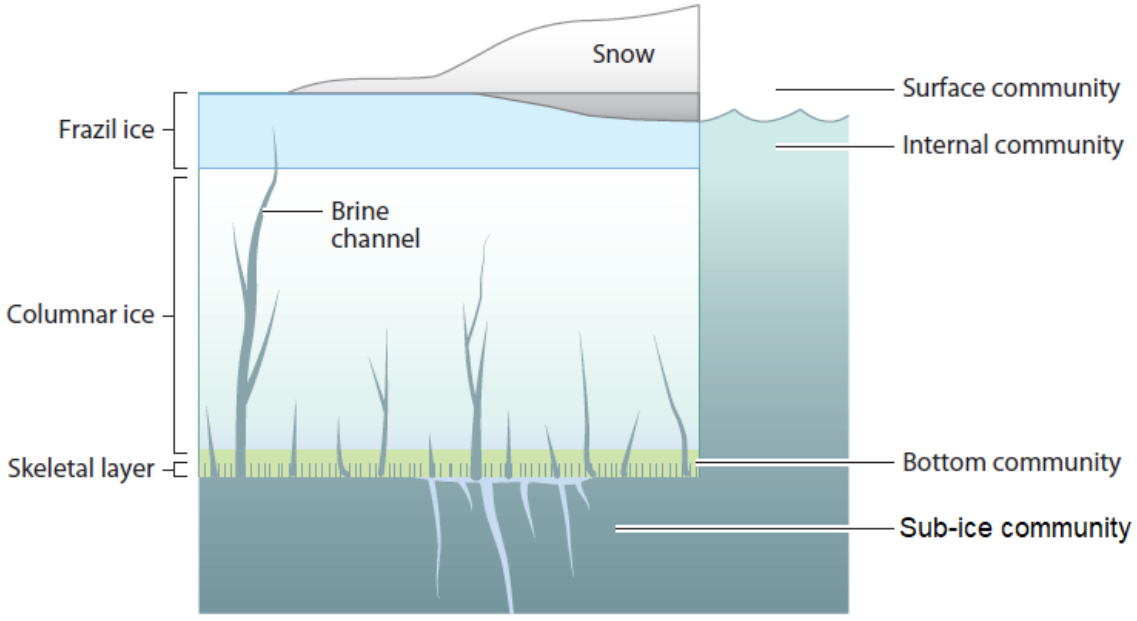

Figure 2. Structure de la banquise de mer comprenant les emplacements typiques des différents types de glace et des communautés microbiennes au sein de la glace de mer ainsi que le système de drainage des canaux de saumure. Modifiée de Arrigo (2014)

BACTÉRIES DANS LA GLACE DE MER ET LA COLONNE D'EAU

Les canaux de saumure de la glace de mer et l'interface glace-eau constituent des micro-habitats abritant une grande variété de microorganismes, des virus aux invertébrés (Figure 3). Les microorganismes présents dans la glace de mer sont exposés à une large gamme de conditions *in situ* dans cet environnement extrême et changeant à la fois dans l'espace et le temps (Bowman 2015). Toutefois, pendant l'hiver, les microorganismes subissent des conditions environnementales moins extrêmes à la base de la glace (températures plus élevées, salinité de la glace et de la saumure plus faibles) que dans les couches supérieures (Collins et al. 2008). Des études récentes réalisées sur la glace pluriannuelle dans l'océan Arctique central ont mis en évidence des communautés microbiennes distinctes entre les différentes couches de glace (i.e., mares de fonte, vieille glace et nouvelle glace) et qui sont elles-mêmes différentes de celles de la colonne d'eau (Bowman et al. 2012, Hatam et al. 2014). Ces résultats indiquent que la glace de mer abrite des assemblages multiples et distincts de bactéries, et que les conditions *in situ* pourraient jouer un rôle moins important dans la structuration des assemblages microbiens que l'âge ou les conditions de la glace au moment de sa formation (Hatam et al. 2014).

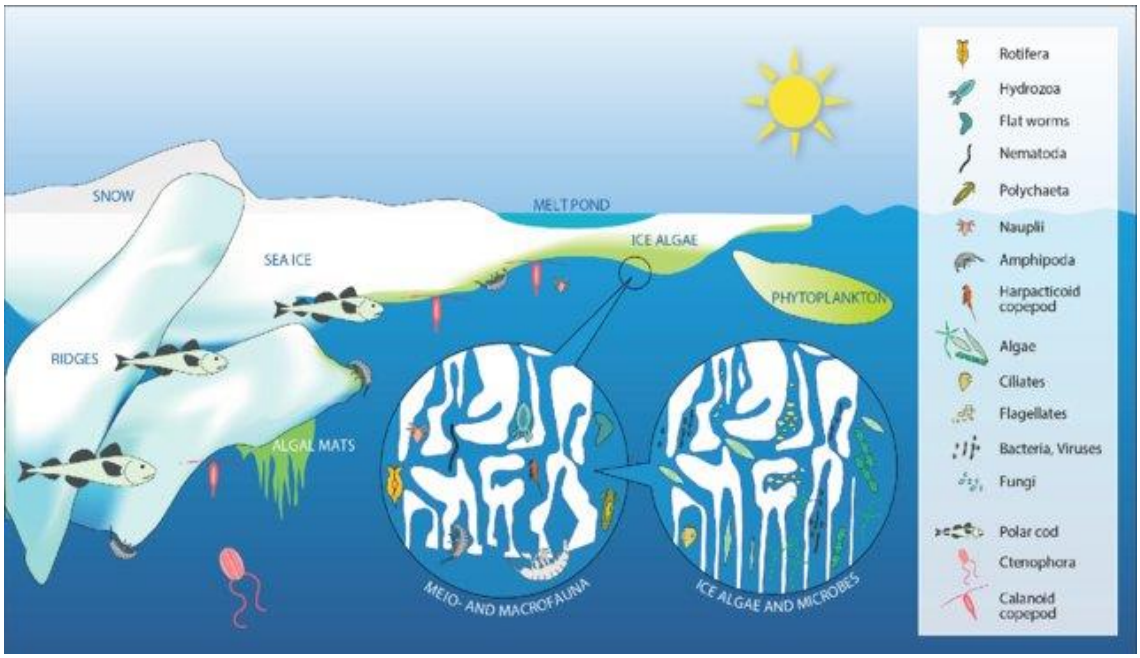

Figure 3. Représentation de la micro-, méio- et macrofaune qui colonisent les interstices de la glace de mer. Tirée de Bluhm et al. (2018)

De nombreuses études réalisées en Arctique et en Antarctique au printemps ont mis en évidence des abondances bactériennes élevées à la base de la glace où les conditions du milieu sont favorables (Sullivan & Palmisano 1984, Bunch & Harland 1990, Gosink et al. 1993, Maranger et al. 1994, Laurion et al. 1995, Gradinger & Zhang 1997, Staley & Gosink 1999, Riedel et al. 2007b, Cowie et al. 2014, Torstensson et al. 2018). Au cours de cette période, l'abondance et la biomasse bactériennes peuvent être dix fois plus élevées à la base de la glace de première année suivant la floraison des algues de glace (Bunch & Harland 1990, Thomas et al. 2001, Riedel et al. 2008).

Les bactéries, ainsi que d'autres organismes microscopiques dont les algues de glace, sont concentrés dans la glace annuelle au moment de sa formation (Riedel et al. 2007a, Collins et al. 2008). Les bactéries peuvent être incorporées dans la nouvelle glace par leur attachement à des plus grosses particules, par exemple des détritus organiques, du sédiment ou des agrégats mais aussi par le biais des algues dont la membrane extérieure collante facilite l'attachement des bactéries (Deming & Collins 2017). L'abondance bactérienne à la base de la glace est généralement corrélée positivement avec celle des algues de glace durant leur

floraison (Riedel et al. 2008, Deming & Collins 2017). Au printemps, l'augmentation du rayonnement solaire favorise la croissance des algues à la base de la glace et, subséquemment ou lorsque les conditions de lumière le permettent, dans la colonne d'eau sous-jacente. L'augmentation de l'abondance bactérienne à l'interface glace-eau est ainsi attribuée à la prolifération des algues qui libèrent de la matière organique dissoute tandis que, dans les couches supérieures de la glace où les algues ne prolifèrent pas ou peu, l'augmentation de l'abondance bactérienne est attribuée à la consommation de carbone organique dissous (COD) concentré dans la glace annuelle au moment de sa formation (Deming & Collins 2017). Riedel et al. (2007b) ont montré que la production bactérienne peut s'avérer supérieure à la production primaire pendant la période qui précède la floraison algale mais non pendant la floraison.

Dans la colonne d'eau, les interactions entre les bactéries et le phytoplancton sont complexes et changent d'une région à l'autre et au cours de l'année. Dans les eaux côtières stratifiées, les bactéries hétérotrophes peuvent soutenir la croissance du phytoplancton en recyclant la matière organique en nutriments azotés. Toutefois, dans les milieux oligotrophes, les bactéries peuvent entrer en compétition avec le phytoplancton pour les ressources nutritives (p.ex., l'azote ou le phosphate) (Legendre & Rassoulzadegan 1995, Bunse & Pinhassi 2017). Au début de la floraison phytoplanctonique, un découplage entre les bactéries et le phytoplancton peut être observé par une diminution initiale de l'abondance bactérienne suivie par une augmentation à mesure que de la matière organique dissoute est produite par le phytoplancton (Riemann et al. 2000, Teeling et al. 2012). Cette diminution de l'abondance bactérienne serait liée à leur prédation par les ciliés et les nanoflagellés hétérotrophes ou encore à la compétition pour les nutriments entre les bactéries et le phytoplancton (Riemann et al. 2000, Castberg et al. 2001, Pernthaler 2005). Lors du déclin de la floraison, la matière organique libérée par le phytoplancton soutient la croissance bactérienne qui devient alors importante (Bratbak et al. 1998). A travers la boucle microbienne, les bactéries hétérotrophes transforment la matière organique dissoute (MOD) et la matière organique particulaire (MOP) dérivées du phytoplancton (Figure 4). Les bactéries hétérotrophes contribuent à la reminéralisation des nutriments organiques notamment l'azote organique dissous et le

phosphate organique dissous en formes inorganiques disponibles pour le phytoplancton. Par ailleurs, la lyse virale contribue à la libération de matières dissoutes et particulaires au niveau des pool phytoplanctonique et bactérien.

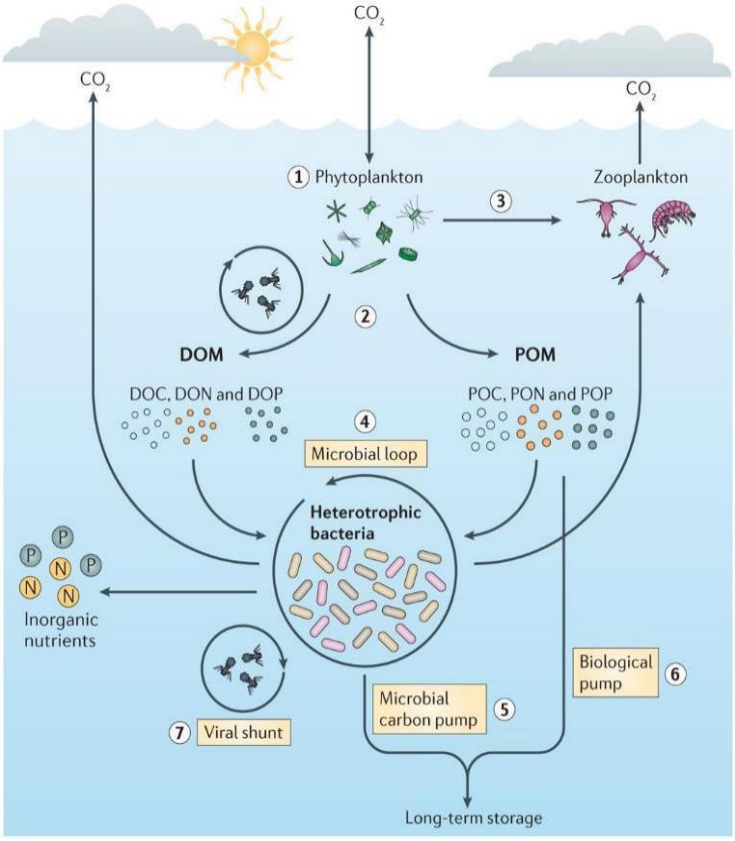

Figure 4. Transformation bactérienne de la matière organique produite par le phytoplancton via la boucle microbienne. Tirée de Buchan et al. (2014)

Le rôle joué par les bactéries hétérotrophes dans le cycle du carbone et de l'azote dans la glace de mer est similaire à celui observé dans la colonne d'eau (Arrigo 2014, Bowman 2015, Deming & Collins 2017). Dans la glace de mer, les bactéries sont actives et abondantes et elles sont étroitement associées à la présence des algues de glace (Bowman 2015). La matière organique dissoute qui provient en grande majorité des algues de glace soutient les assemblages bactériens en stimulant la production bactérienne avec des taux estimés entre

20 et 30 mg C m^{-3} d^{-1} au cours de la floraison algale printanière (Deming & Collins 2017). Malgré ces taux élevés, la production bactérienne représente généralement moins de 10% de la production primaire au printemps et en été dans la glace (Deming & Collins 2017). En effet, Smith & Clement (1990) rapportent des taux de production bactérienne compris entre 3 et 5% de la production primaire à la base de la glace dans le passage de Resolute au cours de la floraison algale. Pour la même région, Vézina et al. (1997) estiment une production bactérienne de 3% de celle de la production primaire et un taux de broutage compris entre 0,1 et 3,5 mg C m^2 d^{-1}. Le carbone dissous produit par les algues de glace, une fois relargué dans les eaux de surface pendant la période de fonte, peut aussi nourrir et modifier les communautés bactériennes présentes dans la colonne d'eau (Niemi et al. 2014, Underwood et al. 2019). Les bactéries hétérotrophes sont également impliquées dans le cycle de l'azote, en reminéralisant l'azote organique dissous sous forme d'ammonium, contribuant possiblement à initier ou allonger la floraison algale en fournissant les ressources aux algues (Deming & Collins 2017). Torstensson et al. (2015) ont mis en évidence que des contacts étroits entre les bactéries et les flagellés hétérotrophes dans la glace peuvent contribuer à un recyclage et à un transfert efficace de l'azote, alors que Riedel et al. (2007b) ont montré qu'une fraction importante de la biomasse bactérienne était consommée par les protistes hétérotrophes dans la glace annuelle.

VIRUS DANS LA GLACE DE MER ET LA COLONNE D'EAU

Les études réalisées au cours des dernières décennies montrent l'importance des virus qui sont la composante la plus abondante, diversifiée et ubiquiste des réseaux trophiques microbiens, et leur rôle essentiel au sein des écosystèmes marins (Bergh et al. 1989, Fuhrman & Noble 1995, Steward et al. 1996, Suttle 2005, 2007). L'abondance des virus dans les écosystèmes aquatiques varie de 10^4 virus mL^{-1} à 10^8 virus mL^{-1} et est typiquement 10 fois plus élevée que celle des bactéries (Middelboe & Brussaard 2017). Généralement, l'abondance virale varie dans l'espace et dans le temps et augmente avec la productivité des systèmes aquatiques (Weinbauer 2004). Ainsi, elle décroît des côtes vers le large, de la

surface vers les couches inférieures de la zone euphotique et augmente avec le degré d'eutrophisation (Fuhrman 1999, Sime-Ngando & Colombet 2009). Par conséquent, les plus fortes abondances virales se retrouvent dans les zones eutrophes où l'abondance bactérienne et les concentrations de chlorophylle *a* sont les plus élevées suggérant que les virus infectent principalement les bactéries et le phytoplancton (Fuhrman & Suttle 1993).

Les recherches menées dans les régions polaires ont mis en évidence une abondance élevée des virus dans la colonne d'eau (Steward et al. 1996, 2007) et la glace de mer (Maranger et al. 1994). Cependant, les quelques études menées dans les eaux de surface des hautes latitudes suggèrent que les concentrations de virus pourraient être environ 10 fois moindre que dans les régions tempérées (Steward et al. 2007). Une étude récente montre toutefois que l'océan Arctique est un point chaud pour la biodiversité du virioplancton (Gregory et al. 2019). Dans la glace de mer, l'abondance virale au printemps peut être plus élevée à la base de la glace (de 10^6 à 10^8 virus mL^{-1}) que dans la colonne d'eau sous-jacente (10^6 virus mL^{-1}) (Maranger et al. 1994). Aussi bien dans la colonne d'eau que dans la glace, les abondances bactériennes et virales peuvent être corrélées positivement avec la biomasse chlorophyllienne (Maranger et al. 1994, Hodges et al. 2005).

À travers les cycles lytique et lysogénique, les virus peuvent contrôler la dynamique de la diversité microbienne, notamment par les processus de perte qui affectent les communautés bactérienne et algale, et par conséquent influencent les cycles biogéochimiques, les flux de carbone, le réseau microbien, la libération de la matière organique dissoute (MOD) et le transfert horizontal de matériel génétique (Sime-Ngando 1997, Wommack & Colwell 2000, Sime-Ngando et al. 2003, Sime-Ngando 2014, Weinbauer 2004, Suttle 2005, 2007). Les virus, à travers la lyse virale, agissent comme catalyseurs des cycles biogéochimiques en transformant la matière particulaire en matière dissoute, assimilable par les bactéries et le phytoplancton comme éléments nutritifs, stimulant ainsi leur croissance et comblant leurs besoins métaboliques (Middelboe et al. 1996, Gobler et al. 1997, Fuhrman 1999, Middelboe & Lyck 2002). Par ailleurs, les virus ont un impact déterminant dans la dynamique de la diversité microbienne. D'après le modèle du " phage

kills the winner " proposé par Thingstad & Lignell (1997) et Thingstad (2000), la diversité au sein des communautés microbiennes serait maintenue par l'activité lytique des virus, qui s'attaquent préférentiellement aux espèces ou souches dominantes.

L'étude de Middelboe et al. (1996) a mis en évidence que l'assimilation bactérienne de COD et l'activité de la phosphatase alcaline augmentent sous l'effet de la lyse virale. Une partie de l'activité de la phosphatase alcaline provient des bactéries hétérotrophes qui la sécrètent tandis qu'une autre partie provient d'enzymes intracellulaires libérées dans le milieu après la mort des cellules ou la lyse virale (Lespilette 2009). De nombreuses bactéries produisent de la phosphatase alcaline notamment dans un milieu limité en phosphate inorganique (Wanner 1993). Au cours d'expériences de cultures algale et virale, Gobler et al. (1997) ont montré que la lyse virale d'une floraison de chrysophytes pouvait libérer environ 40 µmol L^{-1} de COD, augmentant les concentrations ambiantes de 30%. Par ailleurs, à travers la lyse virale, les virus court-circuitent une partie des transferts trophiques, ce qui a pour effet d'augmenter les processus d'oxydation respiratoire et de diminuer l'efficacité du transfert de carbone vers les niveaux trophiques supérieurs (Suttle 2005). Malgré leur importance au sein de l'écosystème marin, on sait relativement peu de choses sur les virus des hautes latitudes, et leur rôle dans le cycle biogéochimique du carbone de la glace de mer n'est pas considéré dans les modèles actuels.

L'ARCTIQUE FACE AUX CHANGEMENTS CLIMATIQUES

L'Arctique, particulièrement vulnérable aux effets du réchauffement climatique, subit une perte significative de l'étendue et de l'épaisseur de la glace de mer (Comiso et al. 2008, Cavalieri & Parkinson 2012, Kwok 2018). L'étendue minimale de glace de mer estivale a diminué d'environ 45% au cours des trois dernières décennies passant de 7×10^6 km² en 1979 à $4{,}2 \times 10^6$ km² au cours de la dernière décennie (Arrigo 2014, NSIDC 2020). Plusieurs facteurs sont à l'origine du déclin du couvert de glace déclenchant une boucle de rétroaction positive qui amplifie le réchauffement climatique aux pôles. D'une part, le faible albédo de

l'océan contribue à augmenter la température des eaux superficielles, ce qui retarde la formation de glace à l'automne et à l'hiver et contribue à sa fonte en été (Perovich et al. 2007, Perovich & Polashenski 2012). D'autre part, la fonte de glace annuelle favorise la formation de mares de fonte dont la superficie peut couvrir jusqu'à 90% de la banquise durant la période de fonte (Perovich et al. 2011). Les faibles reliefs topographiques de la glace annuelle favorisent le développement des mares de fonte dont l'albédo, plus faible que celui de la glace, accentue la pénétration de la lumière à l'intérieur de la glace et dans la colonne d'eau sous-jacente.

Par ailleurs, l'un des changements majeurs dans l'océan Arctique est la perte de glace pluriannuelle qui constitue à ce jour, une composante stable de l'océan Arctique (Maslanik et al. 2011, Perovich et al. 2014). L'étendue minimale de glace en septembre a subi une réduction marquée, avec une perte d'environ 12% par décennie depuis les années 1980 (Nghiem et al. 2007, Serreze & Meier 2019, NSIDC 2020, Figure 5). Certains modèles climatiques prédisent que l'océan Arctique sera libre de glace en été à la fin du siècle voire dans les 30 prochaines années (Overland & Wang 2013, AMAP 2017). À la fin de l'été 2019, l'étendue minimum du couvert de glace était similaire à celle des années 2007 et 2016 comme la deuxième plus faible depuis le début des observations par satellite en 1979 (Perovich et al. 2019). Le déclin de la glace de mer se produit simultanément avec l'allongement de la période d'eau ouverte et des changements dans la formation de glace à l'automne et à l'hiver.

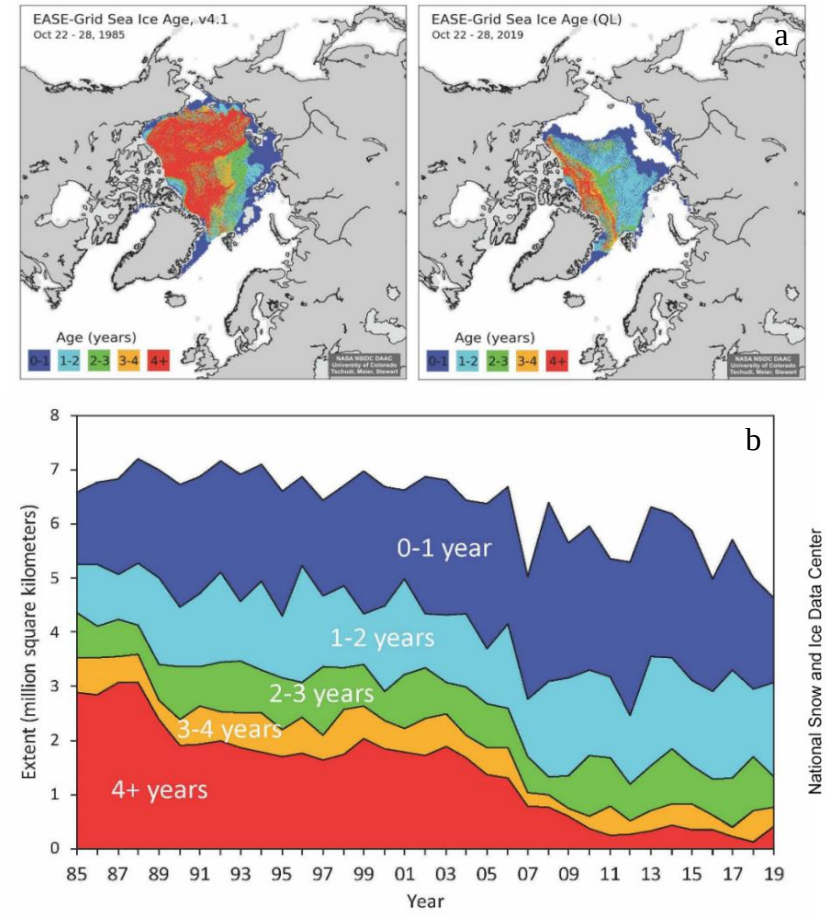

Figure 5. Images satellitaires de (a) l'étendue de la glace de mer annuelle et pluriannuelle en octobre 1985 (à gauche) et 2019 (à droite) et (b) la diminution de l'étendue de la glace de mer annuelle et pluriannuelle de 1985 à 2019 en Arctique. Modifiée de NSIDC (2020)

Le remplacement progressif de la glace pluriannuelle par la glace annuelle a de profonds impacts sur les rétroactions du climat arctique, les processus physiques et biogéochimiques, les écosystèmes et la biodiversité (Kovacs & Michel 2011, Michel 2013, Meier et al. 2014, AMAP 2017). Même s'ils restent difficiles à prévoir, il est attendu que les modifications du couvert de glace continueront d'avoir des impacts sur la production primaire et les écosystèmes marins qui en dépendent. À partir des résultats fournis par les modèles climatiques actuels plusieurs scénarios sont envisagés. D'une part, la diminution de l'albédo dans l'océan Arctique et l'augmentation de la transmission de la lumière à travers la

glace favoriseraient le développement des algues à la base de la glace et du phytoplancton sous la glace. D'autre part, une augmentation de la stratification de la colonne d'eau par la fonte de la glace pourrait diminuer les apports de nutriments provenant des eaux profondes et ainsi réduire la productivité primaire (Arrigo et al. 2012, Tedesco et al. 2012). L'étude menée par Arrigo & van Dijken (2011) a mis en évidence, sur la base des observations satellitaires, une augmentation de la production primaire nette annuelle dans l'océan Arctique entre 1998 et 2009 liée à l'augmentation de la superficie d'eau ouverte ainsi qu'à l'allongement de la période libre de glace. Si cette tendance se poursuit, elle pourrait potentiellement modifier les interactions entre les écosystèmes de la glace de mer, pélagiques et benthiques (Arrigo et al. 2008). Melnikov et al. (2009) suggèrent que des températures plus élevées pourraient intensifier les processus hétérotrophes dans la glace de mer et augmenter le taux de broutage ainsi que la régénération des nutriments. On estime aussi que la diminution du couvert de glace réduira la production annuelle attribuable à la glace de mer au sein des écosystèmes marins arctiques (Melnikov et al. 2009, Johannessen & Miles 2011).

La diminution du couvert de glace de mer représente une perte d'habitat pour l'ensemble des espèces qui y vivent et s'y reproduisent. La perte de glace affecte les processus biologiques et biogéochimiques aux interfaces glace-océan-atmosphère ainsi que la boucle microbienne impliquée dans les réseaux trophiques. Une étude de Melnikov (2008) indique une perte de biodiversité des communautés associées à la glace de mer au cours des trois dernières décennies au profit des écosystèmes pélagiques. Le déclin de la glace pluriannuelle, qui abrite des communautés bactériennes uniques, pourrait ainsi avoir un impact à la fois sur le fonctionnement des assemblages bactériens associés à la glace de mer mais aussi sur l'océan Arctique dans son ensemble.

OBJECTIFS ET HYPOTHÈSES

L'objectif général de cette étude est d'évaluer et de comparer la structure et le fonctionnement des communautés microbiennes ainsi que de réaliser un suivi temporel et dans différentes strates de la glace annuelle et pluriannuelle de la mer de Lincoln au printemps. Les objectifs spécifiques de cette étude sont : (1) de déterminer la distribution verticale des bactéries et des virus et leurs relations avec les facteurs biotiques et abiotiques dans la glace annuelle et pluriannuelle et (2) d'évaluer la structure et le fonctionnement du réseau microbien.

La première hypothèse de travail est que l'abondance et la répartition verticale des bactéries et des virus sont différentes au sein des deux types de glace. La deuxième hypothèse suggère que les virus jouent un rôle sur la dynamique des bactéries de la glace de mer similaire à celui observé chez le bactérioplancton. Cette étude aidera à comprendre les processus biogéochimiques opérant au sein de la glace annuelle et pluriannuelle dans l'Arctique en mutation.

CHAPITRE 1

STRUCTURE AND FUNCTION OF MICROBIAL COMMUNITIES IN FIRST-YEAR AND MULTIYEAR ICE OF THE LINCOLN SEA DURING SPRING

1.1. INTRODUCTION

Sea ice is a unique ecosystem that constitutes one of the largest biomes and coldest marine habitat on Earth, and an important component of the polar and global climate (Junge et al. 2004, Mock & Thomas 2005, Dieckmann & Hellmer 2010). The Arctic is characterized by an annual or first-year ice (FYI) and a perennial or multiyear ice (MYI) cover (Wadhams 2000). Multiyear ice persists over more than one summer and therefore is usually thicker than FYI which is seasonal and melts every year (Maslanik et al. 2007, Comiso 2012). Sea ice is a rich environment for a diverse, active and specialized ice-associated community of microorganisms (e.g., algae, bacteria, protozoa and meiofauna) in which autotrophic algae and heterotrophic bacteria play a key role during the spring productive period (Mock & Thomas 2005, Becquevort et al. 2009).

Sea ice is a complex composite material made of pure ice with brine and gas inclusions, the size and geometry of which depend on the structure of the ice crystals, as well as temperature and bulk salinity (Golden et al. 1998). According to the “law of fives”, sea ice exhibits a marked transition in its fluid transport properties at a temperature of about -5°C, a brine volume fraction of about 5% and a salinity of 5 (Golden et al. 1998). Sea ice is also not vertically uniform and can display strong gradients in temperature, salinity, brine volume, light and nutrient concentrations (Eicken 2003). Microorganisms within sea ice are exposed to a large range of *in situ* conditions in this extreme and variable environment both spatially

and temporally. During autumn freeze-up, microorganisms are incorporated and concentrated within the brine i.e., liquid inclusion in the solid ice (Eicken 2003, Riedel et al. 2007a). During winter, microorganisms experience less extreme environmental conditions in the bottom ice (i.e., higher temperatures, increased brine volume and salinity) than in the upper sea ice horizons (Collins et al. 2010). During spring, increasing solar radiation allows the onset of sea ice-algal growth and an increase in chlorophyll *a* (chl *a*) concentrations, particularly in the bottom ice horizon near the ice-water interface.

Microbes, the smallest and most abundant component in marine ecosystems, play important roles in biogeochemical processes, sustaining every other form of life on Earth (Fuhrman 1999, Cowie et al. 2014). In the water column as well as in the sea ice, heterotrophic bacteria play an essential role in the carbon and nutrient cycling by channelling productivity through the microbial food web (Azam et al. 1983, Steward et al. 1996, Deming & Collins 2017). Bacterial carbon can be transferred to upper trophic levels through grazing and filter feeders. In addition, heterotrophic bacteria remineralize organic matter, providing nutrients for primary producers. Sea ice heterotrophic bacteria typically follow the seasonal development of the ice algal bloom as their abundances increase with increasing chl *a* concentrations in spring (e.g., Riedel et al. 2008).

As bacteria, viruses play essential roles in ecological and biochemical processes (Bergh et al. 1989). For example, virus-induced bacterial lysis leads to the release of inorganic nutrients, which in turn, may be used by primary producers or contribute to the dissolved organic matter pool (Fuhrman 1999, Pearce & Wilson 2003, Weinbauer 2004). Through lytic and lysogenic cycles, viruses could play a role in controlling bacterial and algal populations via transduction (Paul et al. 1993) and transformation (Jiang & Paul 1998). Horizontal gene transfer is a mechanism where viruses act as vectors for genetic transfers between microorganisms (Sime-Ngando & Colombet 2009). Moreover, through lytic infection, viruses attach to cell host and inject their nucleic acid, whereas through the lysogenic infection, the nucleic acid of the virus becomes part of the host cell and reproduces as genetic

material into the host cell (Fuhrman 1999). However, little is known on how environmental conditions influence bacterial and viral abundances in sea ice, and even less in MYI.

The rapid warming of the Arctic Ocean over the past three decades has resulted in major declines in sea ice extent and thickness, with the replacement of old and thick MYI by thinner FYI (Kwok 2018). Very old ice (>4 years) constituted 33% of the Arctic Ocean ice cover in March 1985, but only made up 1.2% in March 2019 (Tschudi et al. 2019a, b). Currently, climate-model simulations predict that the Arctic Ocean will be ice free during summer by the middle or the end of the 21st century (Maslanik et al. 2007, Overland & Wang 2013, AMAP 2017). The replacement of MYI by FYI has profound impacts for Arctic climate feedbacks, physical and biogeochemical sea ice and ocean processes, ecosystems and biodiversity (Kovacs & Michel 2011, Michel 2013, Meier et al. 2014, AMAP 2017). The loss of sea ice represents a fundamental change for microbial communities and ice-associated fauna as well as microbial communities. In addition, sea ice loss affects biological and biogeochemical processes at the sea ice-ocean-atmosphere interfaces and the microbial cycling of key elements in the water column (Bowman 2015, Underwood et al. 2019). While it is recognized that sea ice plays a central role in the Arctic and global marine elemental cycles (Rysgaard et al. 2011, Vancoppenolle et al. 2013, Damm et al. 2015), relatively little is known about the role of bacteria and viruses in sea ice and particularly in MYI. In the context of global warming, uncertainties remain on the impact of the replacement of MYI by FYI on ice-associated microbial communities.

The overall objective of this study is to assess the structure and function of the microbial communities in Arctic FYI and MYI. We hypothesized that the microbial dynamics is different between the two ice types, linked to differences in sea ice characteristics. To test this hypothesis, we (1) determined the vertical distribution of bacteria and viruses and their relationships with biotic and abiotic factors in both ice types, and we (2) assessed the structure and function of the microbial food web, using path analysis which is an extension of multiple linear regression to assess causal relations among variables. This

study provides a better understanding of biogeochemical processes operating within FYI and MYI in the changing Arctic.

1.2. MATERIALS AND METHODS

1.2.1. STUDY AREA AND SAMPLING

This study is part of the Multidisciplinary Arctic Program (MAP) – Last Ice. During a three-week period, from 2 to 23 May 2018, we concomitantly sampled FYI and MYI from an ice camp set up on a FYI floe adjacent to MYI on the consolidated pack, ca. 9 km offshore of Canadian Forces Station (CFS) Alert in the Lincoln Sea (82° 29’ 24” N, 62° 18’ 36” W; Figure 1). During the sampling season, 39 FYI cores and 39 MYI cores were extracted from these two floes. Surface water samples were also collected regularly at the station.

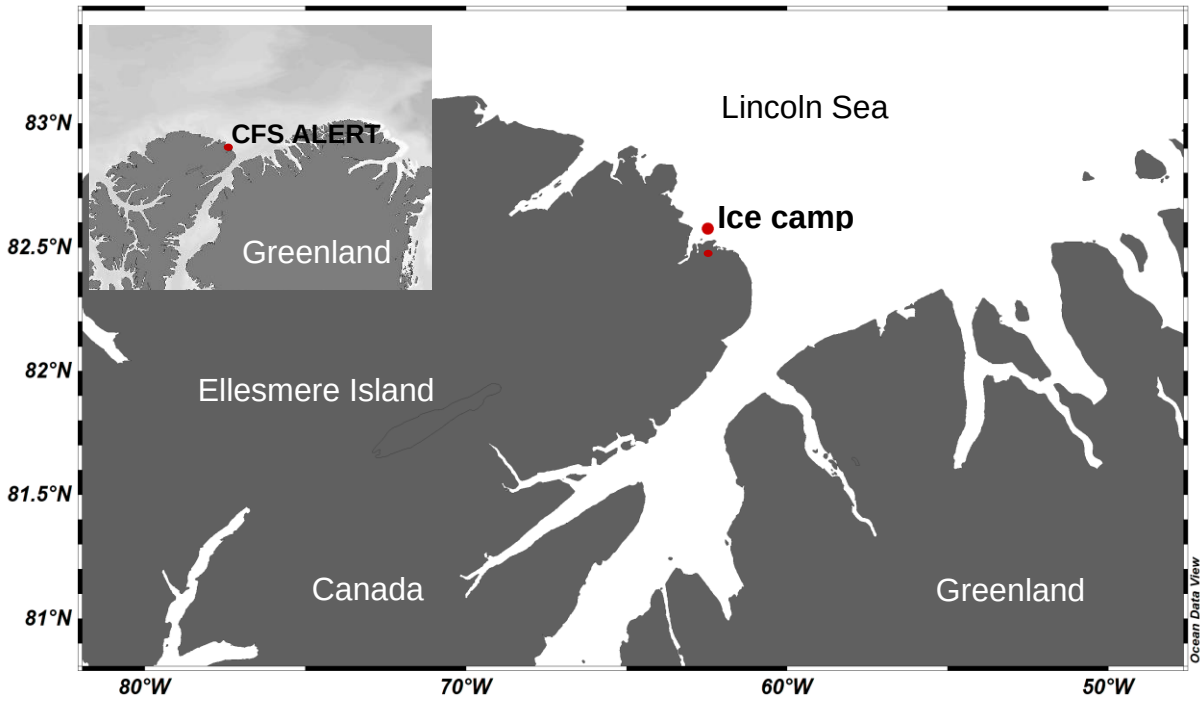

Figure 1. Location of the sampling site in the Lincoln Sea during spring 2018

At each coring site, snow depth and ice thickness were measured (n = 6 to 8) with a graduated stick and an ice thickness gauge (Kovacs Enterprise), respectively. Ice cores were collected using a 9 cm inner diameter ice corer (Mark II Coring System, Kovacs Enterprise). Vertical profiles of temperature and salinity were determined on five and nine full-length FYI and MYI cores, respectively. Ice temperature at 10 cm intervals throughout the length of the core was measured immediately after coring by drilling a 2 mm diameter hole to the center of the core and inserting a temperature probe (Testo 720 RTD Thermometer). The core was thereafter cut in 10 cm sections, which were melted and used for the determination of bulk salinity using a hand-held conductivity meter (Condi 330i, WTW). Brine volume and salinity were calculated for individual 10 cm core sections based on ice temperatures and bulk salinity, according to Cox & Weeks (1983). Daily average, minimum and maximum air temperature records were obtained from Environment and Climate Change Canada weather station at CFS Alert.

From 2 to 22 May, water samples were collected at the ice-water interface every four days using 5 L Niskin bottles. Subsamples were collected for the determination of nutrients, dissolved organic carbon (DOC) and chl *a* concentrations, and for bacterial and viral abundances. On each sampling day, a CTD (conductivity, temperature and depth) probe (SBE Sea-Bird 19plus V2 SeaCAT) was deployed prior water sampling for temperature and salinity vertical profiles.

Sea ice samples were collected every 4 days, between 3 and 23 May. On each sampling day five to seven FYI and MYI cores each were collected for further biochemical analyses. For each core, three sections of 10 cm (top 10-20 cm, middle 100-110 cm and bottom 10 cm) were collected. Core sections were slowly melted in individual sterile Whirl-Pak bags, in the dark over a period of 36-48 h. Subsamples from the first melted core were used for the determination of nutrients, DOC and bacterial and viral abundances. The remaining cores (four or six) were pooled together and used for chl *a* measurements.

1.2.2. LABORATORY ANALYSES

Nutrients, dissolved organic carbon and chlorophyll *a*

Duplicate subsamples were filtered through pre-combusted (450°C, 5 h) Whatman GF/F glass-fiber filters inserted in an acid-washed filter holder and filtrates were immediately frozen at -80°C in acid-cleaned 15 mL polyethylene tubes for subsequent analysis of nitrate plus nitrite referred as NO_x, phosphate (PO_4) and silicic acid ($Si(OH)_4$) concentrations using a Bran-Luebbe 3 autoanalyzer (method adapted from Grasshoff et al. 1999). A correction for the effect of varying salinity was applied for phosphate and silicic acid concentrations, as recommended by Grasshoff et al. (1999). The limit of detection for NO_x, PO_4 and $Si(OH)_4$ are 0.05 µmol L^{-1}, 0.02 µmol L^{-1} and 0.1 µmol L^{-1}, respectively.

Subsamples for DOC determination were filtered in duplicate through pre-combusted (450°C, 5 h) 25 mm Whatman GF/F filters. The filtrates were collected in 20 mL amber EPA glass vials with polypropylene open-top caps and PTFE silicone septas. Samples were acidified with 100 µL of 50% phosphoric acid (H_3PO_4) and stored in the dark at 5°C until analysis using a Shimadzu TOC-VCPH analyzer with a ASI-V auto-sampler, using high-temperature catalytic combustion. Potassium hydrogen phthalate is used for calibration and analytical results are systematically checked against consensus reference material (i.e. deep seawater reference water) and low-carbon water from the Hansell's Certified Reference Materials program.

Two subsamples were filtered onto 25 mm Whatman GF/F filters and extracted (18-24 h) in 90% acetone at 4°C in the dark for fluorometric determination of chl *a* (acidification method; Parsons et al. 1984). Fluorescence was measured on a Turner Designs 10 AU fluorometer calibrated against pure chl *a* extract (*Anacystis nidulans*, Sigma Chemicals).

Flow cytometry analysis

The abundance of free heterotrophic bacteria and virus-like particles was determined by flow cytometry. Duplicate 5 mL subsamples were fixed with 20 µL and 100 µL of 25% of glutaraldehyde (Grade I, Sigma-Aldrich G5882) for bacteria (0.1% final concentration) and viruses (0.5% final concentration), kept in the dark for 15 min at room temperature, and then stored frozen at -80°C until analysis by flow cytometry (Belzile et al. 2008).

Frozen bacteria and viruses samples were quickly thawed in a 30°C water bath, stained with SYBR Green I (Invitrogen) and measured at 525 nm/40 nm BP to detect low and high nucleic acid content (Brussaard et al. 2000, Belzile et al. 2008). In each subsample, microspheres (1 µm Fluoresbrite) were added as an internal standard and allowed to verify there was no degradation of the side scatter signal despite the relatively high flow rate used. Analyses were performed with a CytoFLEX Flow Cytometer (Beckman Coulter Inc.) fitted with blue laser (488 nm) and the results were analysed with CytExpert v2.3 software (Beckman Coulter). Bacterial abundance counted in flow cytometry was compared with bacterial abundance counted in epifluorescence microscopy (n = 22) after staining with DAPI (4.6-diamidino-2-phenylindole) (Sherr et al. 1993). The linear regression of bacterial counts determined from the two methods was significant ($r^2 = 0.62$, $p < 0.01$).

1.2.3. STATISTICAL ANALYSES

Two-way and one-way analyses of variance (ANOVA) were performed to evaluate differences between ice horizons (i.e., top, middle, and bottom) and ice types (i.e., FYI and MYI). Prior to ANOVAs, the homogeneity of variance and the normality of distribution of each variable were tested using Levene's and Shapiro-Wilk tests, respectively. When necessary, data were log-transformed to meet the assumptions of ANOVA. When significant differences were found, *post-hoc* Tukey tests were conducted to identify significantly

different groups. These analyses were performed using R statistical software and SigmaPlot 12.0 (Systat Software Inc.).

Pearson's correlation (r) was used to determine correlations between physical, chemical and biological variables. Model II linear regressions (reduced major axis) were performed to evaluate relationships between viruses, bacteria, physical (temperature, bulk salinity, brine volume) and biochemical (nutrient, DOC and chl *a* concentrations) variables. When necessary, data were log transformed to meet the normality assumptions of model II linear regression analysis. Differences between regression slopes were tested using analysis of covariance. A significant level of $p \leq 0.05$ was used for all statistical tests and analyses. All analyses were performed using R statistical software.

Path analyses were performed to explore causal relations between physical, chemical and biological variables. Path analysis is an extension of multiple linear regressions where hypotheses as to causal relations among variables can be evaluated (Sokal & Rohlf 1995, Legendre & Legendre 2012). The path coefficients are estimated as partial regression coefficients computed on variables normalized to meet conditions of normality when required. The choice of our causal models is based on ecological theory where we assessed the relationships between microbial communities and biological and environmental variables.

1.3. RESULTS

1.3.1. ENVIRONMENTAL CONDITIONS AND CHLOROPHYLL *a*

During the sampling period, air temperature increased progressively with the daily average increasing from -19.4°C to -9.6°C (Figure 2). The average snow depth was 0.12 ± 0.10 m and 0.08 ± 0.10 m in FYI and MYI, respectively. The average ice thickness was 1.63 ± 0.14 m and 3.78 ± 0.54 m in FYI and MYI, respectively. There was no significant difference in snow depth ($p = 0.54$) but a significant difference in ice thickness between FYI and MYI ($p < 0.001$).

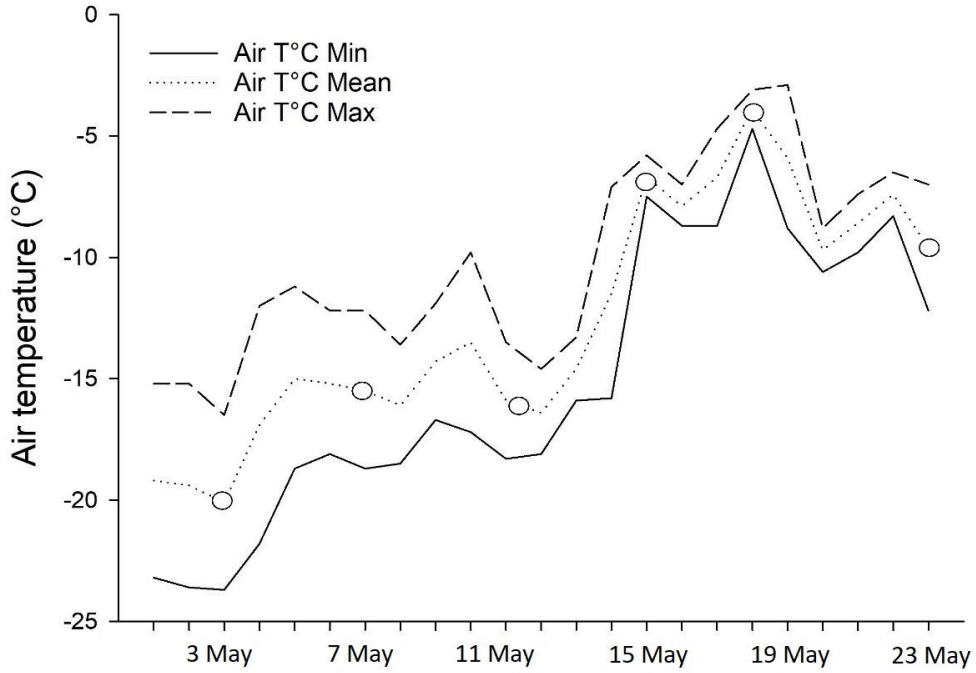

Figure 2. Daily maximum (Max), average (Mean) and minimum (Min) air temperature (T°C) at CFS Alert during spring 2018. Circles identify sampling dates.

Ice temperature, bulk salinity and brine volume fractions changed during the sampling period in both FYI and MYI, as shown by comparative profiles on 7 and 23 May (Figure 3a, b). As the season progressed, FYI temperatures increased by more than 5°C at the snow-ice interface, from -9.7°C to -2.2 °C, whereas virtually no change was observed in the bottom ice where ice temperatures remained stable at -1.6°C. Multiyear ice temperatures at the snow-

ice interface increased by more than 8°C during the season, from -13.6°C to -5.4°C, and remained stable at -1.8°C in the bottom ice (Figure 3a, b). First-year ice bulk salinity (practical salinity, no units) remained stable during the season, with values varying between 4.2 and 4.5 and 7 and 7.3 at the snow-ice interface and the bottom ice, respectively (Figure 3c). Multiyear ice bulk salinity remained 0 at the snow-ice interface during the sampling period and increased from 5.7 to 8.1 in the bottom ice (Figure 3d). First-year ice brine volume fractions varied between 2.4% and 4.7% and 21.6% and 21.2% at the snow-ice interface and the bottom ice, respectively (Figure 3e). Multiyear ice brine volume fractions were 0 at the snow-ice interface and increased from 15.6% to 25.1% in the bottom ice (Figure 3f). Ice temperature, bulk salinity and brine volume fractions were consistently lower than -5°C, 5 and 5% in the top and middle ice horizons, except on 23 May when FYI temperatures were higher than -5°C (Figure 3 a-f).

Throughout the sampling period, ice temperatures, bulk salinity and brine volume of FYI and MYI were significantly lower in the top than in the bottom ice horizon ($p < 0.001$, Table 1).

Table 1. Physical, chemical and biological characteristics in three horizons of first-year ice (FYI) and multiyear ice (MYI) sampled in the Lincoln Sea from 3 to 23 May 2018. NO_x: nitrate + nitrite; PO_4: phosphate; $Si(OH)_4$: silicic acid; DOC: dissolved organic carbon; chl *a*: chlorophyll *a*; VBR: virus-to-bacteria ratio. For each variable, average ± SD is shown

	FYI			**MYI**		
Variable	Top	Middle	Bottom	Top	Middle	Bottom
Temperature (°C)	-7.36 ± 2.59	-4.63 ± 0.90	-1.76 ± 0.25	-9.53 ± 4.57	-9.70 ± 2.45	-1.89 ± 0.25
Salinity	3.70 ± 0.20	4.52 ± 0.71	8.52 ± 1.44	0	1.40 ± 0.35	6.94 ±0.86
Brine volume (%)	2.80 ± 0.87	4.75 ± 1.65	24.29 ± 5.48	0	0.79 ± 0.19	18.38 ± 4.08
NO_x (µmol L^{-1})	0.85 ± 0.47	0.73 ± 0.49	1.20 ± 0.37	0.20 ± 0.09	0.20 ± 0.16	1.39 ± 0.46
PO_4 (µmol L^{-1})	0.09 ± 0.02	0.12 ± 0.02	0.48 ± 0.23	0.04 ± 0.01	0.06 ± 0.02	0.37 ± 0.15
$Si(OH)_4$ (µmol L^{-1})	1.14 ± 0.06	1.45 ± 0.13	2.19 ± 0.36	0.09 ± 0.04	0.37 ± 0.12	2.04 ± 0.34
DOC (µmol L^{-1})	27.37 ± 3.37	30.45 ± 4.09	80.78 ± 30.40	23.70 ± 10.42	23.15 ± 7.65	52.70 ± 12.97
Chl *a* (µg L^{-1})	0.02 ± 0.02	0.48 ± 0.68	11.65 ± 6.02	0.03 ± 0.01	0.03 ± 0.02	8.34 ± 3.67
Bacteria (10^6 cells mL^{-1})	0.04 ± 0.02	0.04 ± 0.02	0.42 ± 0.30	0.05 ± 0.06	0.04 ± 0.03	0.19 ± 0.12
Virus (10^6 cells mL^{-1})	0.53 ± 0.32	0.55 ± 0.32	2.69 ± 1.43	0.58 ± 0.29	0.50 ± 0.13	1.73 ± 0.82
VBR	14.06 ± 0.35	15.65 ± 0.37	6.48 ± 1.61	10.82 ± 0.37	12.84 ± 0.32	9.26 ± 1.09

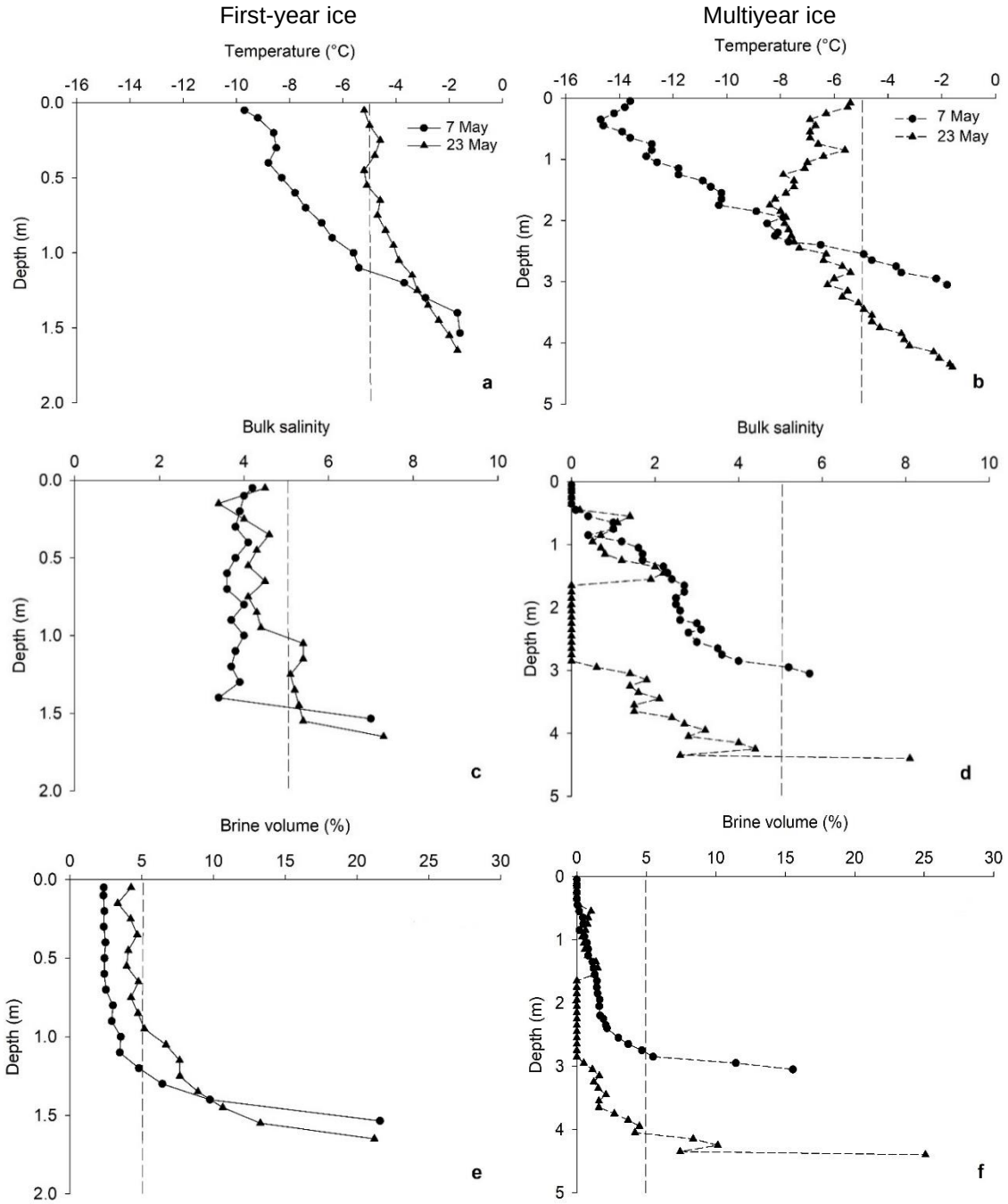

Figure 3. Selected vertical profiles of temperature, bulk salinity and brine volume in (a, c, e) first-year ice and (b, d, f) multiyear ice cores in the Lincoln Sea during 7 and 23 May 2018. Vertical dashed lines indicate ice temperature (negative °C), bulk salinity (no units) and brine volume (%) of 5

Nutrient (NO_x, PO_4 and $Si(OH)_4$) and DOC concentrations were significantly higher in FYI than in MYI ($p < 0.001$, Figure 4a, b, Tables 1 & 2). In both ice types, nutrients and DOC were significantly higher in the bottom horizon (*post-hoc* Tukey test, $p < 0.05$, Table 2). Surface water nutrient concentrations were, on average, 5.02 ± 1.15 µmol L^{-1} for NO_x, 1.01 ± 0.12 µmol L^{-1} for PO_4, 11.81 ± 2.04 µmol L^{-1} for $Si(OH)_4$ and significantly higher in surface waters than in the bottom ice ($p < 0.05$; Figure 4a, b). There was no significant difference in DOC concentrations between surface waters (69.6 ± 26.9 µmol L^{1}) and the bottom ice (Figure 4a, b).

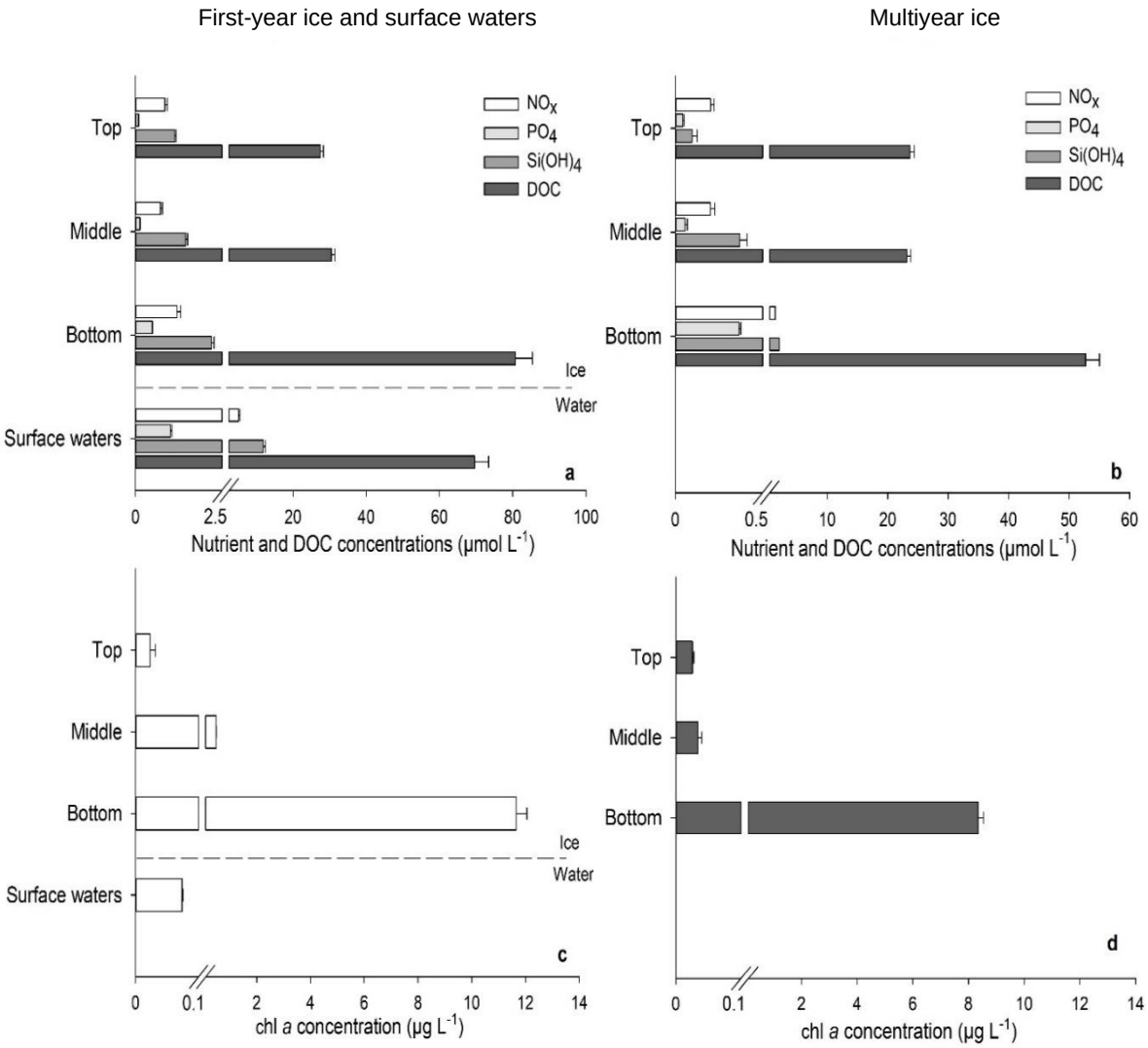

Figure 4. Variations in (a, b) NO_x (nitrate + nitrite), PO_4 (phosphate), $Si(OH)_4$ (silicic acid), DOC (dissolved organic carbon), and (c, d) chl (chlorophyll) *a* concentrations in the top, middle and bottom ice horizons of first-year ice and surface waters and multiyear ice in the Lincoln Sea during spring 2018 (average ± SD)

There was no significant difference in chl *a* concentrations between FYI and MYI (Figure 4c, d, Tables 1 & 2). Hence, the data from both ice types were combined to test differences in chl *a* between ice horizons. Chlorophyll *a* concentrations were significantly higher in the bottom ice horizon (*post-hoc* Tukey test, $p < 0.05$, Tables 1 & 2). Surface waters chl *a* concentration was, on average, 0.07 ± 0.02 µg L^{-1} and significantly lower ($p < 0.05$) than in the bottom ice (Figure 4c, d).

Table 2. Summary of two-way ANOVAs and Tukey test ($\alpha \leq 0.05$) for chemical and biological variables in three horizons of first-year ice (FYI) and multiyear ice (MYI) in the Lincoln Sea during spring 2018. NO_x: nitrate + nitrite, PO_4: phosphate, $Si(OH)_4$: silicic acid, DOC: dissolved organic carbon, and chl *a*: chlorophyll *a*, VBR: virus-to-bacteria ratio. For two-way ANOVAs, ns: not significant and for post-hoc Tukey test A > B > C

	Two-way ANOVA			Tukey test				
Variable	Ice type	Horizon	Horizon × Ice type	FYI	MYI	Top	Middle	Bottom
NO_x (µmol L^{-1})	< 0.001	< 0.001	< 0.01	A	B	B	B	A
PO_4 (µmol L^{-1})	< 0.001	< 0.001	ns	A	B	B	B	A
$Si(OH)_4$ (µmol L^{-1})	< 0.001	< 0.001	< 0.001	A	B	C	B	A
DOC (µmol L^{-1})	< 0.05	< 0.001	ns	A	B	B	B	A
Chl *a* (µg L^{-1})	ns	< 0.001	ns	ns	ns	B	B	A
Bacteria (cells mL^{-1})	ns	< 0.001	ns	ns	ns	ns	ns	A
Virus (cells mL^{-1})	ns	< 0.001	ns	ns	ns	ns	ns	A
VBR	ns	ns	ns	ns	ns	ns	ns	ns

1.3.2. BACTERIAL AND VIRAL ABUNDANCES

There were no significant difference in bacterial and viral abundances between FYI and MYI (Figure 5c, d, Table 1). Hence, the data from both ice types were combined to test the difference in bacterial and viral abundances between ice horizons and between bottom ice horizon and surface waters. Bacteria and viruses were significantly more abundant in the bottom ice than in the top and middle ice horizons (*post-hoc* Tukey test, $p < 0.001$, Figure 5a, b, Table 1). Surface water bacteria and virus concentrations were, on average, $0.11 \pm 0.01 \times 10^6$ cells mL^{-1} and $0.86 \pm 0.10 \times 10^6$ cells mL^{-1}, respectively (Figure 5a, b), and were not significantly different than those in the bottom ice (Table 1).

There was an overall decrease of the virus-to-bacteria ratio (VBR) from the top to the bottom horizon in both ice types (Figure 5c, d, Table 1) although no significant differences were found between sea ice horizons. Maximum VBR values were 60 and 120 in the middle and top horizons and the lowest values were 15 and 12 in the bottom horizon of FYI and MYI, respectively. There were no significant differences in VBR between surface waters and the bottom ice (Figure 5c, d).

Bacterial and viral abundances in the bottom ice horizon of FYI increased as the season progressed, reaching maximum abundances on 19 May (Figure 6a, c) whereas there was no seasonal trend in MYI (Figure 6b, d).

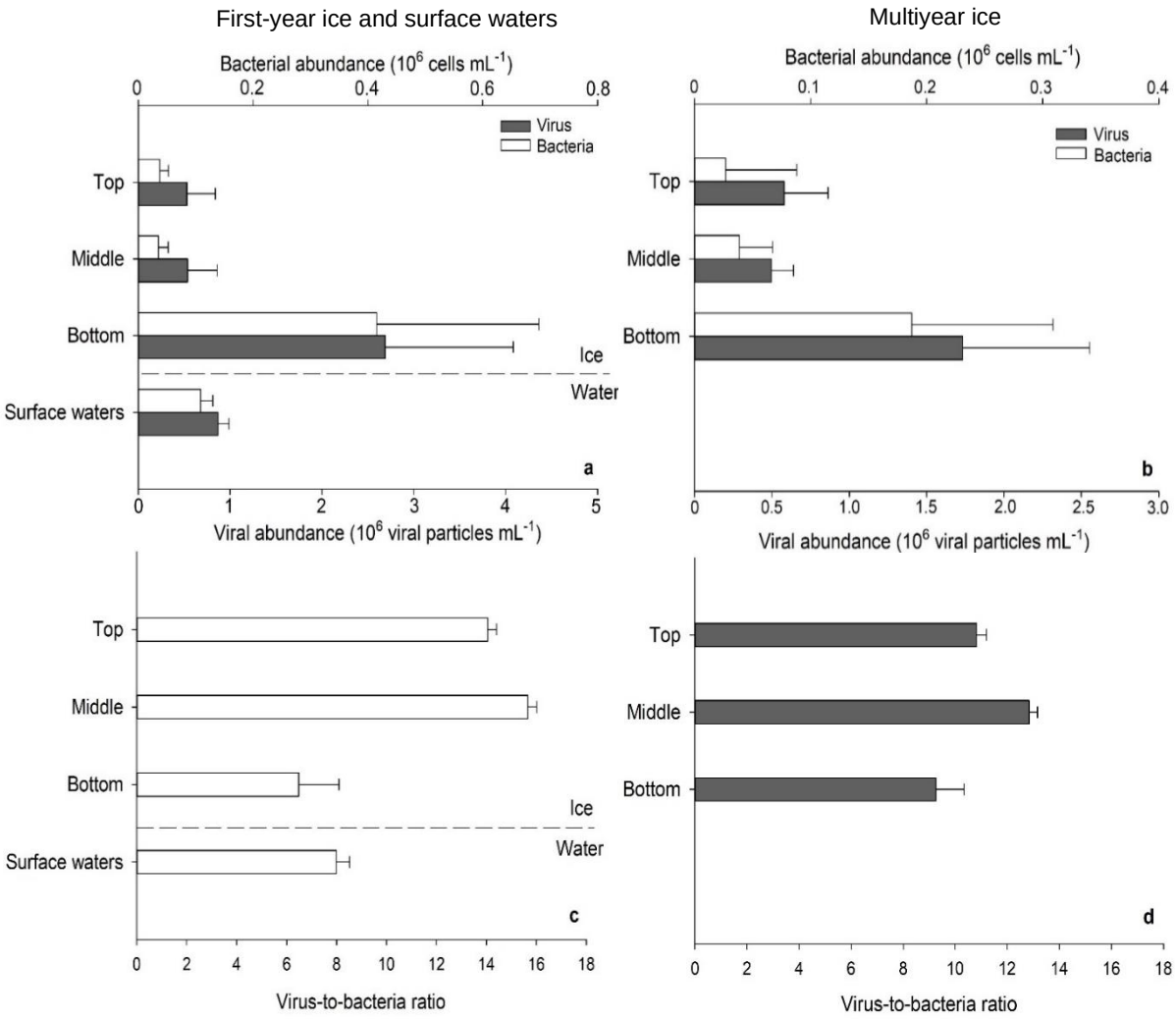

Figure 5. Variations in (a, b) bacterial and viral abundances and (c, d) virus-to-bacteria ratio in the top, middle and bottom ice horizons of first-year ice and surface waters and multiyear ice in the Lincoln Sea during spring 2018 (average ± SD)

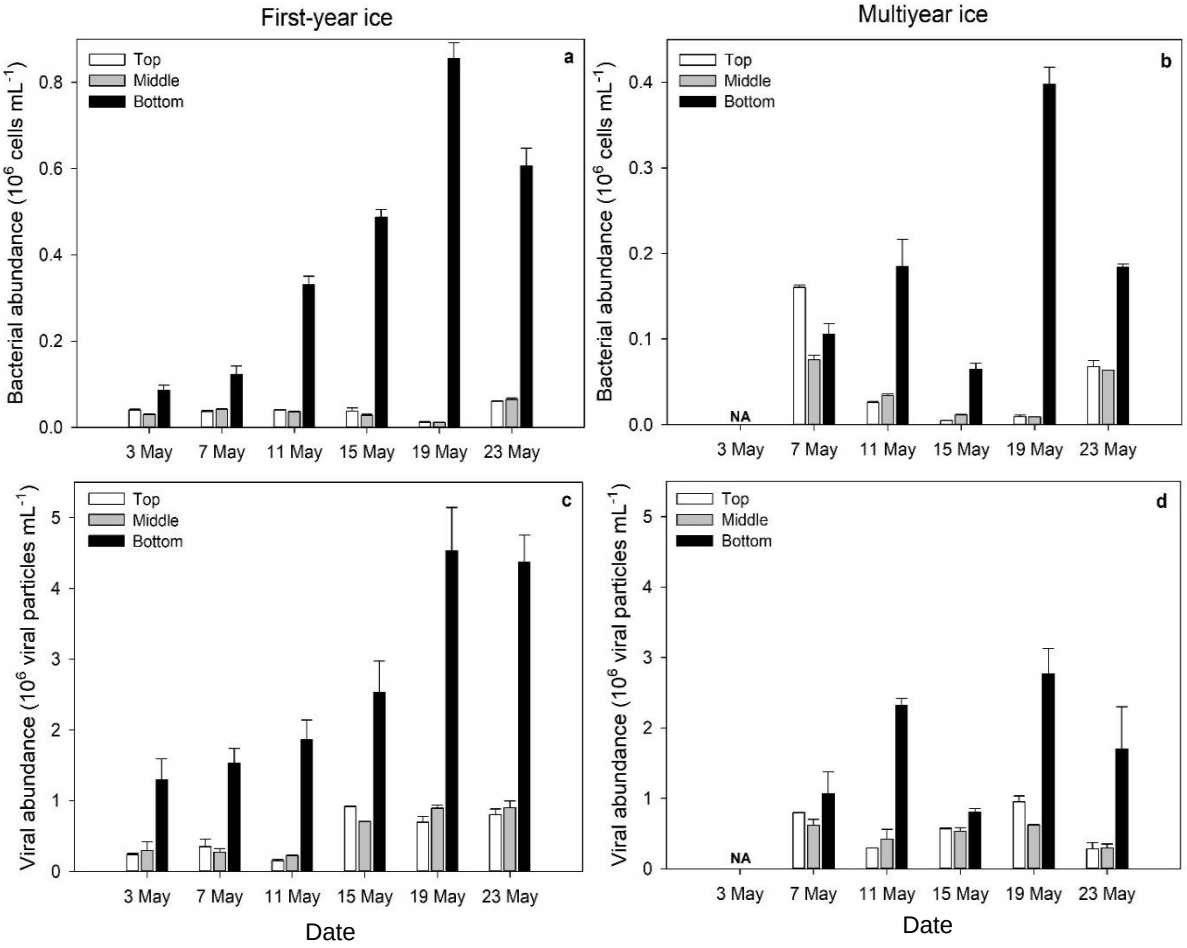

Figure 6. Seasonal variations in (a, b) bacterial and (c, d) viral abundances in the top, middle and bottom horizons of first-year ice and multiyear ice in the Lincoln Sea during spring 2018 (average ± SD)

1.3.3. RELATIONSHIPS BETWEEN SEA ICE MICROBIAL ABUNDANCES AND ENVIRONMENTAL VARIABLES

Bacterial abundance was positively correlated with chl *a*, DOC, PO_4, $Si(OH)_4$ and brine volume fraction in both FYI (Table 3) and MYI (Table 4). Viral abundance in the sea ice was also positively correlated with the same variables as for bacteria. Environmental variables, including chl *a*, were all significantly correlated between each other, as shown in Tables 3 and 4.

In surface waters, bacterial abundance was positively correlated with chl *a* ($r = 0.82$, $p < 0.01$) and DOC ($r = 0.89$, $p < 0.05$; Table 5). In addition, surface waters nutrients (i.e., NO_x, PO_4, $Si(OH)_4$) were inter-correlated ($p < 0.05$, Table 5).

Bacterial abundance was a good predictor of viral abundance for both FYI ($r^2 = 0.91$) and MYI ($r^2 = 0.74$; Figure 7). There was no significant difference between the regression slopes for the two ice types ($p = 0.332$).

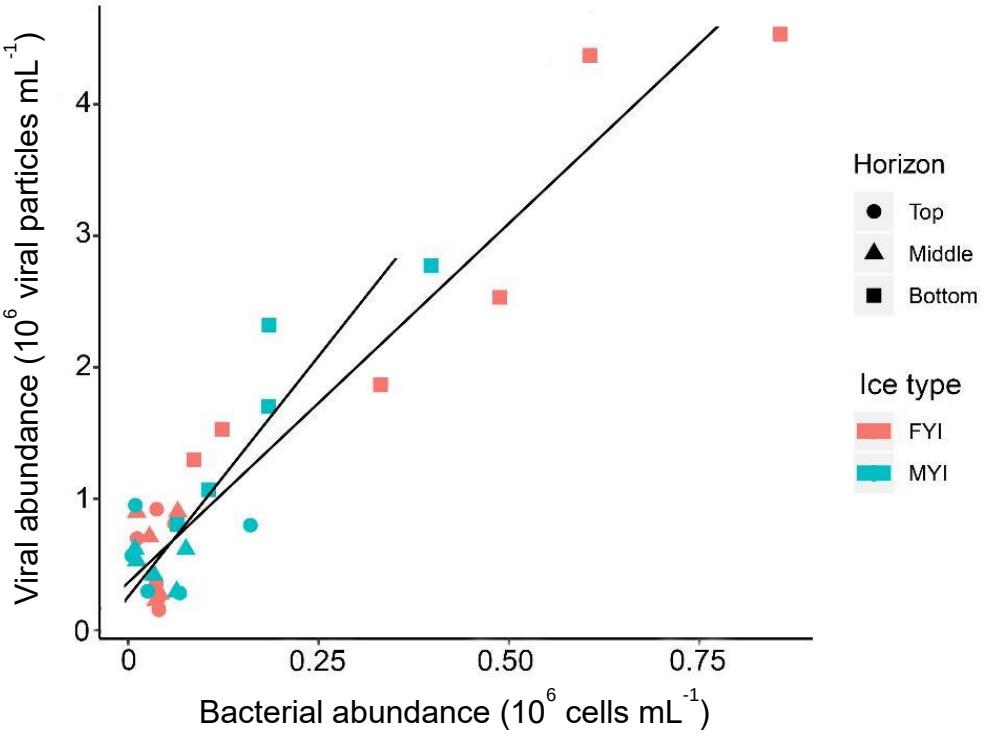

Figure 7. Relationships between viral and bacterial abundances in the top, middle and bottom horizons of first-year ice (FYI) and multiyear ice (MYI) in the Lincoln Sea during spring 2018. Model II linear regressions: $x_2 = 5.38x_1 + 0.37$, $r^2 = 0.91$, $p < 0.001$ (FYI) and $x_2 = 7.17x_1 + 0.27$, $r^2 = 0.74$, $p < 0.001$ (MYI)

Strong significant positive regressions between bacterial abundance and chl *a*, DOC, PO_4 and brine volume fraction were observed for both ice types (Figure 8 a-d). Notably, the bacteria *versus* brine volume regression slope was significantly higher in FYI than in MYI ($p < 0.001$, covariance analysis) whereas the other regression slopes were not significantly different between ice types.

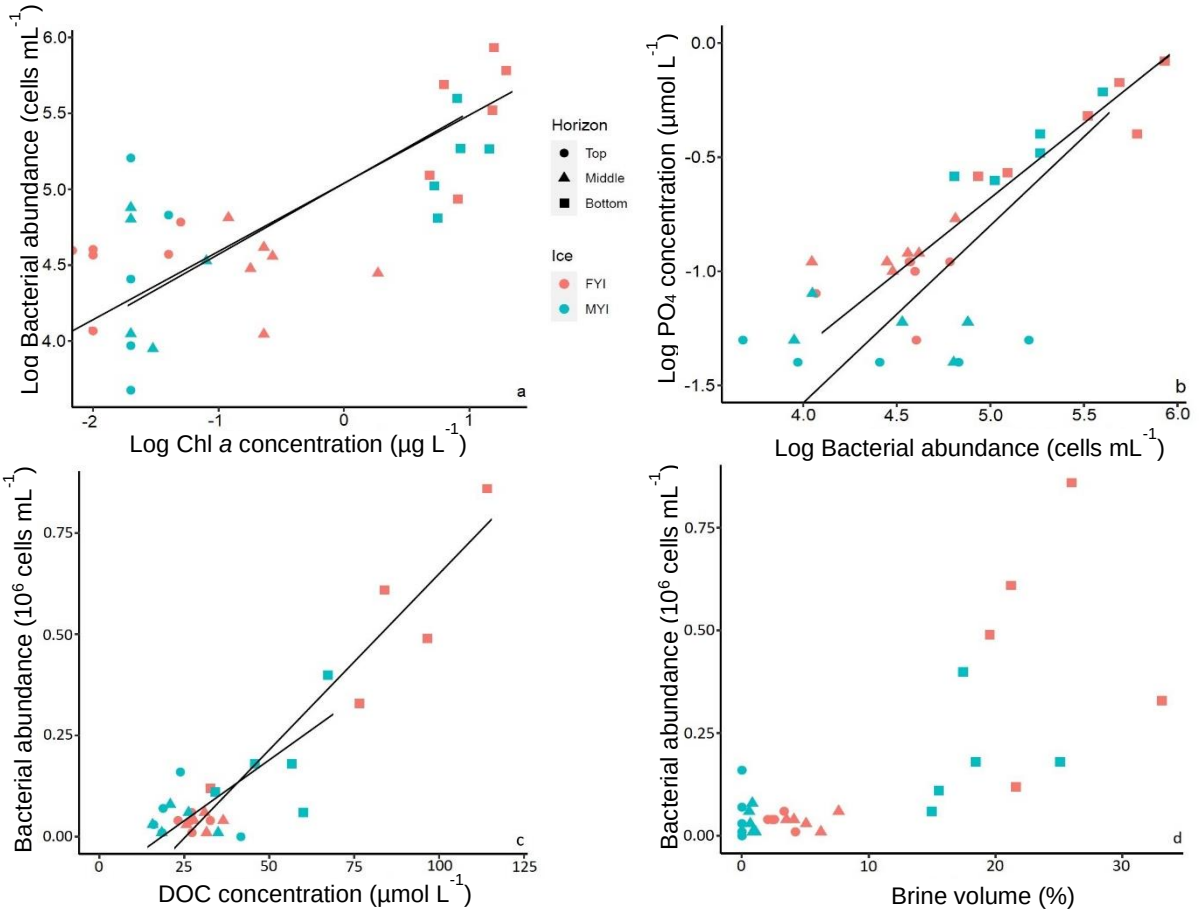

Figure 8. Relationships between bacterial abundance and (a) chl (chlorophyll) *a*, (c) DOC (dissolved organic carbon) and (d) brine volume, and between PO_4 (phosphate) and (b) bacterial abundance in the top, middle and bottom horizons of first-year ice (FYI) and multiyear ice (MYI) in the Lincoln Sea during spring 2018. Model II linear regression: in (a) $Log(x_2) = 0.45 \times Log(x_1) + 5.04$, $r^2 = 0.56$, $p < 0.001$ (FYI) and $Log(x_2) = 0.47 \times Log(x_1) + 5.04$, $r^2 = 0.44$, $p < 0.01$ (MYI); in (b) $Log(x_2) = 0.66 \times Log(x_1) - 3.95$, $r^2 = 0.81$, $p < 0.001$ (FYI) and $Log(x_2) = 0.78 \times Log(x_1) - 4.68$, $r^2 = 0.41$, $p < 0.05$ (MYI); in (c) $x_2 = 0.0087 \times x_1 - 0.2163$, $r^2 = 0.94$, $p < 0.001$ (FYI) and $x_2 = 0.006 \times x_1 - 0.1064$, $r^2 = 0.44$, $p < 0.01$ (MYI); in (d) $x_2 = 0.66 \times x_1 - 3.95$, $r^2 = 0.81$, $p < 0.001$ (FYI) and $x_2 = 0.78 \times x_1 - 4.68$, $r^2 = 0.41$, $p < 0.05$ (MYI)

Table 3. Pearson correlation matrix of biological and environmental variables measured from first-year ice cores in the Lincoln Sea during spring 2018. Chl *a*: chlorophyll *a*, DOC: dissolved organic carbon, NO_x: nitrate + nitrite, PO_4: phosphate, $Si(OH)_4$: silicic acid, BV: brine volume. Correlation coefficients, probability and number of samples (n) are shown. Correlation coefficients in bold are significant at $p < 0.05$

	Virus	Chl *a*	DOC	NO_x	PO_4	$Si(OH)_4$	BV
	0.96	**0.86**	**0.97**	0.43	**0.94**	**0.69**	**0.78**
Bacteria	0.0001	0.0001	0.0001	0.0728	0.0001	0.0013	0.0006
(cells mL^{-1})	n=18	n=18	n=15	n=18	n=18	n=18	n=15
		0.90	**0.90**	0.39	**0.87**	**0.70**	**0.77**
Virus		0.0001	0.0001	0.1120	0.0001	0.0013	0.0008
(cells mL^{-1})		n=18	n=15	n=18	n=18	n=18	n=15
			0.85	**0.51**	**0.79**	**0.64**	**0.88**
Chl *a*			0.0001	0.0314	0.0001	0.0041	0.0001
(µg L^{-1})			n=15	n=18	n=18	n=18	n=15
				0.41	**0.97**	**0.72**	**0.81**
DOC				0.2135	0.0001	0.0026	0.0002
(µmol L^{-1})				n=15	n=15	n=15	n=15
					0.31	0.27	0.47
NO_x					0.2135	0.2732	0.0795
(µmol L^{-1})					n=18	n=18	n=15
						0.82	**0.84**
PO_4						0.0001	0.0001
(µmol L^{-1})						n=18	n=15
							0.81
$Si(OH)_4$							0.0003
(µmol L^{-1})							n=15

Table 4. Pearson correlation matrix of biological and environmental variables measured from multiyear ice cores in the Lincoln Sea during spring 2018. Chl *a*: chlorophyll *a*, DOC: dissolved organic carbon, NO_x: nitrate + nitrite, PO_4: phosphate, $Si(OH)_4$: silicic acid, BV: brine volume. Correlation coefficients, probability and number of samples (n) are shown. Correlation coefficients in bold are significant at $p < 0.05$

	Virus	Chl *a*	DOC	NO_x	PO_4	$Si(OH)_4$	BV
	0.87	**0.67**	**0.66**	**0.73**	**0.87**	**0.71**	**0.67**
Bacteria	0.0001	0.0064	0.0070	0.0001	0.0001	0.0032	0.0066
(cells mL^{-1})	n=15	n=15	n=15	n=15	n=15	n=15	n=15
		0.79	**0.74**	**0.84**	**0.91**	**0.82**	**0.79**
Virus		0.0001	0.0018	0.0001	0.0001	0.0002	0.0004
(cells mL^{-1})		n=15	n=15	n=15	n=15	n=15	n=15
			0.79	**0.87**	**0.87**	**0.89**	**0.98**
Chl *a*			0.0004	0.0001	0.0001	0.0001	0.0001
(µg L^{-1})			n=15	n=15	n=15	n=15	n=15
				0.66	**0.87**	**0.76**	**0.82**
DOC				0.0069	0.0001	0.0011	0.0002
(µmol L^{-1})				n=15	n=15	n=15	n=15
					0.87	**0.96**	**0.91**
NO_x					0.0001	0.0001	0.0001
(µmol L^{-1})					n=15	n=15	n=15
						0.90	**0.90**
PO_4						0.0001	0.0001
(µmol L^{-1})						n=18	n=15
							0.96
$Si(OH)_4$							0.0001
(µmol L^{-1})							n=15

Table 5. Pearson correlation matrix of biological and environmental variables measured from surface waters in the Lincoln Sea during spring 2018. Chl *a*: chlorophyll *a*, DOC: dissolved organic carbon, NO_x: nitrate + nitrite, PO_4: phosphate, $Si(OH)_4$: silicic acid. Correlation coefficients, probability and number of samples (n) are shown. Correlation coefficients in bold are significant at $p < 0.05$

	Virus	Chl *a*	DOC	NO_x	PO_4	$Si(OH)_4$
	0.36	**0.82**	**0.89**	-0.28	-0.13	-0.23
Bacteria	0.482	0.0064	0.0410	0.588	0.802	0.651
(cells mL^{-1})	n=6	n=6	n=5	n=6	n=6	n=6
		-0.10	0.39	-0.79	-0.71	-0.74
Virus		0.841	0.515	0.0615	0.111	0.0923
(cells mL^{-1})		n=6	n=5	n=6	n=6	n=6
			0.86	0.09	0.16	-0.006
Chl *a*			0.0575	0.860	0.763	0.990
(µg L^{-1})			n=5	n=6	n=6	n=6
				-0.24	-0.42	-0.71
DOC				0.694	0.476	0.172
(µmol L^{-1})				n=5	n=5	n=5
					0.92	**0.86**
NO_x					0.0079	0.0280
(µmol L^{-1})					n=6	n=6
						0.96
PO_4						0.0020
(µmol L^{-1})						n=6

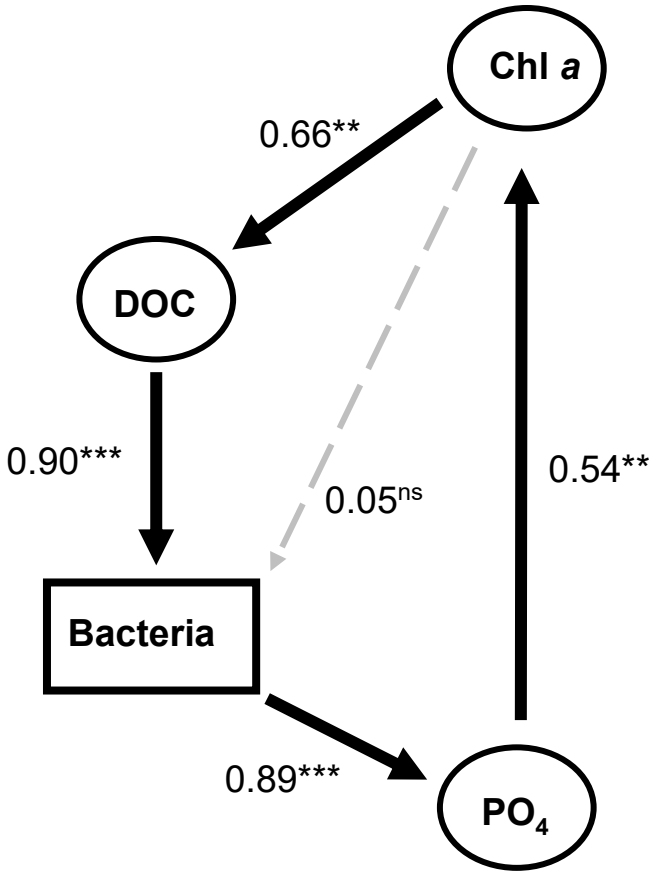

Figure 9. Schematic representation of the path analysis showing interactions between chl (chlorophyll) *a*, DOC (dissolved organic carbon), bacteria and PO_4 (phosphate) in first-year ice and multiyear ice in the Lincoln Sea during spring 2018. Path coefficients (partial correlations) are indicated. Black arrows indicate directions for significant path coefficients between the variables. Gray dashed line indicates non-significant path coefficient. **: $p < 0.01$, *** : $p < 0.001$, ns: not significant

Path analysis was used to evaluate the relationships between chl *a*, DOC, bacterial abundance and PO_4, using data from all horizons in both ice types (Figure 9). All significant path coefficients were positive, showing directional relationships from chl *a* to DOC, DOC to bacteria, bacteria to PO_4, and PO_4 to chl *a*. There was no significant path between chl *a* and bacteria. The strongest path coefficients were from DOC to bacteria and from bacteria to PO_4 (≥ 0.89, $p < 0.001$).

When adding viral abundance and brine volume to the path analysis, new relationships were revealed, of which one of the strongest was between bacteria and viruses (0.93, $p < 0.001$; Figure 10). There were significant path coefficients between brine volume and chl *a*, and between brine volume and PO_4. However, there was no significant relationship between brine volume and DOC or bacteria. In this more complex path analysis, the initial relationships (Figure 9) were mostly maintained, but the path coefficient between DOC and bacteria increased from 0.90 to 0.98 whereas those between chl *a* and DOC, bacteria and PO_4 and PO_4 and chl *a* decreased from 0.66 to 0.64, from 0.89 to 0.60, and from 0.54 to 0.19, a non-significant path value, respectively.

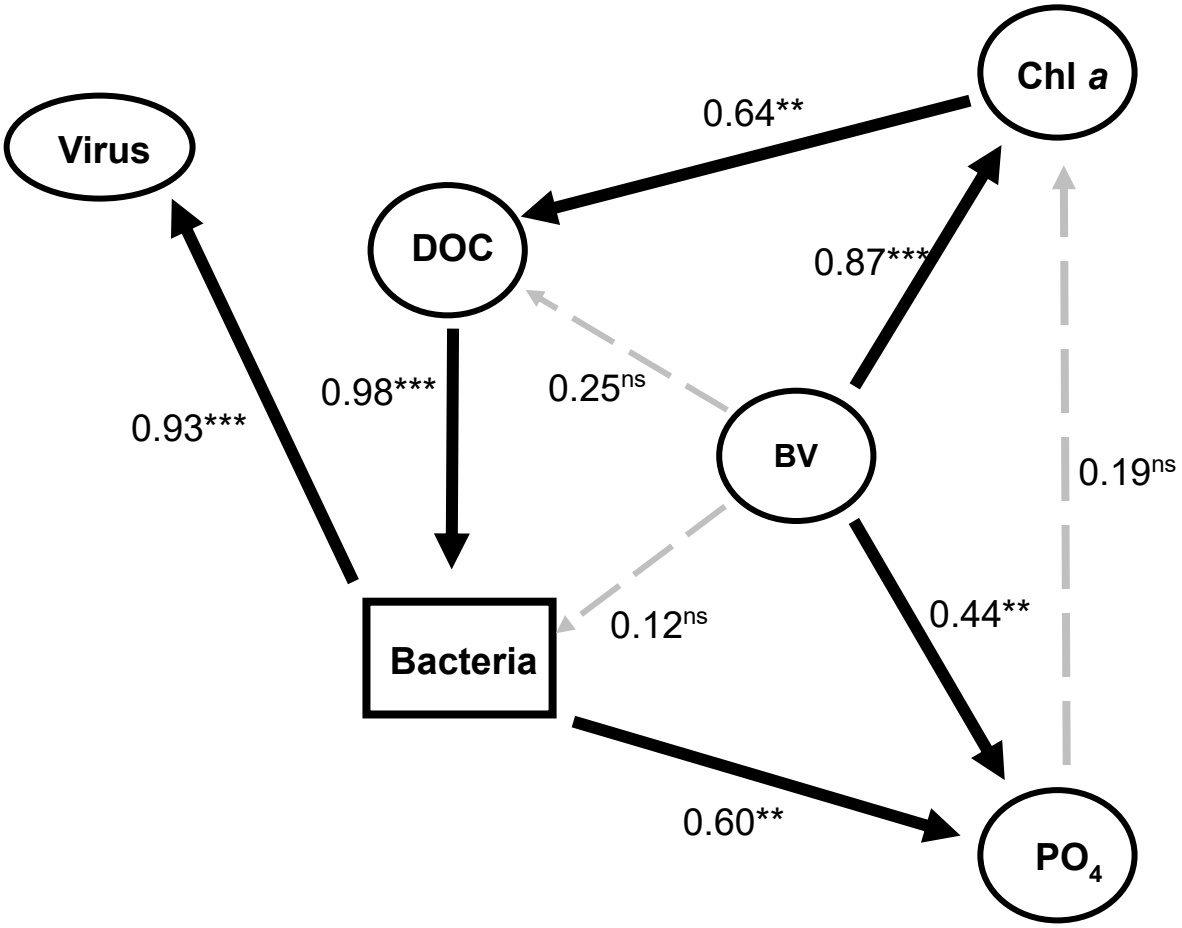

Figure 10. Schematic representation of the path analysis showing interactions between BV (brine volume), chl (chlorophyll) *a*, PO_4 (phosphate), DOC (dissolved organic carbon), bacteria and viruses in first-year ice and multiyear ice in the Lincoln Sea during spring 2018. Path coefficients (partial correlations) are indicated. Black arrows indicate directions for significant path coefficients between the variables. Gray dashed lines indicate non-significant path coefficients. **: $p < 0.01$, ***: $p < 0.001$, ns: not significant

1.4. DISCUSSION

1.4.1. SEA ICE MICROBIAL COMMUNITIES AND ASSOCIATED ENVIRONMENTAL CONDITIONS IN THE LINCOLN SEA

During this study, bacterial and viral abundances in the bottom ice horizon increased seasonally in FYI but not in MYI, showing contrasting seasonality between the two ice types (Figure 6). Similar seasonal trends were observed in FYI in the Canadian Arctic Archipelago, (Smith et al. 1989, Maranger et al. 1994), Frobisher Bay (Bunch & Harland 1990), the Baltic Sea (Kaartokallio 2008), and in McMurdo Sound, Antarctica (Kottmeier et al. 1987). The lack of a seasonal trend in MYI may be explained by the large spatial variability in snow depth (0.02 – 0.30 m), ice thickness (1.37 – 4.58 m) and light conditions in MYI at our sampling stations (Lange et al. 2019).

Higher bacterial and viral abundances in the bottom ice compared to the upper ice horizons and to the surface waters (Figure 5a, b) are consistent with a number of studies conducted across the Arctic (e.g., Beattie et al. 2014, for bacteria in MYI) and Antarctic (Gowing et al. 2004) (see Table 6). However, Eronen-Rasimus et al. (2017) reported that maximum bacterial abundance in the Weddell Sea (Antarctica) during winter generally occurred in the middle horizon of FYI and MYI pack, coinciding with maximum chl *a* concentrations. Another study in Antarctica did not reveal consistent patterns in bacterial abundance between the top, middle and bottom ice horizons in landfast FYI in late spring (Cowie et al. 2014). It is possible that, during our study, sea-ice bacterial and viral abundances remained low throughout the ice including the bottom ice horizon because of the low chl *a* concentrations (< 19.65 µg L^{-1}; Figure 4c, d). These chl *a* concentrations are comparable with those found earlier in the same region (Lange et al. 2015) and in the Weddell Sea (Table 6) and are one to two orders of magnitude lower than chl *a* concentrations in FYI at productive locations in the Canadian Arctic during spring (e.g., Cota et al. 1990, 1991, Michel et al. 1996, Nozais et al. 2001, Lavoie et al. 2005).

Bacteria in the bottom ice horizon were 10 and 100 times more abundant than top and middle ice horizons, respectively. Despite being higher in the bottom ice horizon, sea ice bacterial abundance during our study remained low, comparable to those observed in the Central Arctic Ocean (Bowman et al. 2012, Sazhin et al. 2019) and McClure Strait (Beattie et al. 2014) (Table 6). Bacterial abundances were one to two orders of magnitude lower than those reported in FYI in the Canadian Arctic Archipelago during the spring ice algal bloom (Maranger et al. 1994, Riedel et al. 2007b, Garneau et al. 2016). Viral abundances were similar to values reported in the Weddell and Ross seas (Antarctica), but lower than in Resolute Passage (Table 6).

The lower sea ice bacterial and viral abundances in the top and middle ice horizons compared to the bottom for both ice types (Table 1, Figure 5a, b) are likely explained by the low ice surface temperature and bulk salinity. With sea ice temperatures, bulk salinity and brine volume fraction consistently below -5°C, 5 and 5%, respectively, in the top ice horizon despite the seasonal increase in air temperature (see Figures 2 & 3a, b), conditions within the ice matrix would not be conducive to microbial colonization and growth (e.g., Junge et al. 2001). In the middle ice horizon, ice temperature, bulk salinity and brine volume fraction reached values higher than -5°C, 5, 5%, respectively, only at the end of the sampling period (23 May), whereas they were consistently higher in the bottom ice horizon, allowing for microbial growth (Figure 3). The highest bacterial and chl *a* concentrations in the bottom ice horizon for both ice types (Figure 4c, d), emphasize the role of brine channel space and connectivity for biological communities to thrive within the sea ice environment. Indeed, chl *a* concentrations and brine volume were strongly and positively correlated in FYI and MYI and higher nutrient concentrations were all observed under conditions where the percent of brine volume exceeded 5% (Tables 3 & 4, Figures 3e, f & 10). The movement of brine, which provide inorganic nutrients essential to algal growth can occur under these conditions which coincides with ice temperature at -5°C for a bulk salinity of 5 (Golden et al. 1998, 2007). Moreover, bacterial abundance increased in parallel with chl *a* and DOC concentrations increasing from the top to the bottom of the sea ice cores (see Figures 4 & 5) indicating a vertical gradient in environmental conditions and towards the bottom ice

horizon. It is also likely that the composition of DOC differed between the upper and bottom ice horizons, as reported by Underwood et al. (2013). As in other Arctic regions, during our study, the bottom ice horizon for FYI (Figure 4a, c) provided a suitable habitat with adequate dissolved organic and inorganic nutrients, as well as space for algal colonization and growth (Mundy et al. 2007, Arrigo 2014). Our study also highlights favorable environmental conditions in the bottom ice horizon in MYI (Figure 4b, d).

During this study, low VBR values together with high bacterial and viral abundances were detected in the bottom ice horizon in FYI and MYI (Figure 5c, d) as reported during the spring ice algal bloom near Resolute Passage (Maranger et al. 1994) and austral winter in the Weddell Sea (Luthanen et al. 2018). It is possible that the low VBR in the bottom ice horizon reflects a decoupling between bacterial and viral infection leading to higher bacterial abundance in the bottom ice horizon.

Another explanation is that the low VBR in the bottom ice horizon resulted from changes in bacterial community composition where the proliferation of phage-resistant bacteria may have increased. As explained by Luthanen (2017), bacteria may have virus resistance mechanisms and a dominance of defense strategic bacterial strains would lower the VBR. Alternatively, the disequilibrium between bacterial and phage abundances could be induced by a decrease in host bacterial activity, which could also decrease viral production, possibly because phages may have lysogenized i.e., become prophages (Maranger et al. 1994, Luthanen et al. 2018).

During our study period, sub-ice irradiance of MYI was very low during our study period (0.47 – 0.48 µmol photons m^{-2} s^{-1}; see Table S3 of Lange et al. 2019), at values much lower than theoretical values of 2 – 9 µmol photons m^{-2} s^{-1} for ice algal growth (Gosselin et al. 1985, 1986) is indicative of light limitation of sea ice algae in MYI. Irradiance was higher under FYI (2.7 – 4.3 µmol photons m^{-2} s^{-1}; see Table S3 of Lange et al. 2019), suggesting earlier and possibly higher net growth rate of sea ice algae under FYI than MYI. This is in agreement with the maximum chl *a* biomass observed in FYI (Figure 4c). However, since no

significant difference between chl *a* concentrations was found in ice types, ice algal growth may be limited in both FYI and MYI (Figure 4c, d).

In the Lincoln Sea, nutrient availability in sea ice and surface water may limit the accumulation of sea ice algal chl *a* biomass later in the season when light conditions will improve. Sea ice and surface water nutrient concentrations (NO_x, PO_4, $Si(OH)_4$) were low (< 3 µmol L^{-1} in sea ice and average of 5.02, 1.01 and 11.81 µmol L^{-1} for NO_x, PO_4, $Si(OH)_4$, respectively; Table 1, Figure 4a, b) compared to sea ice nutrient concentrations reported in other regions of the Canadian Arctic Archipelago (e.g., Resolute Passage: 6 – 12 µmol L^{-1}, > 0.60, and 2.8 µmol L^{-1} for NO_x, PO_4, $Si(OH)_4$, respectively; Galindo et al. 2014). Nutrient limitation of sea ice algal growth, in particular by nitrogen or silicic acid, has been linked to nutrient supply at the ice-water interface (Cota et al. 1987, Lavoie et al. 2005). The maximum bottom ice algal biomass attained during the vernal growth season has also been linked to the NO_x surface concentrations (Różańska et al. 2009). The low surface water nutrient concentrations in the sampling region (Table 1, Figure 4a, b) is indicative of an oligotrophic region compared to highly productive regions of the Canadian Archipelago.

During this study, chl *a* concentrations were low in the bottom ice due to light or nutrient limitations and these conditions were not favorable for the development of a sea ice algal bloom. The late start of the growing season of sea ice algae would also explain the low bacterial and viral abundances in the bottom ice horizon in the FYI and MYI of the Lincoln Sea during spring, as discussed in more details in the next section.

1.4.2. MICROBIAL PROCESSES IN FIRST-YEAR ICE AND MULTIYEAR ICE

This study reveals an active microbial food web in FYI and MYI, where DOC released by sea ice algae during photosynthesis is taken up by bacteria. Extracellular enzymes, such as phosphatases, are produced by bacteria and/or heterotrophic and mixotrophic protists preying upon bacteria. Organic matter is remineralized into nutrients, namely phosphate,

which can then accumulate in the sea ice or be taken up by algae or bacteria (Figure 9). These biochemical pathways through the microbial food web are evidenced by regression and path analyses, as discussed below.

The strong positive relationship between bacterial abundance and chl *a* concentrations in both FYI and MYI (Tables 3 & 4, Figure 8a), in agreement with seasonal studies in FYI (Grossi et al. 1984, Maranger et al. 1994, Steward & Fritsen 2004, Comeau et al. 2013) indicates the important role of ice algal DOM substrates. During our study, the bacteria-chl *a* relationship was largely driven by dynamics in the bottom ice rather than in the upper ice horizons for both ice types (see Figure 8a). This could explain inconsistencies between studies in terms of significant relationships between sea ice bacteria and chl *a* concentrations (e.g., Cowie et al. 2014). Indeed, several studies reported no significant relationship between bacteria and algae, in terms of abundance or biomass, in the sea ice (Grossi et al. 1984, Steward & Fritsen 2004, Pusceddu et al. 2009, Cowie et al. 2014). Cowie et al. (2014) proposed a decoupling between bacteria and algae, for example, in the presence of grazers where bacteria are less dependent on substrates produced by sea ice algae and more dependent on DOM produced during grazing. This process may explain, in part, the heterotrophic activity observed in newly formed sea ice in fall when photosynthetic activity is declining (Riedel et al. 2007a).

In FYI, sea ice algae are known to produce DOM, which can make up to 34% of total ice algal production (Gosselin et al. 1997). Several studies reported high accumulation of DOM within sea ice, with DOC concentrations > 3300 µmol C L^{-1} during the ice algal bloom in FYI, either landfast ice or pack ice (Smith et al. 1997a, Riedel et al. 2008, Aslam et al. 2016). The sea ice DOC concentrations in FYI and MYI during our study (< 100 µmol L^{-1}, Table 1, Figure 4a, b) remain much lower than those values. However, these values are similar to those observed in MYI from the Fram Strait in late spring (mostly below < 100 µmol L^{-1}, Thomas et al. 1995) and the northeastern Beaufort Sea in late summer (15 – 110 µmol L^{-1}, Beattie et al. 2014).

Strong correlations between DOC and bottom ice algal biomass, established for a wide range of sea ice conditions in the Arctic and the Antarctic clearly indicate an algal origin for DOC (Underwood et al. 2013). Our results agree with these findings and support that sea ice algae are the main producers of DOC, which is further used by bacteria, in both FYI and MYI in the Lincoln Sea (see Figures 9 & 10). It is well-established that sea ice bacteria are largely heterotrophic and assimilate DOC to produce biomass and energy (Riedel et al. 2007b, Bowman 2015). During our study, we did not characterize the composition of sea ice DOM. It is possible that the composition of sea ice DOM was different between FYI and MYI and that differences in DOM composition could impact the activity and diversity of bacterial communities, as shown by Underwood et al. (2019). Interestingly, despite potentially different sea ice DOM pools in FYI and MYI, microbial web processes appeared to be consistent across the ice types (Figures 9 & 10).

The path analyses provide insights into microbial processes in both FYI and MYI (Figures 9 & 10). In the simplified model, DOC produced by sea ice algae is identified as a determining factor for bacterial abundance in both ice types, as discussed earlier. This model also suggests that PO_4 regeneration from dissolved organic phosphorus (DOP) compounds by enzymes released by bacteria could also support ice algal production. Cowie et al. (2014) measured bacterial enzyme activity in Antarctic landfast sea ice at the beginning of the ice algal spring bloom. They showed that ice bacteria responded to changing nutrient conditions by regulating the synthesis and activity of their enzymes. During their study, bacterial phosphatase activity was higher than protease activity, indicating that sea ice was more P-limited than N-limited.

When incorporating brine volume as a forcing factor into the path analysis, relationships between bacteria, PO_4 and algae, and their interpretations, change significantly (see Figure 10). Here, the model reveals that brine volume (a proxy of sea ice permeability which facilitates fluid and nutrient transport), also linked to habitat space in the ice, is more important than PO_4 for ice algal biomass. The second path analysis suggests that bacteria could either produce or use PO_4 and that PO_4 regeneration could also be from excretion by

herbivorous protists. Riedel et al. (2007b) found that bacterivorous protists are active throughout the spring season in the Canadian Arctic. Hence, remineralization of sea ice PO_4 could involve both bacterial enzymes and heterotrophic grazing. In the water column as well as in sea ice, algae and heterotrophic bacteria take up PO_4 for their metabolic functions. In the open ocean, the inorganic phosphorus is rapidly assimilated by phytoplankton whereas some of the organic phosphorus compounds can be hydrolyzed by enzymes synthesized by bacteria and phytoplankton and then assimilated (Paytan & McLaughlin 2007). Therefore, in oligotrophic waters especially, bacteria would compete with microalgae for inorganic nutrients (Fuhrman et al. 1988, Danovaro 1997). In nutrient-rich waters, a larger fraction of the nutrients is consumed by phytoplankton (Bratbak & Thingstad 1985).

As mentioned in the previous section, sea-ice nutrient concentrations in the Lincoln Sea were low when compared to values reported in other regions of the Canadian Arctic. The NO_x:PO_4 and NO_x:$Si(OH)_4$ molar ratios in the sea ice (Table 1) were generally lower than the Redfield-Brzezinski values (16 and 1, respectively; Redfield et al. 1963, Brzezinski 1985), indicating that nitrogen was potentially the limiting nutrient for ice algal growth, as shown in Resolute Passage (Smith et al. 1997b) and in the Beaufort Sea (Różańska et al 2009). Silicon may also be limiting for sea ice diatoms (Lavoie et al. 2005), especially since the sea ice concentrations of $Si(OH)_4$ ranging from < 0.10 to 2.62 µmol L^{-1} are within the range of reported values for the affinity constant of diatoms for dissolved silicon (K_s = 0.8 to 3.4 µmol L^{-1}; Paasche 1973, Azam & Chisholm 1976). In contrast, phosphate concentrations in the bottom ice horizon (from 0.25 to 0.83 µmol L^{-1} and a mean of 0.43 µmol L^{-1}) are relatively high compared to the affinity constant for dissolved phosphorus (K_s = 0.14 to 0.18 µmol L^{-1}; Perry & Eppley 1981). This indicates that without nutrient regeneration or replenishment from the under-ice water column, the sea ice algae biomass may become co-limited by nitrogen and silicon supply later in the season.

Few studies have characterized the role of bacteria in the remineralization of PO_4 in sea ice, especially in MYI, while other studies have described this process in marine waters (e.g., Paytan & McLaughlin 2007). Within platelet ice, which accumulates under FYI,

Dieckmann et al. (1992) and Arrigo et al. (1995, 2003) reported high PO_4 concentrations indicating active heterotrophic remineralization. However, in their studies they could not distinguish bacterial from protozoan remineralization. Interestingly, this study shows a significant positive relationship between bacteria and PO_4 in both FYI and MYI in the Lincoln Sea indicating that bacteria are involved in phosphate recycling. During this study, the accumulation of PO_4 in the bottom ice horizon may be explained by enhanced ice permeability and/or higher bacterial remineralization, low light conditions limiting photosynthetic activity, and the excess phosphate availability relative to bacterial nutrient requirement.

As anticipated and based on results from earlier studies in Arctic FYI (Maranger et al. 1994) and open waters (Middelboe & Lyck 2002, Hodges et al. 2005), sea ice viral and bacterial abundances were tightly coupled (Tables 3 & 4, Figures 7 & 10). The second path analysis indicates that viruses in FYI and MYI were essentially bacteriophages as shown by the strong and significant path coefficient (0.93, Figure 10). However, this was not the case in surface waters (Table 5), possibly due to the low bacterial abundances and/or to low virus-bacteria contact rates. The low bacterial abundances in surface waters are likely related to the chemical composition of DOM rather than its availability, since surface waters DOC concentrations were comparable to those in the bottom ice (Figure 4a, b). Aslam et al. (2016) report a significantly different carbohydrate composition in DOM between FYI and surface waters at 23 stations in the Canadian Arctic Archipelago, with a dominance of glucose *versus* mannose, respectively.

This study indicates that despite differences in sea ice properties and biochemical conditions in FYI and MYI, the key processes influencing microbial activity are similar for both ice types.

Table 6. Abundance of free-living bacteria and free viral particles, and chl (chlorophyll) *a* in the bottom ice horizon at various locations in the Arctic and the Antarctic. Note that full profiles of bacterial abundance (from surface to bottom) are presented in Beattie et al. (2014) for multiyear ice (MYI) and Eronen-Rasimus et al. (2017) for first-year ice (FYI) and MYI. Cowie et al. (2014) and this study, data are presented for the top, middle and bottom ice horizons. nd: no data

Location	Season	Ice type	Thickness of bottom ice horizon or full core (m)	Bacteria ($\times 10^6$ mL^{-1})	Virus ($\times 10^6$ mL^{-1})	Chl *a* concentration (µg L^{-1})	Reference
Lincoln Sea	Mid-spring	MYI	0.10	0.06 – 0.40	0.81 – 2.77	5.26 – 14.38	This study
Central Arctic Ocean	Early spring & mid-summer	MYI (second year)	0.12 – 0.15	0.025 – 0.095	0.091	nd	Sazhin et al. 2019
Central Arctic Ocean		MYI	Full core: 3.0− 3.3	0.017 – 0.084	nd	nd	Bowman et al. 2012
McClure Strait	Late summer	MYI (pack ice)	0.10	0.2 – 0.45	nd	0.01 – 4	Beattie et al. 2014
Lincoln Sea	Mid-spring	FYI (landfast)	0.10	0.09 − 0.86	1.30 – 4.53	4.84 – 19.65	This study
Lincoln Sea	Mid-spring	FYI	0.86	Core range: 0.01 – 0.1	nd	nd	Hatam et al. 2014
Central Arctic Ocean	Early spring	FYI	0.12 – 0.15	0.025	nd	nd	Sazhin et al. 2019
Resolute Passage	Spring	FYI (landfast)	0.04	1.5 – 6.0	nd	10 – 2000	Laurion et al. 1995

Resolute Passage	Mid-spring	FYI (landfast)	0.04	0.15 – 10	9.0 – 150	125 – 3000	Maranger et al. 1994
Resolute Passage	Mid-spring	FYI (landfast)	0.03	16	nd	4563	Garneau et al 2016
Barrow Strait	Spring	FYI	0.04	0.4 – 7.9	nd	1500 – 3000	Smith et al. 1989
Dease Strait	Late winter – late spring	FYI (landfast)	0.05	0.1 – 10	nd	0.2 – 240	Campbell et al. 2018
Amundsen Golf	Early spring – early summer	FYI (pack and landfast ice)	0.045	0.071 – 0.574	nd	0.70 – 1.970	Nguyen & Maranger 2011
Amundsen Golf	Spring	FYI (pack and landfast ice)	0.1	0.139 – 1.383	nd	7 – 1187	Comeau et al. 2013
Franklin Bay	Winter − early spring	FYI (landfast)	0.3 – 1.0	0.004 – 0.09	nd	nd	Collins et al. 2008
Franklin Bay	Late winter – mid-spring	FYI (landfast)	0.04	0.3 – 2.7	nd	0.3 – 22	Riedel et al. 2007a
Franklin Bay	Late winter/late spring	FYI (landfast)	0.04	0.3 – 4.3	nd	0.01 – 700	Riedel et al 2006
Mackenzie Shelf	Autumn	Newly formed sea ice	Full core or 0.03 for sea ice thicker than 0.07 m	0.2 – 2.0	nd	0.3 – 496	Riedel et al 2007b
Beaufort Sea	Winter	FYI	0.1	0.1 − 2 (scaled to brine volume)	80 – 300 (scaled to brine volume)	nd	Collins & Deming 2011
Barents and Laptev seas	Spring/Summer	FYI	0.1	0.04 – 3.67	nd	0.6 – 17.3	Gradinger & Zhang 1997

Greenland Sea	Spring	FYI	0.1	0.3 − 1.2	nd	0.5 – 1.93	Gradinger et al. 1991
Weddell Sea, Antarctica	Austral winter	FYI (pack ice) and MYI	0.05	0.05 – 1.2	0.19 – 9.70	0.41 – 16.59	Luthanen et al. 2018
Weddell Sea, Antarctica	Winter	Pancake ice	Interval: 0.10 Bottom: 0.10	Core range: 0.05 – 0.3 0.08 – 0.12	nd nd	0.1 – 3.7 0.1 – 1.6	Eronen-Rasimus et al. 2017
Weddell Sea, Antarctica	Winter	FYI (pack ice)	Interval: 0.10 – 0.20 Bottom: 0.15 – 20	Core range: 0.03 – 1.8 0.05 – 0.27	nd nd	0.8 – 18 0.3 – 15	Eronen-Rasimus et al. 2017
Weddell Sea, Antarctica	Winter	MYI (second year ice pack)	Interval: 0.10 – 0.30 Bottom: 0.10	Core range: 0.15 – 11 1.23	nd nd	1.5 – 114 6.15	Eronen-Rasimus et al. 2017
Ross Sea, Antarctica	Austral winter	FYI (pack ice)	0.2	0.18 – 6.71	0.63	2.1	Gowing et al. 2004
Granite Harbour, Antarctic	Late ausral spring	FYI (landfast)	0.1	0.007 – 0.1	nd	40.1 – 400	Cowie et al. 2014

1.5. CONCLUSION

This study discusses the structure and functioning of microbial communities in FYI and MYI in the Lincoln Sea in spring 2018 during the Multidisciplinary Arctic Program (MAP) – Last Ice. This study is the first to characterize and compare the vertical distribution of bacteria and viruses between FYI and MYI in the Arctic during spring, as well as microbial processes in the sea ice of the Lincoln Sea. This research has improved biological knowledge on this changing ecosystem.

This study shows that bacterial and viral abundances were comparable in FYI and MYI, but that the maximum concentrations were higher in FYI. The vertical distribution of sea ice bacteria and viruses was linked to environmental conditions and ice algal-derived substrates. The highest bacterial abundance, found in the bottom ice horizon, was associated with the enrichment in organic matter associated with sea ice algae.

Strong significant positive relationships between bacterial abundance and chl *a* concentrations indicate an active microbial food web in both FYI and MYI. Our results are consistent with an ecological model where bacteria assimilate DOC and regenerate PO_4 in the ice, increasing the inorganic phosphorus pool available for sea ice algae. Furthermore, viruses in sea ice appear to be likely bacteriophages, which is possibly related to the semi-closed environment of the brine channels, which increases the contact rate with bacteria when their abundance increases in spring. Despite differences in environmental and biological conditions in FYI and MYI, our results show that similar microbial processes apply to both ice types. In the context of climate change in the Arctic, the replacement of MYI by FYI could lead to a shift in bacterial community and diversity, thus having potential consequences on ecological processes.

In order to characterize more accurately and better understand microbial processes within FYI and MYI, it is essential to determine the bacterial community composition and the activity of free and attached bacteria. In this context of climate change, it is important to carry out additional studies, such as metagenomic studies, to extend our knowledge and understanding of this unique ecosystem. Thus, it will lead to a better insight into the ecological functioning of sea ice, which is a crucial habitat for the feeding and reproduction of ice-associated, pelagic and benthic fauna of the Arctic.

CONCLUSION GÉNÉRALE

Cette étude traite de la structure et du fonctionnement des communautés microbiennes dans la glace de mer annuelle et pluriannuelle de la mer de Lincoln au printemps. Elle est la première à caractériser et comparer la répartition verticale des bactéries et des virus dans les glaces de cette région en plus de décrire les processus biogéochimiques intervenant au sein de la glace de mer. Cette recherche a permis d'améliorer les connaissances biologiques sur cet écosystème en mutation en regard des changements climatiques qui le fragilise.

Les résultats montrent que, de façon générale, la répartition verticale des virus est similaire à celle des bactéries à la fois dans la glace annuelle et la glace pluriannuelle avec des abondances plus élevées à la base de la glace. Les plus fortes concentrations de nutriments, COD et chlorophylle *a* se retrouvent également à la base de la glace, où la perméabilité de la glace est la plus grande, pour les deux types de glace.

La répartition verticale des bactéries semble déterminée par la disponibilité et la répartition de la matière organique disponible ainsi que les conditions environnementales favorables à la base de la glace. En effet, l'abondance élevée de bactéries à la base de la glace est associée à l'enrichissement en matière organique due à la prolifération d'algues de glace au printemps. Les virus se retrouvent dans les milieux où se retrouvent les cellules (bactéries notamment) qu'ils sont capables d'infecter.

Bien que la salinité et le volume de saumure ainsi que les concentrations en nutriments inorganiques et en COD soient plus élevés dans la couche de la glace annuelle que dans celle de la glace pluriannuelle, on observe néanmoins des processus biogéochimiques similaires dans les deux types de glace. À la lumière de nos résultats s'appuyant sur des relations fortes entre les variables physico-chimiques et biologiques et l'analyse des coefficients de direction, nous pouvons identifier un réseau microbien actif dans ces deux types de glace. Notre modèle

causal suggère que les bactéries hétérotrophes assimilent du COD, produit par les algues de glace, et le transforme en biomasse bactérienne. En retour, les bactéries hétérotrophes ou leur brouteur reminéralisent la matière organique dissoute en nutriments inorganiques, notamment en phosphate, qui s'accumule à la base de la glace et peut être consommé par les algues. Par leur activité, les bactéries peuvent ainsi contribuer à soutenir la production primaire.

Finalement, cette étude a mis en évidence le rôle joué par les virus sur la dynamique bactérienne. L'augmentation de la concentration des particules virales à la base de la glace suit les abondances bactériennes. Par ailleurs, notre second modèle causal suggère que dans la glace de mer, les virus sont essentiellement bactériophages, possiblement lié à l'environnement semi-fermé des canaux de saumure qui augmentent le taux de contact avec les bactéries quand leur abondance augmente au printemps. Ces résultats suggèrent qu'à travers la lyse virale exercée sur les bactéries, les virus ont un rôle dans le contrôle de la dynamique bactérienne et des cycles biogéochimiques.

Afin de mieux comprendre le rôle des bactéries dans le cycle du carbone de la glace de mer, il serait intéressant de déterminer la production des bactéries libres et attachées. Les bactéries attachées peuvent avoir des concentrations locales très élevées par rapport aux bactéries libres (Fernández-Gómez et al. 2013). Par ailleurs, les communautés bactériennes libres et attachées peuvent présenter des différences taxonomiques et physiologiques. Les bactéries attachées ont généralement un taux d'activité spécifique par cellule supérieur à celui des bactéries libres (Kirchman 1993). La contribution des bactéries attachées à l'activité bactérienne totale est très variable mais elle est généralement de 20% dans les milieux oligotrophes et peut dépasser 30% dans les milieux eutrophes (Simon et al. 2002). Dans la glace de mer arctique (Smith et al. 1989) et antarctique (Sullivan & Palmisano 1984), les bactéries attachées représentent environ 30% des bactéries totales.

Dans le même ordre d'idées, il serait intéressant de mieux quantifier les variations spatiale et temporelle de la mortalité des bactéries induites par le broutage (prédation) par les protistes hétérotrophes et mixotrophes notamment les nanoflagellés hétérotrophes et les

ciliés. En effet, le broutage par les protistes hétérotrophes est un facteur important de la mortalité bactérienne. Les études menées dans l'archipel arctique Canadien ont mis en évidence des taux élevés de bactérivorie au cours de la floraison algale printanière qui supportent la croissance des protistes hétérotrophes notamment les flagellés < 10 µm (Laurion et al. 1995, Sime-Ngando et al. 1997, Riedel et al. 2007b). En étudiant plus précisément la dynamique saisonnière du broutage bactérien, Riedel et al. (2007b) ont montré que les bactéries satisfont les besoins en carbone des protistes hétérotrophes avant la floraison algale printanière.

D'autre part, la métagénomique et les études d'expression génétiques sont des alliés importants dans la compréhension de la dynamique des communautés bactériennes. Ces techniques sont des atouts essentiels qui nous permettraient de déterminer et comparer la composition taxonomique des bactéries et des virus dans la glace annuelle et pluriannuelle. Des études récentes menées en Arctique et en Antarctique ont permis de mettre en évidence des assemblages bactériens distincts, aussi bien sur le plan taxonomique que fonctionnel, non seulement entre les différents types de glace (nouvelle glace, vieille glace) et couches de la glace (incluant les mares de fonte) (Collins et al. 2010, Bowman et al. 2012, Cowie et al. 2014, Hatam et al. 2014) mais aussi avec la colonne d'eau. Les communautés bactériennes présentes dans la glace pluriannuelle ont une structure et une composition plus stables que celles présentes dans la glace annuelle (Hatam et al. 2016).

Il est attendu que le remplacement progressif de la glace pluriannuelle par la glace annuelle entraînera des changements majeurs et potentiellement irréversibles sur la communauté de la glace de mer en général (Hop et al. 2020) et la communauté bactérienne en particulier. La perte d'habitat liée à la diminution du couvert et de l'étendue de glace de mer pourrait entraîner des changements au sein des communautés bactériennes. Ces changements de communautés pourraient avoir des conséquences sur les fonctions écosystémiques qu'elles remplissent au sein des régions polaires.

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