Rôle des propriétés physiques et chimiques du milieu dans la succession des protistes marins lors de la floraison printanière en baie de Baffin

Mémoire

Pierre-Luc Grondin

Maîtrise en biologie - avec mémoire
Maître ès sciences (M. Sc.)

Québec, Canada

Résumé (Français)

Une diminution de l'étendue du couvert de glace et de neige au printemps a été observée en Arctique. Il est attendu que ceci affectera la phénologie des floraisons printanières, de même que la succession des groupes et espèces parmi les producteurs primaires. Les principaux objectifs étaient (i) de caractériser les communautés d'algues de glace et de phytoplancton et (ii) d'identifier les principaux forçages environnementaux associés à la succession des principaux groupes taxonomiques d'algues unicellulaires pendant une floraison printanière en baie de Baffin en 2015 et en 2016. Avec des mesures de variables environnementales à haute résolution temporelle et utilisant un cytomètre en flux imageur submersible (Imaging FlowCytobot) pour l'identification et le décompte des algues (<150 μm), nous avons évalué le rôle de la lumière et de la disponibilité en nutriments dans le contrôle des floraisons printanières d'algues unicellulaires. Les diatomées pennées représentaient principalement les communautés sympagiques. Les communautés phytoplanctoniques étaient initialement semblables à celles observées dans la glace, suggérant un possible ensemencement des floraisons phytoplanctoniques par les algues de glace. Une augmentation de l'intensité lumineuse, principalement causée par la fonte de la neige et l'apparition de cuvettes d'eau de fonte, semble avoir favorisé les diatomées centriques, ces dernières dominant les communautés pélagiques pendant les floraisons phytoplanctoniques des deux années. La disponibilité en lumière semble être le forçage principal limitant le déclenchement des floraisons sympagiques et pélagiques, avec une valeur journalière minimale de 0.1 mol photons m^{-2} d^{-1}. Une limitation en nutriments dans la glace n'a pas clairement été observée, alors que les nitrates semblent avoir joué un rôle prépondérant dans le déclin de la floraison dans la colonne d'eau. Nos résultats suggèrent qu'il y a un fort potentiel pour des floraisons printanières sous la glace, qui sont actuellement principalement limitées par la lumière tôt dans la saison.

Résumé (Anglais)

With ongoing climate change in the Arctic, a decrease in the extent of sea ice and in the spring snow cover thickness has been observed. A modification of the ice and snow dynamics is predicted to impact the onset, the duration and the decline of microalgae spring blooms, as well as the succession among groups and species of primary producers. The main goals of the present study were (i) to characterize the ice-associated algae and phytoplankton communities and (ii) to identify the main drivers associated with the microalgal main taxonomic groups succession during an under-ice bloom in Baffin Bay in 2015 and 2016. With high-resolution time series of environmental parameters and using an Imaging FlowCytobot for the identification and enumeration of algal cells (<150 µm) within the sea ice bottom and in the underlying water column, we address the role of light and nutrients availability in controlling spring bloom phenology. Pennate diatoms dominated the sympagic community, with different genera dominating for each year. The phytoplankton community was initially alike that found in sea ice, suggesting a possible seeding of the pelagic bloom by the ice algal community. Light availability seemed to be the main factor controlling the onset of both sympagic and pelagic blooms, with a threshold value of 0.1 mol photons m^{-2} d^{-1}. Through spring, snow and sea ice melting in association with melt pond onset caused the decline of the sympagic bloom, while the increase in under-ice irradiance likely favored centric diatoms, which dominated the protists assemblage during the phytoplankton blooms. Nutrients limitation in sea ice was not observed, while nitrate seemed to play a major role in the decline of the phytoplankton bloom. Our results suggest that there is a potential for early and massive under ice blooms, which are mostly light limited early in the season.

Table des matières

Liste des figures

Remerciements

J'aimerais tout d'abord remercier mon directeur de recherche, Marcel Babin, pour son appui et ses conseils tout au long de ma maîtrise, mais aussi pour les années précédentes au sein de son laboratoire où j'ai pu développer mes aptitudes en recherche. Par le fait même, je suis reconnaissant pour les opportunités qu'il m'a offertes tant pour les collaborations, congrès que pour la participation à des missions scientifiques sur le terrain. Enfin, merci pour avoir contribué à ma formation scientifique, au développement de ma pensée critique et de ma rigueur au travail.

Je voudrais aussi remercier ma co-directrice, Lee Karp-Boss, avec qui j'ai pu échanger longuement sur l'analyse de mes données et avec qui j'ai eu la chance de collaborer dans un projet international, *Tara Oceans Polar Circle*. Je voudrais aussi la remercier pour m'avoir reçu à quelques reprises chez elle dans le Maine dans le cadre du travail et pour m'avoir fait découvrir son coin de pays.

Pour le projet *Green Edge* en particulier, j'aimerais remercier des membres de Takuvik sans qui tout cela n'aurait pas été possible : Joannie Ferland, Marie-Hélène Forget et Flavienne Bruyant. Une mention spéciale à ces trois collègues qui m'ont supervisé pendant mon baccalauréat et ma maîtrise, tout au long des différents projets auxquels j'ai participés et pendant mon travail en laboratoire et sur le terrain. Je ne voudrais pas oublier de souligner l'important travail de coordination de Marie-Hélène Forget, Debra Christiansen-Stowe et Julie Sansoulet, sans qui la chaire de recherche et tous les projets associés n'auraient pu fonctionner. Un merci aussi pour toutes les heures passées à revoir mes textes de demande de financement, et spécialement à Debra pour tous les travaux en anglais. Je voudrais mentionner le travail incroyable de Claudie Marec pour la réparation du Imaging FlowCytobot, sans lequel je n'aurais pu mener à terme mon projet de maîtrise. De même, le soutien de Marc Picheral pour l'utilisation du logiciel Ecotaxa, de Heidi Sosik et Rob Olson pour la formation sur l'Imaging FlowCytobot et l'utilisation de MATLAB et de Philippe Massicotte sur R et dans l'analyse de données ont joué un rôle important dans la réussite de mon projet. De plus, une mention spéciale à Sylvie Lessard et Marie Parenteau pour leur aide en taxonomie.

J'aimerais remercier mes collègues et amis Philippe-Israël Morin, Jade Larivière et Théo Sciandra pour leurs conseils et commentaires, notamment pour ce manuscrit, ainsi que plusieurs collègues pour leur aide durant toutes ces années : Virginie Galindo, Martí Gali Tapias, Guislain Bécu, José Lagunas, Maxime Benoît-Gagné, Nicolas Schiffrine, Pierre Coupel, Laurent Oziel, Thibaud Dezutter, Moritz Schmid et tous les autres membres de Takuvik.

Pour terminer, je voudrais remercier mes amis et ma famille pour leur soutien et encouragements pendant toutes ces années.

Avant propos

La soumission de l'article inséré est prévue pour l'automne 2019. L'étudiant Pierre-Luc Grondin est le principal auteur du manuscrit présenté. Il a contribué en majeure partie à toutes les étapes menant à la publication de l'article inséré. Les coauteurs listés ont participé à l'acquisition ou l'analyse de données et/ou à la révision du manuscrit.

Introduction

Mise en situation

Alors que les changements climatiques observés depuis plusieurs décennies semblent s'intensifier avec le temps, l'étude de la réponse des écosystèmes à ces changements est de première importance (Comiso and Hall 2014). Avec le réchauffement climatique, une fonte précoce et amplifiée des glaces pluriannuelles est observée en Arctique (Comiso *et al.* 2008, Comiso 2012, Stroeve *et al.* 2014). On s'attend à ce que ces modifications aient à long terme une influence sur les organismes photosynthétiques, en passant par les maillons supérieurs de la chaîne alimentaire, allant même jusqu'aux communautés humaines présentes (Stroeve and Notz 2015); il est donc primordial de bien comprendre la dynamique qui existe au sein de ces écosystèmes marins polaires.

En raison de la forte connectivité entre les niveaux trophiques de l'écosystème arctique (Grebmeier *et al.* 2006), une simple perturbation du milieu pourrait entraîner des répercussions importantes sur l'ensemble des composantes du système. À la base de ce réseau trophique se retrouvent des protistes unicellulaires autotrophes, hétérotrophes et mixotrophes qui forment les communautés sympagiques – associées aux glaces de mer – et phytoplanctoniques. Les algues sympagiques composent une partie non-négligeable de la production primaire à la base de la chaîne alimentaire (3-25% sur les plateaux continentaux (Legendre *et al.* 1992), et jusqu'à 57% dans le bassin arctique central (Gosselin *et al.* 1997). Ensemble, les algues unicellulaires sympagiques et le phytoplancton sont un facteur limitant pour la croissance des niveaux trophiques supérieurs (Behrenfeld *et al.* 2002) et jouent également un rôle crucial dans les cycles biogéochimiques dont celui du carbone.

Les microalgues arctiques sont soumises à une dynamique bien particulière. L'océan Arctique étant en grande partie couvert de glace près des deux tiers de l'année (Markus *et al.* 2009), la période de croissance des organismes photosynthétiques est assez limitée. Toutefois, une modification du régime annuel des glaces (fonte et gel) tend à changer cette dynamique (Arrigo *et al.* 2008, Kahru *et al.* 2011, Ardyna *et al.* 2014). Cette modification a un impact sur des propriétés physiques telles que la température, la salinité ou l'éclairement dans la colonne d'eau, mais aussi sur la chimie du milieu en affectant la dynamique des nutriments. Ainsi, il est attendu qu'une modification de ces paramètres influence la

répartition spatio-temporelle, l'abondance ainsi que la composition des communautés sympagiques et phytoplanctoniques (Hill *et al.* 2005, Li *et al.* 2009). Comme ces différentes communautés influencent l'écosystème de façons distinctes (Petrou *et al.* 2016), il est nécessaire de comprendre les caractéristiques et la dynamique qui leur sont associées.

L'océan Arctique

Vaste et caractérisé par une grande variabilité environnementale, l'océan Arctique présente des réponses différentes aux changements climatiques selon l'échelle temporelle et spatiale considérée. L'étendue géographique importante explique la grande gamme de conditions environnementales, de régimes hydrographiques et de communautés biologiques y étant associés.

Il est d'usage de considérer deux grandes entités : le bassin arctique central et les plateaux continentaux (<200 m), ces derniers totalisant à eux seuls plus de 50% de la superficie de l'océan Arctique (Carmack *et al.* 2006).

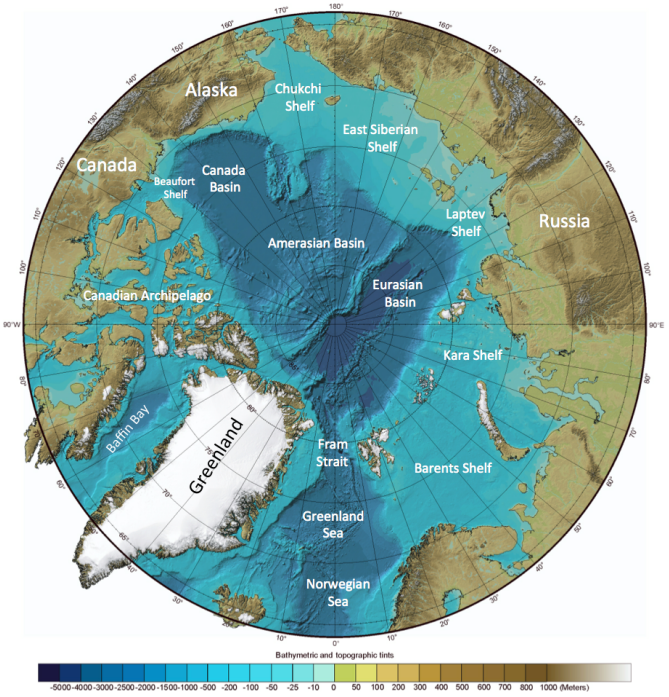

Figure 1. Carte bathymétrique de l'océan Arctique de l'«International Bathymetric Chart of the Arctic Ocean». Modifiée de http://geology.com/world/arctic-ocean-bathymetry-map.shtml

La glace pluriannuelle (2 ans et plus) caractérise le bassin arctique central (Carmack *et al.* 1997). En raison de sa présence, en plus de la décharge d'eau douce par certains

grands fleuves tel que le Mackenzie, le mélange hivernal y est moins prononcé et la zone est plutôt oligotrophe (Ardyna *et al.* 2011). Le bassin central est par ailleurs très profond, atteignant plus de 4000 m par endroit. De leur côté, les plateaux continentaux présentent une dynamique très variable selon l'environnement local et régional. Les plateaux eurasiens sont assez stratifiés en raison de la décharge importante d'eau douce par les fleuves et par l'eau de fonte, ce qui limite le mélange vertical (Sakshaug 2004). Un fort apport d'eau chaude de l'Atlantique par la mer de Norvège (Beszczynska-Moller *et al.* 2011) limite la formation du couvert de glace en hiver en mer de Barents. En plus d'être plus chaudes que les eaux arctiques, les eaux atlantiques sont moins stratifiées. Ceci permet le mélange vertical de la colonne d'eau jusqu'au fond (<250 m) (Olsen *et al.* 2003) et la remontée de nutriments dans les eaux de surface. Une production primaire élevée est observée en mer de Chukchi, reflétant l'arrivée d'eaux riches en nutriments en provenance de la mer de Béring (Sakshaug 2004). Finalement, l'archipel arctique canadien présente des conditions environnementales bien différentes d'est en ouest (Ardyna *et al.* 2011). L'hydrographie y est complexe, caractérisée par la présence de plusieurs seuils et détroits séparant de nombreuses îles. Les eaux du Pacifique et de l'Arctique s'y fraient un chemin, puis s'écoulent jusque dans la baie de Baffin (Carmack *et al.* 2006). À l'est de celle-ci, le courant du Groenland occidental longe la côte ouest du Groenland, apportant de l'eau d'origine Atlantique du détroit de Davis au sud, jusqu'au détroit de Smith au nord. Il y bifurque vers l'ouest et rejoint le courant de l'île de Baffin sur sa côte est, pour finalement suivre le courant du Labrador vers le sud jusqu'à la mer du Labrador (Bacle *et al.* 2002, Ingram *et al.* 2002). En définitive, c'est près du tiers du volume d'eau s'écoulant de l'océan Arctique qui chemine via l'archipel canadien (Coachman and Aagaard 1974), modifiant ainsi les propriétés physiques et chimiques de la baie de Baffin (Tremblay *et al.* 2002). Il est aussi possible d'y noter la présence de glace de première année, mais également de glace pluriannuelle s'écoulant de l'Arctique.

Paramètres physiques et chimiques

Glace

Le réchauffement global se faisant sentir de manière accentuée en Arctique, une étude de l'étendue de la superficie de la glace de 1979 à 2006 par Serreze *et al.* (2007) indique une tendance à la baisse de la couverture de la banquise, Comiso *et al.* (2008) soutenant même une accentuation de la fonte de 10% par décennie. De même, Markus *et al.* (2009) ont montré qu'en 2008, 73% du bassin canadien était couvert de glace annuelle, la glace pluriannuelle ayant presque complètement disparu.

L'albédo de l'eau libre de glace (~0,07) est beaucoup plus faible que celui de la neige recouvrant la glace (~0,85) ou de la glace elle-même (~0,65; 0,2 à 0,4 si présence de cuvettes d'eau de fonte) (Pegau and Paulson 2001, Perovich and Richter-Menge 2009, Perovich 2011). Ainsi, une diminution de la banquise au profit d'eau libre augmentera la quantité d'énergie absorbée par l'océan (Perovich *et al.* 2007, Perovich *et al.* 2008). Cela aura pour effet de repousser la formation de la glace à l'automne de 1 à 7 jours par décennie, avec une moyenne de 2,2 jours (Markus *et al.* 2009). Cette boucle de rétroaction positive s'accentue, ce qui favorise la formation d'une glace de première année plutôt que pluriannuelle. La glace de première année étant moins épaisse, elle fond plus facilement l'année suivante (Figure 2).

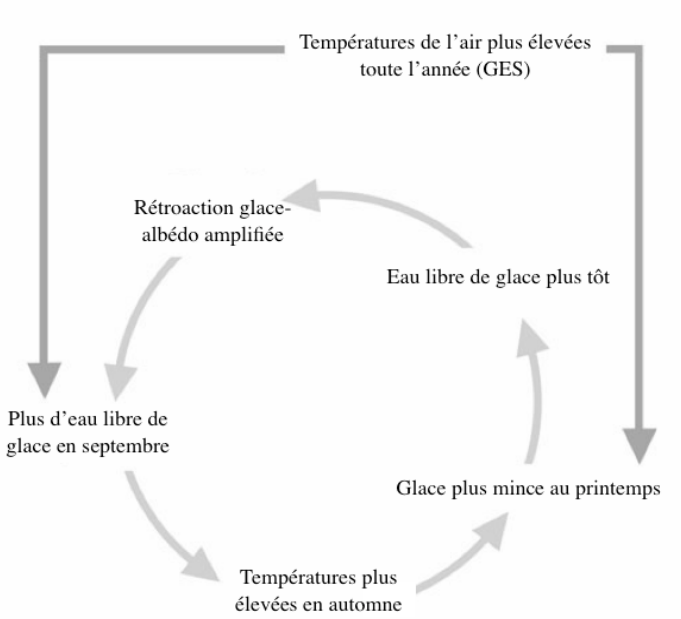

Figure 2. Boucle de rétroaction glace-albédo. Modifiée de Stroeve *et al.* (2012).

La fonte accentuée de celle-ci a un impact à plusieurs égards. Il y a le relargage d'eau douce en peu de temps sur une grande surface ce qui modifie la structure physique de la colonne d'eau. L'accumulation d'une couche d'eau douce en surface contribue à la stratification haline de la colonne d'eau, qui est ensuite amplifiée par la stratification thermique de l'océan, résultant d'un réchauffement des couches superficielles par le rayonnement solaire et par l'atmosphère.

Lumière

Les régions polaires sont caractérisées par des variations saisonnières extrêmes de l'intensité lumineuse et de la durée du jour (Sakshaug and Slagstad 1991, Popova *et al.* 2012). La réduction accrue de la banquise en été induite par les changements climatiques modifie ce régime lumineux dans la colonne d'eau. Effectivement, la fonte de la neige et de la glace permet à une plus grande proportion du rayonnement d'atteindre la surface de l'océan. En plus des effets thermiques, cet apport accentué en lumière (durée et intensité) favorise la production primaire (Popova *et al.* 2012), notamment en déclenchant l'initiation de la floraison (Tremblay and Gagnon 2009), terme définissant une forte croissance du phytoplancton et souvent établie à partir d'une concentration en chlorophylle (ex : >0,5 mg m^{-3}, Perrette *et al.* 2011). En plus des variations saisonnières de l'éclairement, il faut aussi tenir compte du gradient vertical de la lumière dans la colonne d'eau, lié aux propriétés optiques inhérentes de l'eau et à la matière dissoute et en suspension.

Couche de mélange de surface

Bien que les méthodes employées pour déterminer sa profondeur varient et ne fassent pas consensus (Thomson and Fine 2003, Montegut *et al.* 2004, Holte and Talley 2009, Thomson and Fine 2009, Nahavandian Esfahani 2014, Peralta-Ferriz and Woodgate 2015), la couche de mélange est souvent définie comme étant la couche superficielle de l'océan où un mélange convectif et/ou turbulent assure une homogénéité des propriétés physiques telles que la température et la salinité (Nahavandian Esfahani *et al.* 2013). L'océan Arctique étant stratifié une grande partie de l'année en raison de l'apport d'eau douce et du réchauffement en surface, ceci crée une barrière pour le mélange vertical pendant la saison de croissance. Cette stratification a un impact significatif sur le phytoplancton en modifiant l'accessibilité à la lumière, mais aussi la disponibilité des

nutriments qui sont en plus grande concentration dans les eaux profondes (Thingstad and Sakshaug 1990, Ardyna *et al.* 2011, Popova *et al.* 2012). Cette stabilisation permet l'initiation de la floraison au printemps dans la couche de surface en raison d'un apport suffisant en lumière et en nutriments. Toutefois, la stratification limite l'apport nouveau en nutriments en réduisant le mélange vertical, ce qui devient un inconvénient lorsque le phytoplancton a consommé tous les nutriments de la couche de surface.

Nutriments (azote, phosphore, silice)

L'apport de nutriments dans l'océan Arctique se fait majoritairement via le mélange hivernal. Ce dernier est causé par le rejet de saumures lors de la formation de la glace pendant l'automne et l'hiver (Peralta-Ferriz and Woodgate 2015). Plus denses, ces saumures coulent et engendrent un appel d'eau vers la surface, apportant des nutriments depuis les masses d'eaux en profondeur. L'advection horizontale d'eau du Pacifique et de l'Atlantique ainsi que les tempêtes qui engendrent un mélange suffisant ou encore des remontées d'eaux profondes sont aussi responsables d'apports nouveaux en nutriments (Carmack and Chapman 2003, Arrigo *et al.* 2008, Li *et al.* 2009, Popova *et al.* 2012). Dans une moindre mesure, l'apport des fleuves (surtout sur les plateaux continentaux) est aussi une autre source de nutriments, et ce, principalement au printemps (Le Fouest *et al.* 2013).

Parmi les différents nutriments dans l'océan, l'azote et le phosphore sont les principaux éléments chimiques régulant la production primaire, parce que souvent présents en quantités limitantes, et ayant donc un impact considérable sur le cycle du carbone (Yamamoto-Kawai *et al.* 2006). Toutefois, de nombreuses études rapportent que dans l'océan Arctique, l'azote, sous forme de nitrates, serait le principal élément limitant (Kattner and Budeus 1997, Reigstad *et al.* 2002, Tremblay *et al.* 2002, Simpson *et al.* 2008, Tremblay *et al.* 2008, Li *et al.* 2009, Tremblay and Gagnon 2009). La silice peut aussi devenir limitante dans certaines régions pour les diatomées qui l'utilisent pour leur frustule (Sakshaug 2004). La croissance des algues unicellulaires nécessite des nutriments, toutefois les demandes pour ceux-ci dépendent des taxons. De plus, les ratios de ces nutriments varient selon les masses d'eau (Tremblay *et al.* 2002). Ainsi, il importe d'aborder la dynamique associée à une floraison en intégrant les paramètres physiques et chimiques, tout en tenant compte de la composante spatiale et temporelle.

Dynamique d'une floraison

D'une part, les floraisons en Arctique ont lieu au printemps, dès que l'intensité lumineuse est suffisante pour permettre la croissance des algues (Tremblay and Gagnon 2009). D'autre part, l'appauvrissement en nutriments limite la croissance et éventuellement met fin à celle-ci. La formation de la glace à l'automne et pendant l'hiver qui entraîne un mélange hivernal favorise un apport nouveau en nutriments dans la couche de surface pour l'année suivante.

En présence de glace annuelle, l'initiation d'une floraison phytoplanctonique se fait normalement à la lisière de celle-ci (*Marginal Ice Zone,* MIZ), en formant une bande de plusieurs kilomètres (Perrette *et al.* 2011). Leur formation en lisière de banquise est favorisée par la couche d'eau de fonte qui stabilise la colonne d'eau et par la concentration élevée en nutriments au début de la saison de croissance (Carmack and Wassmann 2006). Toutefois, de nouvelles études démontrent aussi l'importance de floraisons sous la banquise dans la production primaire printanière (Arrigo *et al.* 2012, Arrigo *et al.* 2014, Assmy *et al.* 2017).

Les floraisons sont caractérisées par une forte production primaire, principalement nouvelle (>90%) (Kristiansen and Lund 1989), faisant référence à la production primaire reposant sur un apport nouveau en nutriments. Une partie de la production primaire est assurée par les algues sympagiques qui se développent à la base de la banquise à des éclairements très faibles (Kirst and Wiencke 1995), même lorsque le couvert de glace est d'une épaisseur appréciable. Un éclairement de 1-2 µmol de photons m^{-2} s^{-1} est suffisant pour supporter une croissance nette des diatomées (Tremblay *et al.* 2006). Or, c'est souvent la fonte de la neige et l'apparition de cuvettes d'eau de fonte qui initient la floraison dans la colonne d'eau grâce à un apport de lumière suffisant pour la croissance du phytoplancton (Arrigo *et al.* 2012, Perovich and Polashenski 2012). Les espèces sympagiques sédimentent lors de la fonte de la glace et il est alors possible d'observer une transition «communauté de glace» vers «communauté phytoplanctonique». Toutefois, certaines espèces de glace participent aussi à cette transition et il est possible de les retrouver dans la colonne d'eau par la suite (Booth and Horner 1997). En Arctique, les floraisons phytoplanctoniques, souvent associées à un milieu riche en nutriments (Ardyna *et al.* 2011), sont principalement représentées par des diatomées centriques des genres *Thalassiosira*

Cleve et *Chaetoceros* Ehrenberg (Horner 1984, Booth and Horner 1997, Hasle and Heimdal 1998, Sukhanova *et al.* 1999). Les communautés présentes après la floraison sont composées essentiellement d'espèces de petite taille ayant une forte affinité pour les nutriments (Kristiansen *et al.* 1994, Cota *et al.* 1996). Les conditions à ce moment présentent typiquement une faible concentration en nutriments en surface, séparée par une pycnocline prononcée, laquelle est souvent le lieu d'une accumulation de biomasse («Subsurface Chlorophyll Maximum», SCM) (Sakshaug 2004). Bien qu'il puisse rester des diatomées, surtout au niveau de ce SCM où les concentrations en nutriments sont plus élevées (Hill *et al.* 2005, Laney and Sosik 2014), on retrouve principalement en conditions post-floraison des dinoflagellés et d'autres groupes comme des petits flagellés verts, des chrysophytes et des prymnésiophytes telles que *Phaeocystis pouchetii* (Hariot) Lagerheim (Baumann *et al.* 1994, Zingone *et al.* 1999, Sakshaug 2004). Des évènements de mélange vertical se produisant parfois en automne et apportant des nutriments en surface peuvent aussi donner naissance à de secondes floraisons (Sakshaug 2004, Ardyna *et al.* 2014). Toutefois, ces floraisons automnales sont généralement de plus faible intensité.

Succession des espèces

Tel que décrit par Margalef (1978), la lumière et les nutriments sont les facteurs régulant la croissance et la composition des communautés phytoplanctoniques. Toutefois, il avance que le tout est lié à la turbulence du milieu. De même, une analyse de la composition des communautés en relation avec les paramètres environnementaux permet de reconnaître une séquence allant des eaux turbulentes et riches en nutriments à des eaux pauvres et stratifiées, le long de laquelle sont classés les genres ou espèces (Figure 3) (Margalef 1978). L'évolution des paramètres environnementaux, liée à la stratification de la colonne d'eau lors de la transition hiver-printemps-été, entraîne donc des changements dans la composition des communautés phytoplanctoniques.

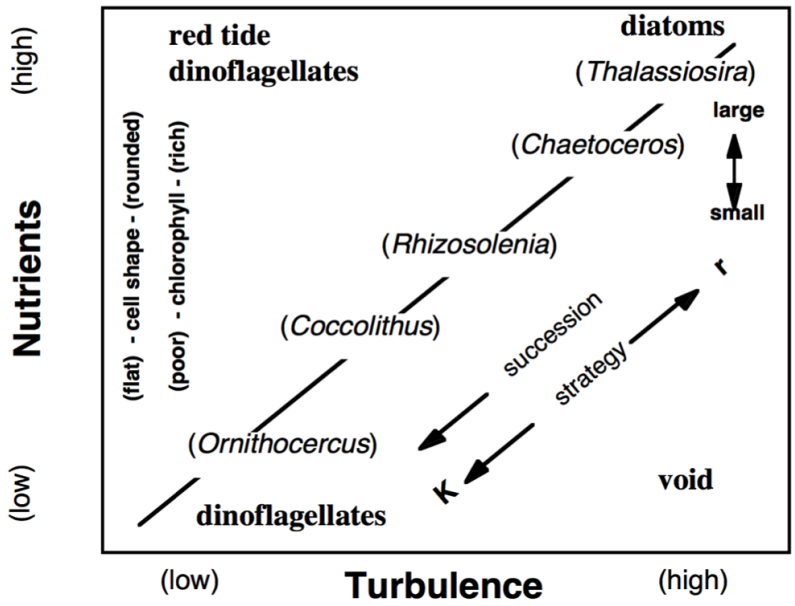

Figure 3. Représentation de la succession des espèces en fonction de la turbulence et de la disponibilité des nutriments selon Margalef (1978). Tiré de Cullen and Macintyre (1998).

Dans les eaux stratifiées, les organismes autotrophes consomment les nutriments à un rythme plus élevé que l'apport nouveau en nutriments (Dugdale 1967, Harrison 1980). Ceci entraîne une compétition interspécifique et les nutriments limitent alors le taux de croissance (Falkowski and Raven 2007). Les diatomées ont une forte capacité à consommer les nutriments, ce qui leur permet de croître plus vite et même de les stocker dans des vacuoles. Ainsi, elles sont avantagées lorsque les nutriments sont en abondance en début de saison dans la couche de surface (Turpin and Harrison 1979, Mccarthy 1980, Tozzi *et al.* 2004), ou encore près de la nitracline au niveau du SCM. Les petites cellules, grâce à leur rapport surface-volume plus élevé, sont plus compétitives lorsque les concentrations en nutriments sont faibles; elles sont donc plus abondantes vers la fin de la floraison.

Cytomètre en flux imageur submersible (Imaging FlowCytobot, IFCB)

Dans le passé, les efforts de recherche à l'aide d'instruments automatique ont surtout été dirigés vers l'identification du picophytoplancton (0.2-2 µm, Olson *et al.* 2003, Sosik *et al.* 2003) et sur le plancton de plus de 100 µm (Davis *et al.* 1992, Huller *et al.* 1994, Gallager *et al.* 1996, Thwaites *et al.* 1998). Toutefois, peu d'études ont mis l'emphase sur le plancton de 10-100 µm avec une résolution suffisante pour permettre une compréhension précise de la dynamique d'un écosystème dans toutes ses subtilités. Basé

sur les taux métaboliques et de croissance, Maranon *et al.* (2013) avancent qu'une plus grande diversité spécifique des cellules de taille intermédiaire peut être attendue, ces dernières étant de meilleures compétitrices. Pour mieux comprendre comment les facteurs environnementaux régulent la composition des communautés phytoplanctoniques, des observations détaillées et répétées sont nécessaires (Olson and Sosik 2007).

Un cytomètre en flux imageur submersible (Imaging FlowCytobot, IFCB) combine la microscopie et la cytométrie en flux pour produire à cadence élevée des images des organismes phytoplanctoniques présents dans l'eau de mer. Ces images sont utilisées pour l'identification des espèces (Olson and Sosik 2007). L'IFCB offre un détail d'environ 1 µm et une résolution temporelle allant jusqu'à l'heure (Olson and Sosik 2007, Sosik and Olson 2007). Selon Olson and Sosik (2007), les autres instruments disponibles sur le marché pour faire un suivi du phytoplancton offrent une moins bonne résolution et endurance sur le terrain (ex : FlowCAM (Sieracki *et al.* 1998) et CytoSub (Cunningham *et al.* 2003).

Problématique

Bien que la diminution de l'étendue du couvert de glace en Arctique ait bien été documentée, les conséquences sur les principaux processus biologiques restent inconnues (Soreide *et al.* 2010). Le peu de données historiques et la disparité spatiale de ces dernières contribuent aux carences dans nos prédictions de la dynamique de l'écosystème arctique (Wassmann *et al.* 2011).

Nous nous attendons à des modifications majeures dans la disponibilité de lumière et de nutriments, qui exerceront certainement un contrôle sur l'initiation, la durée et la fin des floraisons phytoplanctoniques. Il est attendu qu'une modification de la dynamique associée à la glace et à la neige augmentera la période de croissance des algues par 40% ou plus (Wassmann and Reigstad 2011). Entre autre, un couvert de neige et de glace plus mince permet à une plus grande quantité de lumière d'atteindre le dessous de la glace et de se propager dans la colonne d'eau, favorisant ainsi la croissance des organismes photoautotrophes. Des études ont démontré une croissance hâtive des algues de glace et même le déclenchement de la floraison phytoplanctonique sous la glace (Fortier *et al.* 2002, Mundy *et al.* 2009, Wassmann and Reigstad 2011, Arrigo *et al.* 2012, Arrigo *et al.* 2014, Assmy *et al.* 2017).

Non seulement pourrions-nous observer un changement dans la phénologie, mais la succession parmi les groupes et les espèces de microalgues pourraient être affectée. Ceci pourrait causer un décalage entre les producteurs primaires et les consommateurs de premier ordre, tel que l'espèce clé *Calanus glacialis* Jaschnov. Cette dernière est dépendante du moment, de la durée ainsi que de la composition spécifique des floraisons d'algues unicellulaires afin de compléter son cycle vital (Soreide *et al.* 2010). Perrette *et al.* (2011) démontrent que les floraisons printanières de phytoplancton représentent la majeure partie de la production primaire annuelle dans l'océan Arctique. De plus, elles sont associées à un transfert important de matière vers les niveaux trophiques supérieurs et vers le fond.

Les études sur les floraisons printanières ont principalement mis l'accent sur les changements dans la concentration en chlorophylle, alors que des études sur la composition spécifique et sur la succession saisonnière des espèces en relation avec leur environnement dans l'océan Arctique sont manquantes. Très peu est connu en ce qui concerne la

dynamique temporelle des algues de glace, plus particulièrement l'éclairement requis pour supporter une croissance nette (Hancke *et al.* 2018). En raison du faible nombre d'observations de floraisons d'algues de glace et leur dynamique saisonnière, il est difficile de quantifier leur importance pour la production primaire (Leu *et al.* 2015), et de définir leur rôle dans l'ensemencement de la floraison phytoplanctonique (Selz *et al.* 2018, Van Leeuwe *et al.* 2018). La réponse des différentes espèces aux conditions de croissance est requise afin de mieux prédire comment les changements attendus affecteront les écosystèmes marins (Campbell *et al.* 2018).

Objectifs et hypothèses de l'étude

Cette étude a été réalisée pendant les missions océanographiques *Green Edge*, qui ont eu lieu à un camp de glace (67.48˚N, 63.79˚W) dans la baie de Baffin de mai à juillet 2015 et 2016. Des mesures de paramètres environnementaux ainsi que de diversité et de physiologie d'algues unicellulaires (1-150 µm) ont été répétées aux deux jours pendant la période d'étude. Ceci procure une résolution temporelle qui permet de suivre les changements rapides dans la composition spécifique des communautés sympagiques et phytoplanctoniques en Arctique en relation avec les variables du milieu.

Les principaux objectifs étaient (i) de caractériser les communautés d'algues de glace et de phytoplancton et (ii) d'identifier les principaux forçages environnementaux associés à la succession des principaux groupes taxonomiques d'algues unicellulaires pendant une floraison printanière en baie de Baffin. Le tout a été réalisé avec une approche innovante qui repose principalement sur des mesures à haute fréquence à l'aide d'un cytomètre en flux imageur submersible (Imaging FlowCytobot).

Chapitre 1. Algal taxonomic succession and its drivers during under-ice spring blooms in Baffin Bay

Pierre-Luc Grondin[1], Joannie Ferland[1], Philippe Massicotte[1], Virginie Galindo[2], Joséphine Ras[3], Hervé Claustre[3], Nicole Garcia[4], Patrick Raimbault[4], Pierre Coupel[1,4,5], Jean-Éric Tremblay[1], Marie-Hélène Forget[1], Lee Karp-Boss[6], Marcel Babin[1]

[1] Takuvik Joint International Laboratory, Laval University (Canada) - CNRS (France), UMI3376, Université Laval, Québec, Québec G1V 0A6, Canada
(pierre-luc.grondin.1@ulaval.ca; joannie.ferland@takuvik.ulaval.ca; philippe.massicotte@takuvik.ulaval.ca; pierre.coupel@takuvik.ulaval.ca; jean-eric.tremblay@bio.ulaval.ca; marie-helene.forget@takuvik.ulaval.ca; marcel.babin@takuvik.ca)

[2] Centre for Earth Observation Science, Faculty of Environment, Earth and Resources, University of Manitoba, Winnipeg, Manitoba, Canada
(virginie.galindo@gmail.com)

[3] Sorbonne Universités, UPMC Univ Paris 06, CNRS, Observatoire Océanologique de Villefranche (OOV), Laboratoire d'Océanographie de Villefranche (LOV), Villefranche-sur-Mer, France
(Josephine.ras@obs-vlfr.fr; claustre@obs-vlfr.fr)

[4] Mediterranean Institute of Oceanography, MIO UMR110, Aix-Marseille Université, CNRS/INSU, Université de Toulon, IRD, 13288 Marseille, France
(nicole.garcia@mio.osupytheas.fr; patrick.raimbault@mio.osupytheas.fr)

[5] Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada

(Pierre.Coupel@dfo-mpo.gc.ca)

[6] School of Marine Sciences, University of Maine, Orono ME, USA
(lee.karp-boss@maine.edu)

1.1 Résumé

Avec des mesures de variables environnementales et utilisant un cytomètre en flux imageur submersible pour l'identification et le décompte des algues unicellulaires, nous avons évalué le rôle de la lumière et de la disponibilité en nutriments dans le contrôle de la phénologie et de la composition taxonomique des floraisons printanières en baie de Baffin en 2015 et en 2016. Les diatomées pennées représentaient principalement les communautés sympagiques, alors que les diatomées centriques dominaient dans les communautés pélagiques. Les communautés phytoplanctoniques étaient initialement semblables à celles observées dans la glace, suggérant un possible ensemencement des floraisons phytoplanctoniques par les algues de glace. La disponibilité en lumière semble être le forçage principal limitant le déclenchement des floraisons sympagiques et pélagiques. Une limitation en nutriments dans la glace n'a pas clairement été observée, alors que les nitrates semblent avoir joué un rôle prépondérant dans le déclin de la floraison dans la colonne d'eau.

1.2 Abstract

With ongoing climate change in the Arctic, a decrease in the extent of sea ice and in the spring snow cover thickness has been observed. A modification of the ice and snow dynamics is predicted to impact the onset, the duration and the decline of microalgae spring blooms, as well as the succession among groups and species of primary producers. The main goals of the present study were (i) to characterize the ice-associated algae and phytoplankton communities and (ii) to identify the main drivers associated with the microalgal main taxonomic groups succession during an under-ice bloom in Baffin Bay in 2015 and 2016. With high-resolution time series of environmental parameters and using an Imaging FlowCytobot for the identification and enumeration of algal cells (<150 µm) within the sea ice bottom and in the underlying water column, we address the role of light and nutrients availability in controlling spring bloom phenology. Pennate diatoms dominated the sympagic community, with different genera dominating for each year. The phytoplankton community was initially alike that found in sea ice, suggesting a possible seeding of the pelagic bloom by the ice algal community. Light availability seemed to be the main factor controlling the onset of both sympagic and pelagic blooms, with a threshold value of 0.1 mol photons m^{-2} d^{-1}. Through spring, snow and sea ice melting in association with melt pond onset caused the decline of the sympagic bloom, while the increase in under-ice irradiance likely favored centric diatoms, which dominated the protists assemblage during the phytoplankton blooms. Nutrients limitation in sea ice was not observed, while nitrate seemed to play a major role in the decline of the phytoplankton bloom. Our results suggest that there is a potential for early and massive under ice blooms, which are mostly light limited early in the season.

1.3 Introduction

Ice-edge blooms of sympagic and planktonic microalgae provide a crucial food source to pelagic and benthic organisms. The phytoplankton spring blooms that develop at the ice-edge account for a large fraction of annual primary production in the Arctic Ocean (AO) and are generally associated with both large energy transfer to higher trophic levels and export of carbon to the sea floor (Morata *et al.* 2011, Perrette *et al.* 2011). These blooms are ubiquitous during spring in the AO; understanding their dynamics is essential to the comprehension of Arctic marine ecosystems and their responses to environmental changes.

With ongoing climate change in the Arctic, a decrease of 50% in the minimum annual extent of sea ice has been observed between 1978 and 2017 (Stroeve *et al.* 2012, Stroeve *et al.* 2014), as well as a shift from multi-annual to first-year sea ice (Comiso 2012), and a decreased spring snow cover thickness by as much as 2.12% per decade for the period 1967-2012 (Comiso and Hall 2014). Although receding of the Arctic sea ice extent has been well monitored, the consequences on key biological processes remain largely unknown (Soreide *et al.* 2010). The thinner snow and sea ice covers allow for higher irradiances at the bottom of the sea ice and in the underlying water column, promoting the growth of autotrophic organisms. These changes are expected to increase the productive period by 40% or more (Wassmann and Reigstad 2011), and impact the onset, the duration and the decline of algal blooms.

Recent studies showed an earlier growth of ice algae and even the onset of under-ice phytoplankton blooms (Fortier *et al.* 2002, Mundy *et al.* 2009, Wassmann and Reigstad 2011, Arrigo *et al.* 2012, Arrigo *et al.* 2014, Assmy *et al.* 2017). Spring increased light intensities and warmer air temperatures trigger snow and ice melt, creating a surface meltwater layer that stratifies the upper part of the water column (Carmack and Wassmann 2006), reducing vertical mixing and thus preventing nutrient replenishment of surface waters (Ardyna *et al.* 2014). Light and nutrient availability along with water column stability are major environmental factors governing species succession, the latter being determined by ecological strategies and capacities of algae to acclimate to their environment (Margalef 1978, Cullen and Macintyre 1998). Not only we might observe a shift in the phenology, but the succession among groups and species that thrive during the

spring bloom might be affected. This could lead to a mismatch between primary producers and first order consumers, such as the keystone zooplankton species *Calanus glacialis* Jaschnov, which is dependent on the timing, duration and composition of the algal blooms to complete its life cycle (Soreide *et al.* 2010).

Microalgae are incorporated into the ice matrix during its formation in late fall (Syvertsen 1991, Reimnitz *et al.* 1992, Reimnitz *et al.* 1993, Weissenberger and Grossmann 1998, Rozanska *et al.* 2008) and initiate the spring sympagic algal bloom the year after (Horner and Schrader 1982, Rozanska *et al.* 2009, Niemi *et al.* 2011). The ice algal community is mainly dominated by pennate diatoms (Rozanska *et al.* 2009, Poulin *et al.* 2011), with species of the genera *Nitzschia* Hassal, *Navicula* Bory and *Fragilariopsis* Hustedt (Leu *et al.* 2015). Ice algae are adapted to low irradiances (Cota and Smith 1991), thus sustaining net photosynthetic growth at low light intensities, even under thick snow and ice covers (0.17 µmol photons m^{-2} s^{-1}, Hancke *et al.* 2018). Despite being found in the water column during the ice melting period, some studies suggest that their contribution to the phytoplankton bloom is small (Booth and Horner 1997), although isolated blooms dominated by pennate diatoms have been reported (Galindo *et al.* 2014, Mundy *et al.* 2014). Some species such as *Fragilariopsis cylindrus* (Grunow ex Cleve) Frenguelli have also been shown to contribute significantly to the phytoplankton biomass at the ice edge (Barber *et al.* 2015). Most of phytoplankton blooms are dominated by centric diatoms, in particular species of the genera *Thalassiosira* Cleve and *Chaetoceros* Ehrenberg (Horner 1984, Booth and Horner 1997, Hasle and Heimdal 1998, Sukhanova *et al.* 1999, Poulin *et al.* 2011). Centric diatoms favor nutrient-replete conditions (Ardyna *et al.* 2011) and perform better under high irradiances (Campbell *et al.* 2017, Campbell *et al.* 2018). Low nutrient availability due to ice algae and phytoplankton consumption forces the assemblage to shift toward species having smaller cell sizes and higher nutrient affinity (Kristiansen *et al.* 1994, Cota *et al.* 1996). Post-bloom community is generally dominated by dinoflagellates and other small-sized flagellates such as chlorophytes, chrysophytes and prymnesiophytes (Hsiao 1992, Baumann *et al.* 1994, Sakshaug 2004).

Under-ice phytoplankton blooms studies have largely focused on changes in chlorophyll *a* biomass, while detailed studies on both ice algal and phytoplankton community composition and seasonal succession patterns are lacking. Little is known about

the onset of ice algae blooms, especially the irradiance required to support active growth (Hancke *et al.* 2018). The low number of time series on ice algal and under-ice phytoplankton blooms makes it hard to quantify the importance of under-ice primary production (Leu *et al.* 2015). Furthermore, the role of ice algae in seeding pelagic blooms remains uncertain (Selz *et al.* 2018, Van Leeuwe *et al.* 2018).

Here we present results from the *Green Edge* campaigns, conducted at an ice camp (67.48°N, 63.79°W) in Baffin Bay from March to July 2015 and May to July 2016. The main goals of the study were (i) to characterize the ice-associated microalgal and phytoplankton communities and (ii) to identify the main environmental drivers associated with the microalgal main taxonomic groups succession during an under-ice bloom in Baffin Bay. With high-resolution time series of algal communities composition in the bottom ice and the underlying water column, using an Imaging FlowCytobot (IFCB) (Olson and Sosik 2007, Sosik and Olson 2007), we address the role of light and nutrient availability in controlling the under-ice spring bloom phenology. Further, we address the potential seeding of the under-ice phytoplankton bloom by sympagic algae during spring.

1.4 Material and Methods

1.4.1 Study site

Sampling took place during the *Green Edge* campaign, from an ice camp (67.48° N, 63.79° W) located on first-year landfast ice (water depth at ice camp location: 360 m) near the community of Qikiqtarjuaq, off Broughton Island, Nunavut, in Baffin Bay (Figure 4) from March 28th to July 14th 2015 and from April 27th to July 22nd 2016 . Air temperature and irradiance were measured, while sea ice and water column were sampled to assess the role of physical and chemical drivers on the ice algae and phytoplankton community composition and the bloom phenology.

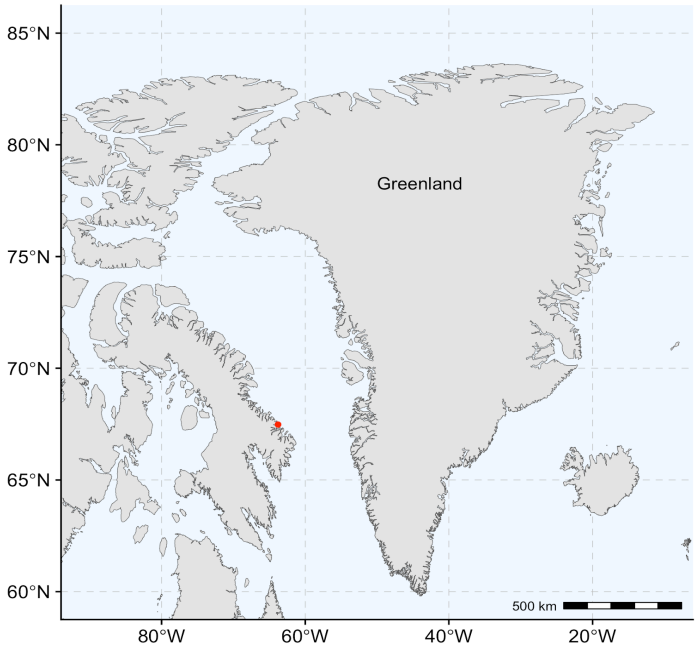

Figure 4. Map of the study area. Ice camp location is identified by the red dot.

1.4.2 Air temperature and sea ice concentration

A meteorological tower located at the ice camp was used to measure air temperature every 10 minutes (HC2S3 probe, Campbell Scientific, 0.1˚C precision). Note that the meteorological tower was installed before ice and water sampling started. Sea ice concentration (SIC) was obtained from the AMSR2 radiometer on a 3.125 km grid, using the pixel closest to the ice camp and not contaminated by land, located at 566 m from the ice camp position (Kaleschke and Tian-Kunze 2016).

1.4.3 Ice cores

Ice cores were collected every 2-3 days for physical, chemical and biological analyses. Ice coring was done at an average distance of 250 m in 2015 (range: 100-1220 m) and 220 m in 2016 (range: 40-509 m) away from the main tent location to avoid disturbance of the light field caused by other measurements. Snow depth and ice thickness were measured at each coring site using a measuring stick and an ice thickness gauge (Kovacs Enterprises), respectively. Ice cores were extracted using a 14-cm internal diameter ice corer (Mark V Coring System, Kovacs Enterprises) in 2015 and a 9-cm internal diameter ice corer (Mark II Coring System, Kovacs Enterprises) in 2016. Vertical profiles of temperature and ice bulk salinity were measured on two full ice cores. Ice temperature was measured every 10 cm with a temperature probe (Testo Inc. model 720) inserted into 2 mm holes drilled toward the center of the ice core, starting at 5 cm from the top of the core. To determine ice bulk salinity, the ice core was cut into 10-cm sections as quickly as possible to avoid brine drainage, and melted into Whirl-Pak bags. Ice bulk salinity was measured with a hand-held conductivity meter (Cond 330i, WTW) in 2015 and a portable salinometer (Thermo Scientific Orion portable salinometer, model WP-84TPS) in 2016. Brine salinity and volume fraction of each 10-cm section were calculated using the recorded ice bulk salinity and temperature following Cox and Weeks (1983) and Petrich and Eicken (2010).

For biological analyses, two ice cores were collected in 2015, and two to four ice cores at high snow depth sites in 2016. The bottom 10 cm was sectioned (0-3 cm and 3-10 cm) and placed into Whirl-Pak bags in a cooler. The ice cores were melted overnight in 0.22 μm filtered seawater (FSW) (three part FSW to one part melted ice) to minimize osmotic stress on the microbial community during melting (Bates and Cota 1986, Garrison and Buck 1986). Analyses of pigments and protist assemblage were performed the next day, as soon as ice was melted to diminish the impact on algal physiology. Bulk salinity of each melted ice core section was also recorded. For physiological algal measurements (^{14}C photosynthesis *versus* irradiance curves), at least two ice cores were collected and the bottom 1-cm was cut and melted in filtered seawater. Another ice core was collected for nutrient analyses (0-3 cm section) and placed into sterile Whirl-Pak bags. The nutrient ice

cores were melted in FSW in 2015 and in artificial seawater (ASW) in 2016 (3 part FSW/ASW to one part melted ice).

1.4.4 Water column measurements

Salinity and temperature profiles were measured every sampling day, through a hole in the sea ice from inside a Polarhaven tent, using a conductivity-temperature-depth (CTD) probe (Seabird SBE 9plus V2).

Downward irradiance [$E_d(\lambda,z)$, µmol photon m^{-2} s^{-1}] vertical profiles were measured using an underwater multispectral radiometer usually in triplicate (C-OPS, ICE-Pro version, Biospherical Instruments Inc.) deployed 50-100 m away from the Polarhaven tent through a 25-cm circular hole. The photosynthetically available radiation for downward irradiance [$PAR_{Ed}(z)$] was calculated by trapezoidal integration of $E_d(\lambda)$ measured between 400 and 700 nm. The daily scalar PAR at any depth, $PAR_{Ed,24h}(z)$ (mol photon m^{-2} d^{-1}), was calculated using the following equation:

$$PAR_{Ed,24h}(z) = PAR_{Ed,24h}(0^+) \cdot T_{snow+ice} \quad (1)$$

where $PAR_{Ed,24h}(0^+)$ is the downward daily PAR measured in air right above the snow and ice cover, and $T_{snow+ice}$ is the ratio between instantaneous $PAR_{Ed}(0^-)$ and $PAR_{Ed}(0^+)$. In 2015, $PAR_{Ed,24h}(0^+)$ was derived from continuous recording of shortwave downwelling irradiance K (W m^{-2}) using a pyranometer (CNR4, Kipp & Zonen; see Oziel *et al.* (submitted) for details). In 2016, $PAR_{Ed,24h}(0^+)$ was directly measured using a LI-190SA instrument (Li-COR). When not available due to instrument failure, $PAR_{Ed,24h}(0^+)$ was estimated from satellite observations (sensor MODIS Aqua) of cloud optical thickness, cloud fraction and total ozone column, used as input to an atmospheric radiative transfer model (SBDART; Ricchiazzi *et al.* 1998). SBDART was implemented as described by Belanger *et al.* (2013) and Laliberte *et al.* (2016).

Water samples were collected at typically 1.5, 5, 10, 20, 40 and 60 m using 10- or 20-L Niskin bottles, while under-ice water (*ca.* 30 cm below the ice) was collected with a small electric submersible pump (12 V Cyclone ®) tethered to an under-ice arm (Galindo *et*

al. 2016). The water was poured into cooler jugs and brought back rapidly to the laboratory in Qikiqtarjuaq for analyses of pigments and protist assemblage.

1.4.5 Nutrient and pigment analyses

Melted sea ice and water samples were filtered onto 0.7 µm Whatman GF/F filter and the filtrate was collected into sterile 20-mL polyethylene vials. The samples were poisoned with 100 µL of mercuric chloride (600 mg/ 100mL) and stored in the dark until analyses (Kirkwood 1992) of nitrate, nitrite, phosphate and silicate concentrations. The nutrient concentrations were determined using an automated colorimetric procedure (detection limit: ± 0.05 µmol L^{-1}) (Aminot and Kérouel 2007).

Chlorophyll *a* (chl *a*) and degradation pigments (i.e. *chlorophyllide a* and *phaeophorbide*) pigments concentrations were determined by High Performance Liquid Chromatography (HPLC) following Ras *et al.* (2008). 0.1 to 1 L of melted ice and 1 to 2.5 L of seawater were filtered onto Whatman GF/F 25-mm filters (nominal porosity of 0.7 µm), and stored at -80˚C for later analysis. Extraction was done in 100% methanol for 2 h, disrupted by sonication and clarified by filtration (Whatman GF/F). Pigments were analyzed the same day using an Agilent Technologies 1200 Series system with a narrow reversed-phase C8 Zorbax Eclipse XDB column (150 × 3 mm, 3.5 µm particle size) which was maintained at 60°C.

1.4.6 Photosynthetic parameters

Photosynthetic parameters were derived from the ^{14}C photosynthesis *versus* irradiance (P *vs* E) curves according to Babin *et al.* (1994), with minor changes in the incubator design (longitudinal instead of radial display of incubation chambers, LED instead of metal-halide lamp; Flavienne Bruyant, pers. comm.). Measurements were made on melted sea ice samples (bottom 1-cm) (typically 1-3 h after ice sampling) and on water samples (immediately after sampling) from four depths (typically under-ice, 1.5, 5 and 20 m). The model proposed by Platt *et al.* (1980) was fitted to the data. The light-saturation index [E_k, µmol photon m^{-2} s^{-1}] was calculated for each curve using the following equation:

$$E_k = P_{max} / \alpha \quad (2)$$

where P_{max} [mg C m^{-3} h^{-1}] is the maximum carbon fixation rate at saturating irradiance and α [mg C m^{-3} h^{-1} [µmol photon m^{-2} s^{-1}]$^{-1}$] is the initial slope of the P *vs* E curve.

1.4.7 Protist assemblage

For each melted ice (0-3 cm section) and seawater samples, the protist assemblage was determined using an Imaging FlowCytobot (IFCB, manufactured at Heidi Sosik's lab, Woods Hole Oceanographic Institute, serial number 013). This instrument allows for the identification and enumeration of nano- and microphytoplankton (Olson and Sosik 2007, Sosik and Olson 2007). The targeted size range was between 1 and 150 µm, while the image resolution of ~3.4 pixels/µm limited the identification of < 10 µm cells to broad functional groups. 5 mL samples were analyzed and Milli-Q® water was run between samples with high biomass in order to prevent contamination between samples. A 150 µm Nitex mesh was used to avoid clogging of the fluidics system by large particles, although this might have induced a bias in the results by preventing large cells to be sampled. Image acquisition was triggered by chlorophyll *a in vivo* fluorescence, with excitation and emission wavelengths of 635 and 680 nm, respectively. Grayscale images were processed to extract regions of interest (ROIs) and their associated features (e.g.: geometry, shape, symmetry, texture, etc.), using a custom made MATLAB (2013b) code (Sosik and Olson 2007); processing codes are available at *https://github.com/hsosik/ifcb-analysis*). A total of 231 features (e.g.: geometry, shape, symmetry, texture, etc; see full list and description at *https://github.com/ hsosik/ifcb-analysis/wiki/feature-file-documentation*) were derived on the resulting ROIs and were used for automatic classification using random forest algorithms with the EcoTaxa application (Picheral *et al.* 2017). A learning set was manually prepared for each year, with *ca.* 20,000 images annotated and used for automatic prediction. Each automatically annotated image was further validated by visual examination and corrected when necessary. The final datasets consist of 124,247 and 57,397 annotated images in 2015 and 2016, respectively, and their associated features. Images were classified into 39 (2015) or 35 (2016) categories (Table S1) that were binned into 6 broader taxonomic categories (centric diatoms, dinoflagellates, flagellates, other

phytoplankton, pennate diatoms, prymnesiophytes). Calibration beads (9 µm red-fluorescing beads; Duke Scientific, Inc.) were run to verify the instrument's performance and ensure that particles were in focus. Size calibration was performed after the fieldwork, during image processing.

1.4.8 Cell abundance and carbon estimates

As it was impossible to count the number of cells on each IFCB image, we assumed a ratio of 1 cell per image. However, this leads us to potentially underestimate cell abundances when colonies or chains were imaged, with many cells present on one image. To account for such bias, the biovolume of each cell (or chain or colony) on IFCB images was computed during image processing according to Moberg and Sosik (2012). Using carbon to volume ratios from Menden-Deuer and Lessard (2000), biovolume was converted into carbon estimates as in Laney and Sosik (2014).

1.4.9 Statistical analyses

Statistical analyses were carried out on R v3.5.1 (R Core Team 2018), with a significance level of 0.05. Average values are presented with ± 1 SD, and were compared using Welch's t-test for (un)equal variances (*stats* package, v3.5.1). Correlation coefficients were computed using Pearson's correlation test (*Hmisc* package, v4.2.0). A redundancy analysis (RDA) was performed on transformed protist assemblage data (Hellinger transformation) and environmental variables to identify the main environmental parameter(s) controlling the bloom phenologyn(*vegan* package, v2.5.5). Further analysis by forward selection allowed us to identify the best explanatory variables (*adespatial* package, v0.3.7).

1.5 Results and Discussion

1.5.1 Air temperature and sea ice concentration

Air temperature increased gradually over the study period for both years, 2015 being colder than 2016, especially during the first two weeks of April (Figure 5A). For both years, the sea ice concentration in the closest AMSR2 pixel was nearly 100% until mid-July. At the ice camp location, the concentration was always at 100% until mid-July (visual observations). Since the sea ice concentration was obtained from the closest AMSR2 pixel (*ca.* 500 m from the ice camp location), the variability in the sea ice concentration further away led to values under 100% on a few occasions. It then decreased rapidly to <1% by the end of July (Figure 5B), matching with the ice break-up.

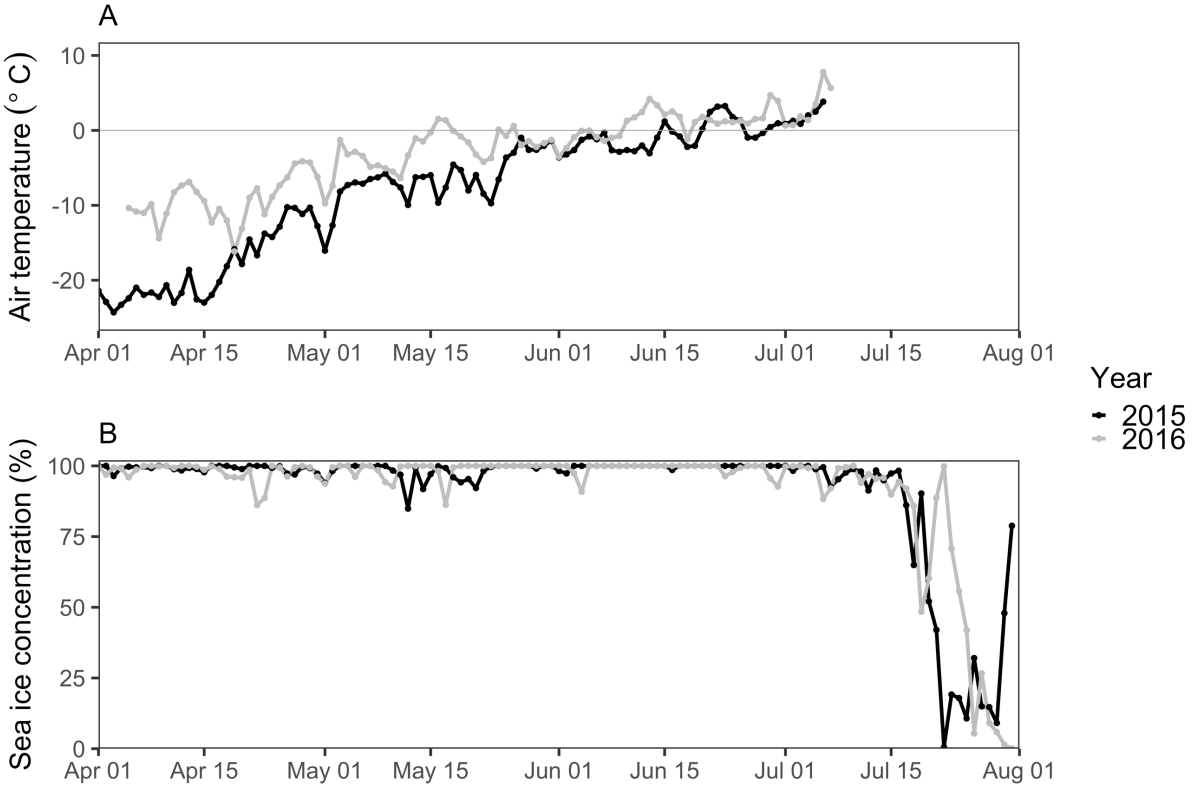

Figure 5. **A.** Daily mean air temperature (˚C) and **B.** sea ice concentration (%) from the AMSR2 radiometer in 2015 and 2016.

1.5.2 Physical parameters

Snow cover depth was not significantly different between both years (t-test, t = 0.53725, df = 60, p-value > 0.05), with seasonal average values of 20.80 ± 11.03 cm in 2015 and 19.09 ± 13.97 cm in 2016 (Figure 6A). In 2015, snow cover depth increased suddenly in mid-May as a result of a snowfall event. For both years, snow cover depth decreased progressively until a marked decrease during the two first weeks of June. Snow melt onset was on June 8th 2015 and June 3rd 2016, matching with a rapid decrease in snow cover depth and air temperatures above 0˚C (Oziel *et al.* submitted). Average sea ice cover was thinner in 2015 (120.98 ± 7.44 cm) than in 2016 (128.11 ± 11.15 cm) (t-test, t = -2.9423, df = 50.101, p-value < 0.01) (Figure 6B). Melt pond onset, associated with increased under-ice PAR levels and snow cover depth <10 cm, was on June 22nd 2015 and June 15th 2016, roughly two weeks after snow melt onset for each year (Oziel *et al.* submitted).

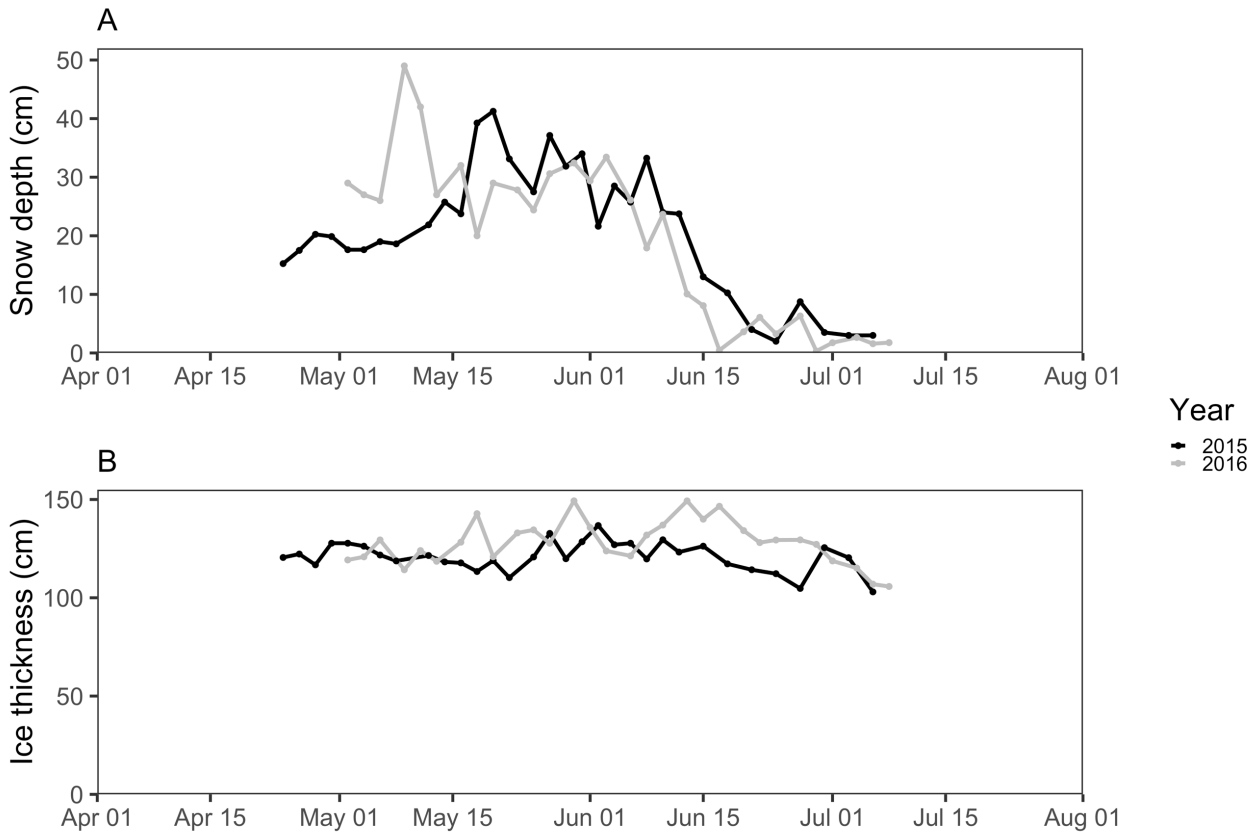

Figure 6. Time series of average **A.** snow cover depth (in cm) and **B.** sea ice thickness (in cm) at ice coring sites in 2015 and 2016.

Brine salinity in the bottom 10-cm of sea ice was in the same range in 2015 and 2016 with seasonal averages of 29.76 ± 8.63 and 30.36 ± 6.43, respectively (t-test, t = -0.30025, df = 57, p-value > 0.05) (Figure 7A), suggesting that the salinity in the bottom layer was mainly influenced by the underlying seawater. The decrease of salinity in brines after mid-June during both years could be associated to the melting of snow, which was flushed through the brine channels. However, the brine volume fraction of the bottom 10-cm of sea ice was significantly higher in 2015 (23.22 ± 4.46%) than in 2016 (11.86 ± 3.02%) (t-test, t = 11.545, df = 53.027, p-value <0.001) (Fig 7B). The observed differences may be due to sea ice thermodynamic history, with lesser autumnal precipitations and colder winter air temperatures in 2015 than in 2016, impacting the ice growth rate and therefore its physical properties (Oziel *et al.* submitted). This suggests that ice algae grew in two different environment between both years, the bottom sea ice being more porous in 2015 than 2016.

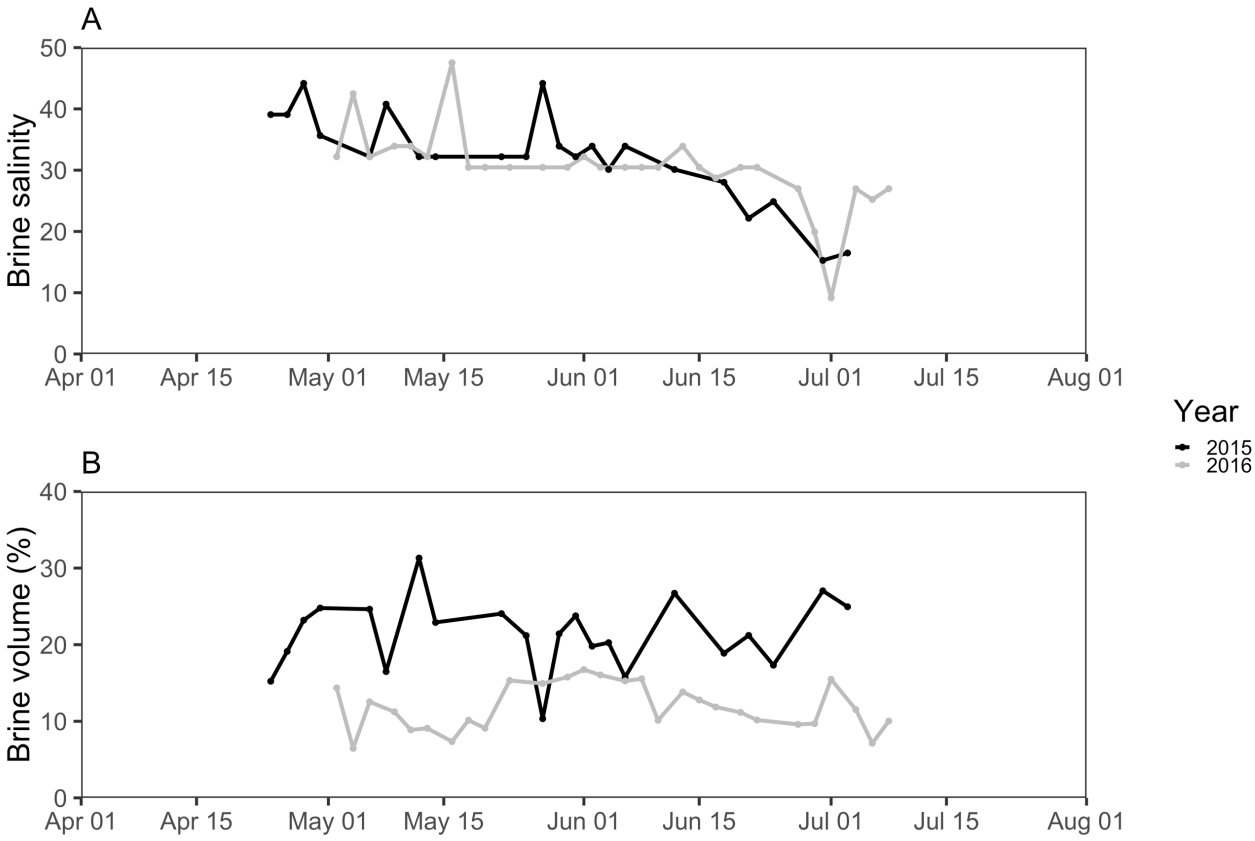

Figure 7. Time series of **A.** brine salinity and **B.** brine volume fraction (%) for the bottom 10 cm in sea ice in 2015 and 2016.

Average salinity (Figure 8A,B) and temperature (Figure 8C,D) in the water column (0-60 m) were not significantly different between both years (salinity 32.38 ± 1.08 (2015) and 32.16 ± 1.26 (2016), t-test, t = 8.0085, df = 7584, p-value < 0.001; temperature: -1.68 ± 0.13 (2015) and -1.63 ± 0.12 (2016), t-test, t = -19.177, df = 7600, p-value < 0.001). We observed a thin melt water layer (<5 m) just below the ice at the surface of the water column, as of mid-June for both years, associated with low salinity values (<10) caused by meltwater from snow melt draining through brine channels. The influence of melt water was also associated with an increase in temperature within just below sea ice (Figure 8C,D). While differences in salinity and temperature were important between the surface melt water and underlying the water mass, they were not sufficient to prevent vertical mixing from occurring, thus allowing cells to be brought at greater depths (Oziel *et al.* submitted).

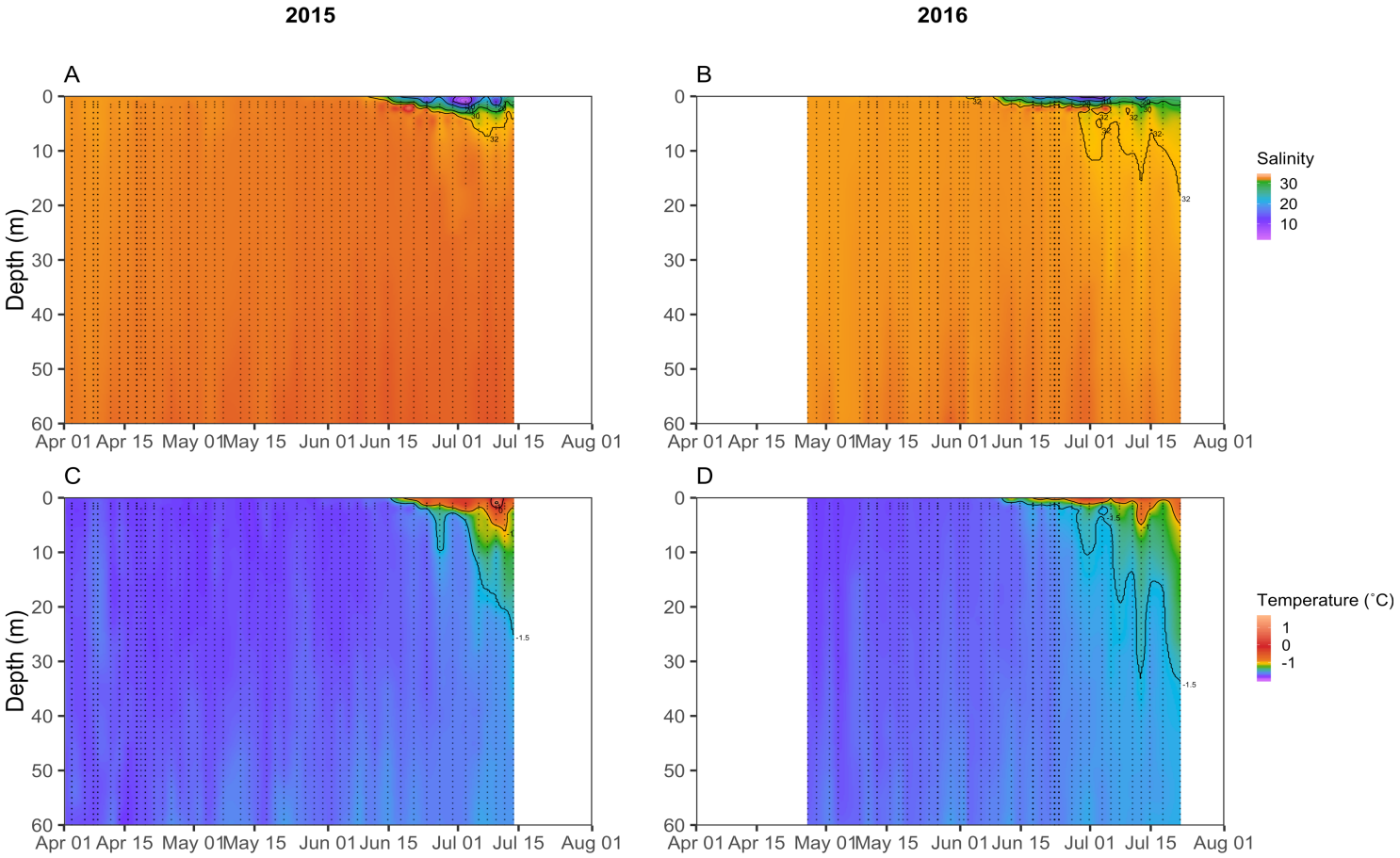

Figure 8. **A. B.** Salinity, **C. D.** temperature (˚C) for the upper 60 m of the water column in 2015 (left panels) and 2016 (right panels). Black dots represent samples.

As expected, the available PAR under ice was negatively correlated to the variation in the snow cover depth (Pearson's correlation, r = -0.76, p-value < 0.001 in 2015; r = -0.79, p-value <0.001 in 2016). Light levels just below ice (defined as 1.3 m) represent minimum PAR values experienced by ice algae, and maximum values for phytoplankton. In 2015, daily mean under-ice PAR was <0.1 mol photons m^{-2} d^{-1} from the beginning of the sampling period until April 26th, where it oscillated for a few days, and then dropped due to a snowfall event at mid-May (Figure 9). The 0.1 mol photons m^{-2} d^{-1} threshold was reached again on June 8th 2015, matching with the snow melt onset, increasing gradually to 3.31 mol photons m^{-2} d^{-1} by the end of the sampling period. In 2016, the 0.1 mol photons m^{-2} d^{-1} threshold was observed on May 17th, two weeks before the snow melt onset (June 3rd 2016). The increase of melt pond fraction in late spring (Figure S1) favored the penetration of light through sea ice, further increasing the PAR values observed under-ice (Oziel *et al.* submitted). The release of ice algae, during snow cover and sea ice melt, might also have contributed to the observed increase in under-ice PAR. Even though phytoplankton cells could have been exposed to higher light intensities in open water areas (>200 km away from ice camp), it is unlikely to have impacted the physiology of phytoplankton cells as observed at the ice camp. Biomass advected from the ice edge did not contribute, or to a limited extent, to the biomass observed at the ice camp due to the time required for cells to be advected and the sinking velocities of phytoplankton cells (Oziel *et al.* submitted). Thus, we assume that light field measured at the ice camps are representative of the light history experienced by phytoplankton.

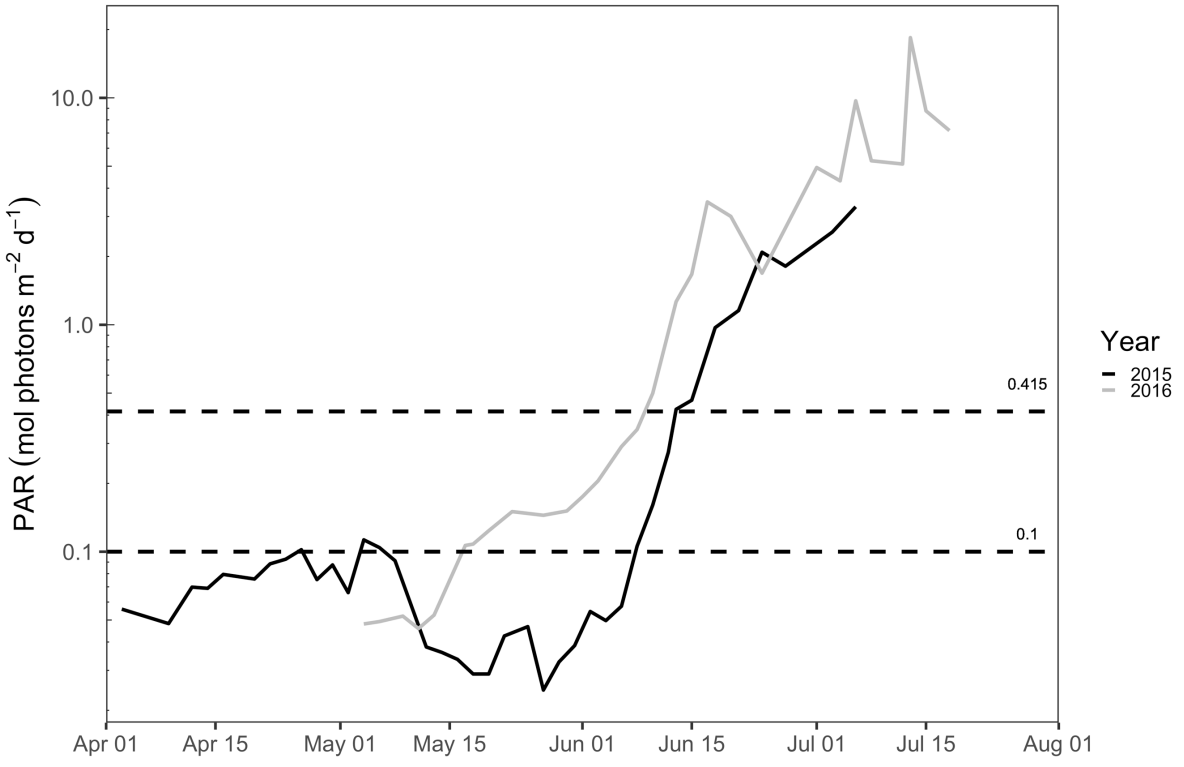

Figure 9. Time series of the daily mean PAR (mol photons m^{-2} d^{-1}) under-ice at 1.3 m in 2015 and 2016. Black dashed lines represent the 0.1 and 0.415 mol photons m^{-2} d^{-1} isolumes.

1.5.3 Nutrients

In the bottom 3-cm of sea ice, the average nitrate concentration (µmol L^{-1}) was significantly higher in 2015 (8.48 ± 8.05) compared to 2016 (1.81 ± 1.40) (t-test, t = 4.6021, df = 33.215, p-value < 0.001) (Figure 10A). While a constant decrease until depletion was observed in 2016, an increase in nitrate was observed in 2015 until June 8th, where it drastically decreased to <1 µmol L^{-1}. This parallel increase in nitrate was correlated with biomass, and was likely a result of the release of intracellular pools due to osmotic stress during ice core melt (Cota *et al.* 1990, Mundy *et al.* 2014, Oziel *et al.* submitted). The rapid decrease matched the snow melt onset, where melted snow and brines were most probably drained, thereby lowering the observed nitrate concentrations. Phosphate average concentration was higher in 2015, with a value of 2.31 ± 1.80 µmol L^{-1} compared to 1.81 ± 1.40 µmol L^{-1} in 2016 (t-test, t = 4.6486, df = 36.881, p-value < 0.001) (Figure 10B). In 2015, phosphate concentration seemed to increase gradually until the first

week of June, where it then started to decrease until it reached null concentration at the end of the sampling period. In 2016, no particular trend was observed. Silicate average concentrations were not significantly different between both years (t-test, t = 1.3279, df = 55, p-value >0.05), with values of 5.00 ± 6.80 µmol L^{-1} (2015) and 2.83 ± 5.31 µmol L^{-1} (2016) (Figure 10C). High concentrations (>20 µmol L^{-1}) of silicate were observed on a few occasions, and were most likely caused by dense diatoms populations in the bottom 3-cm of sea ice, either from natural *in situ* mortality of cells or contamination during sampling. Although the exact process would be hard to identify, we think that upon melting of ice samples, degraded cells in the ice matrix could have led to the release of silicate in the sample, thereby reflecting concentrations above that of available silicate for ice algae (P. Raimbault, pers. comm.).

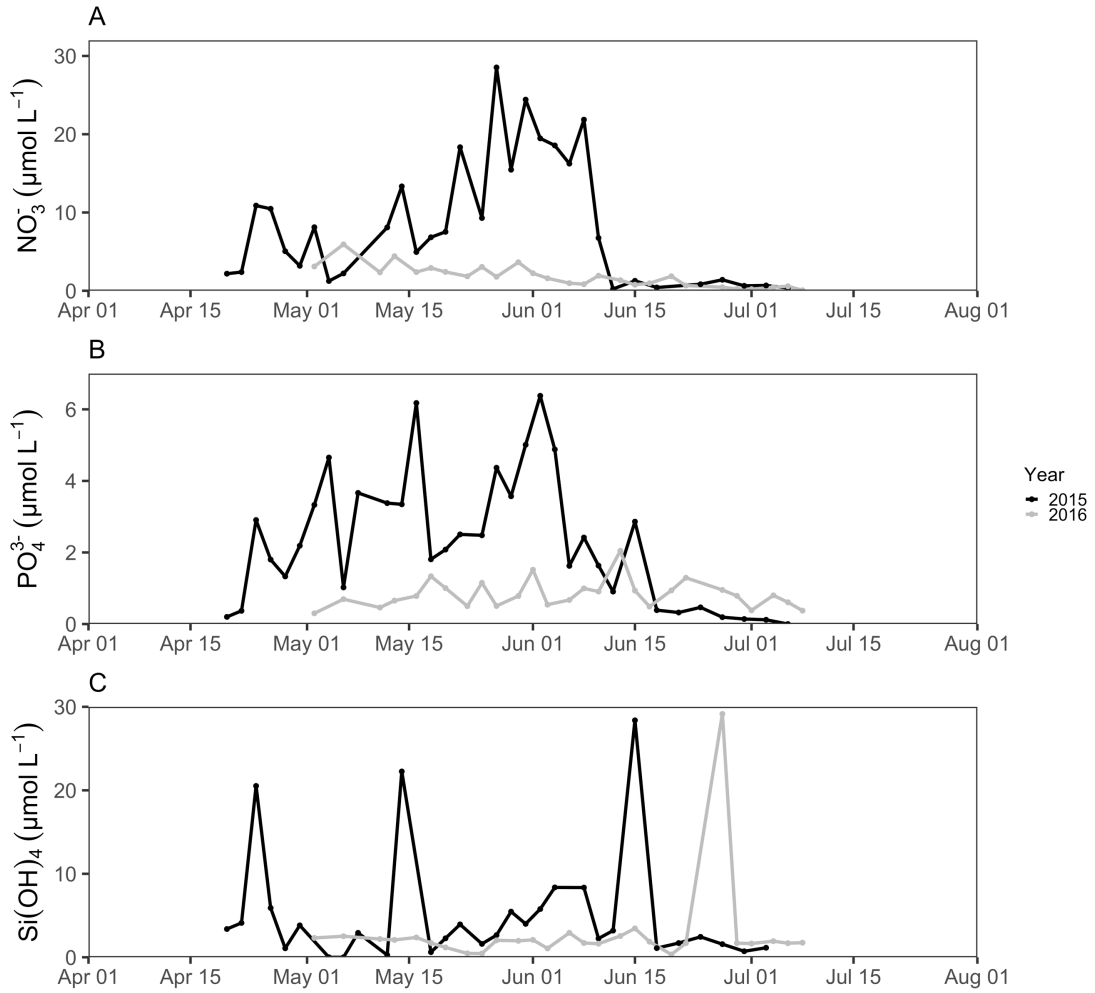

Figure 10. Time series of **A.** nitrate (NO_3, µmol L^{-1}), **B.** phosphate (PO_4, µmol L^{-1}) and **C.** silicate ($Si(OH)_4$, µmol L^{-1}) concentrations in the bottom 3 cm of sea ice in 2015 and 2016.

In the upper 60 m of the water column, average nitrate concentration (µmol L^{-1}) was not significantly different between both years (t-test, t = 5.6751, df = 417, p-value < 0.001), with average concentrations of 4.59 ± 1.10 (2015) and 3.80 ± 1.69 (2016) (Figure 11A,B). Average phosphate concentration (µmol L^{-1}) was slightly lower in 2015 (0.81 ± 0.11) than in 2016 (0.82 ± 0.14) (t-test, t = -1.4791, df = 418, p-value > 0.05) (Figure 11C,D), but average silicate concentrations (µmol L^{-1}) were similar between both year (2015: 6.91 ± 1.30, 2016: 5.89 ± 1.32; t-test, t = 8.0257, df = 418.61, p-value <0.001) (Figure 11E,F). Except for a few samples at the beginning of both sampling periods, N:P and N:Si ratios were lower than the Redfield ratio throughout the whole study period, with values under 16 and 1, respectively (data not shown). This further supports the limitation in nitrate, especially towards the end of the sampling period.

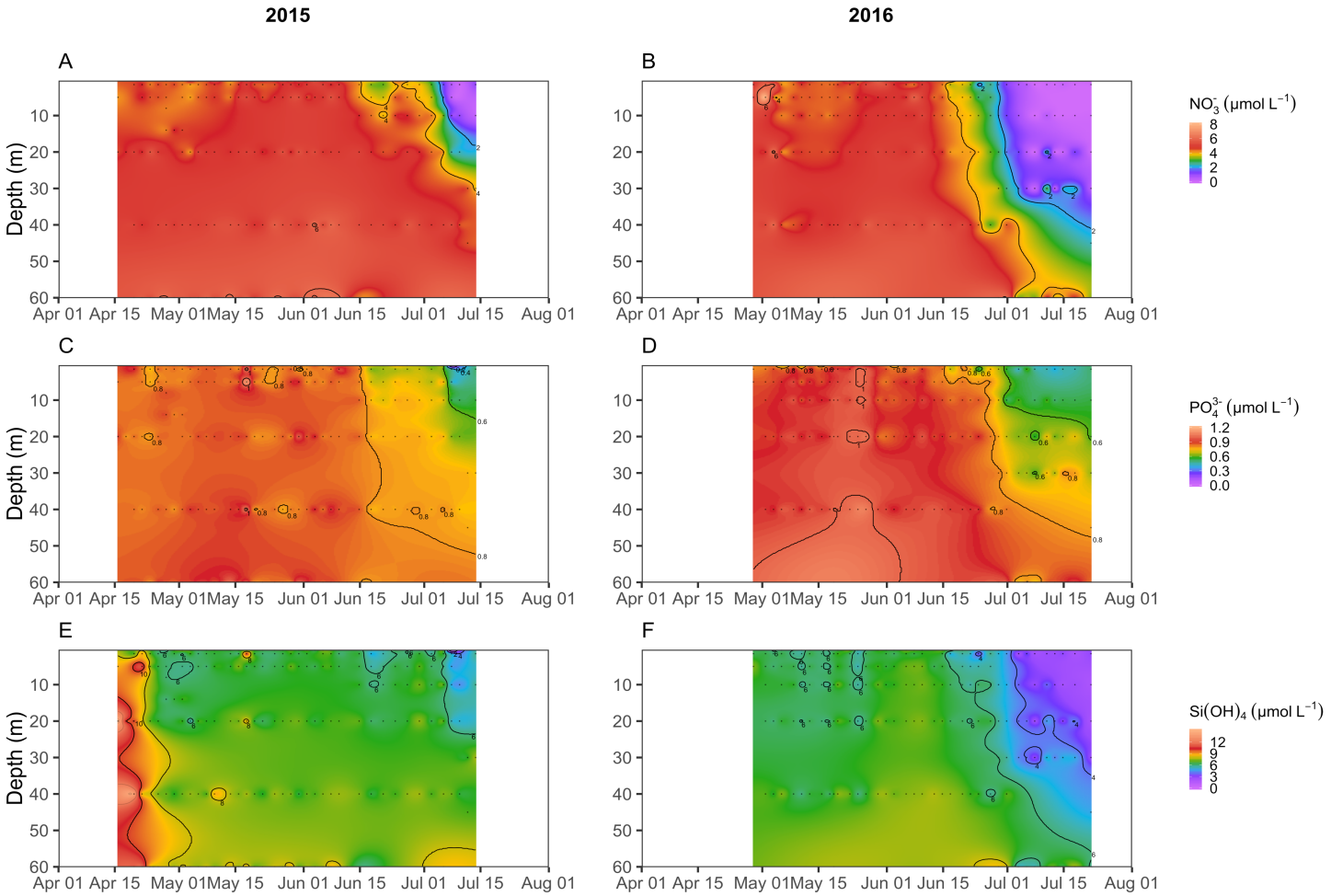

Figure 11. **A. B.** Nitrate (µmol L^{-1}), **C. D.** phosphate (µmol L^{-1}) and **E. F.** silicate (µmol L^{-1}) for the upper 60 m of the water column in 2015 (left panels) and 2016 (right panels). Black dots represent samples.

1.5.4 Chlorophyll a biomass (Tchla)

Integrated chlorophyll *a* biomass (Tchl*a*) in the bottom 3 cm of sea ice differed significantly between the two years (t-test, t = 4.914, df = 61, p-value < 0.001), ranging from 0.19 to 29.25 mg chla m^{-2} (mean ± SD: 7.92 ± 6.37) in 2015, and from 0.06 to 6.04 mg chla m^{-2} (mean ± SD: 2.07 ± 1.46) in 2016 (Figure 12A,B). With sympagic algae growing mainly within the brine channels (Mundy *et al.* 2011), the difference in biomass in the bottommost horizon of sea ice observed between both years may be due to the significant difference in brine volume, allowing for more space for algae to develop in 2015 (Figure 7B). As such, higher (lower) nitrate and phosphate concentrations within brines in 2015 (2016) could explain the higher (lower) ice algae biomass observed in the bottom 3 cm of ice.

Integrated Tchl*a* in the upper 60 m of the water column was similar for both years (t-test, t = -1.6753, df = 62.949, p-value >0.05), ranging from 1.41 to 151.35 mg chla m^{-2} (mean ± SD: 20.42 ± 39.76) in 2015, and from 1.08 to 182.37 mg chla m^{-2} (mean ± SD: 38.61 ± 52.40) in 2016 (Figure 12A,B). Biomass accumulation started in the second half of June for both years, when PAR values where higher due to snow melt and melt pond onset (Figure 6). While Tchl*a* concentrations in water were higher in 2015 than in 2016 (Figure 9 C,D), higher integrated Tchl*a* biomass in 2016 is explained by the expansion of the bloom at greater depths in July. Hence, the bloom was initially more intense in 2015 than in 2016, but we cannot compare the end of it due to the absence of data at the end of July 2015.

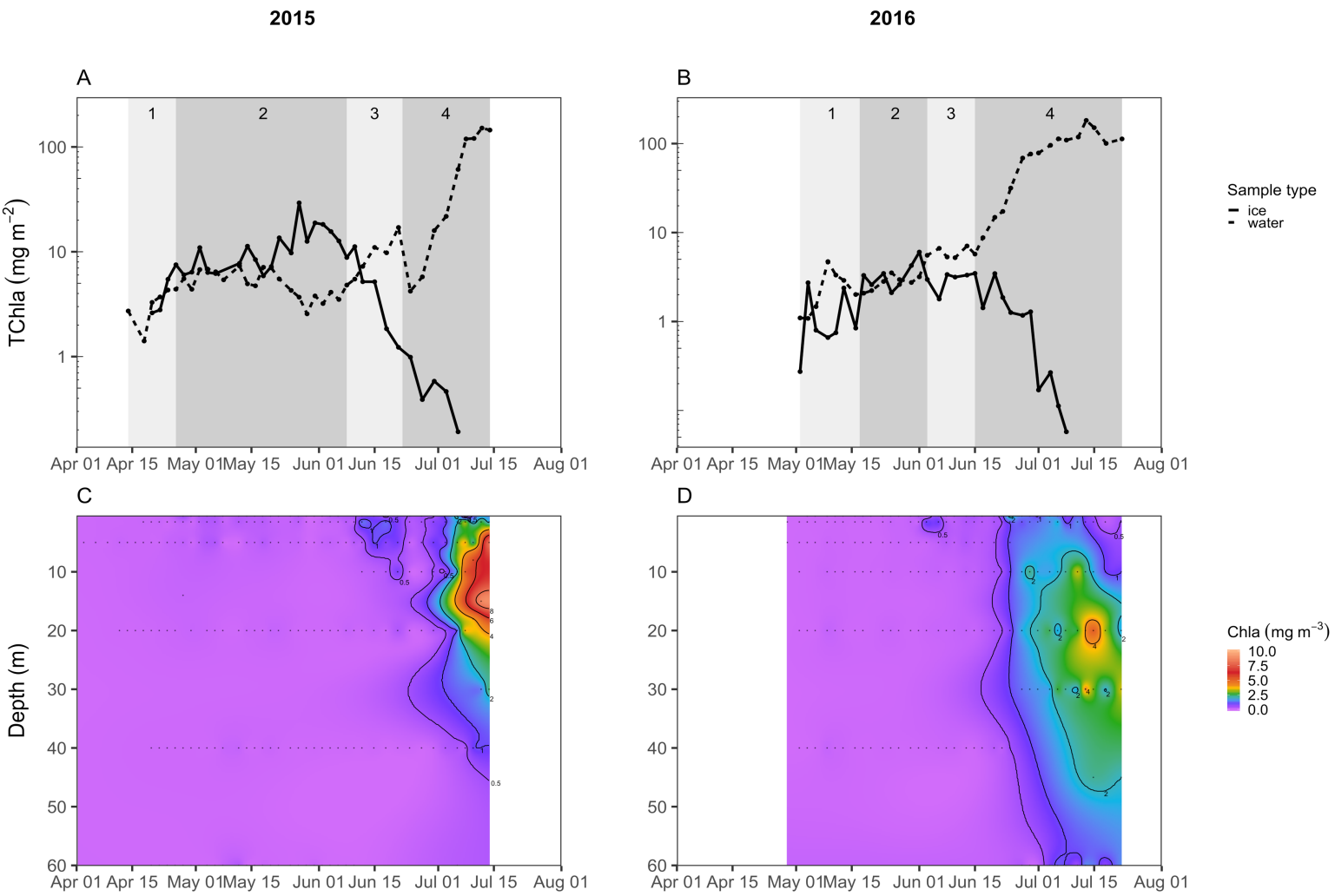

Figure 12. **A. B.** Tchl*a* (mg m^{-2}) in the bottom 3 cm of sea ice (solid line) and the upper 60 m of the water column (dashed line), and **C. D.** Tchl*a* (mg m^{-3}) for the upper 60 m of the water column, in 2015 (left panels) and 2016 (right panels). Numbered grey rectangles on **A** and **B** identify phases of the phenology (1. Pre-bloom, 2. Ice algae bloom, 3. Ice algae bloom collapse, 4. Phytoplankton bloom). Black dots on **C** and **D** represent samples**.**

1.5.5 Bloom phenology

Based on physical parameters, we defined four different phases to describe both the ice algae and phytoplankton bloom phenology (Table S2, Figure 12A,B). The first phase (*pre-bloom*) was associated with under-ice $PAR_{24h,\ 1.3m}$ levels <0.1 mol photons m^{-2} d^{-1} and low biomass accumulation. Even if under-ice PAR values decreased in May 2015 due to a snowfall event (Figure 6A), the first day at which the threshold of 0.1 mol photons m^{-2} d^{-1} was observed was defined as the end of this phase. This threshold was chosen based on the

value used by Lacour *et al.* (2015) to define the euphotic zone, and on Hancke *et al.* (2018) showing algae growth at 0.17 µmol photons m^{-2} s^{-1} (~0.1 mol photons m^{-2} d^{-1}). The second phase (*ice algae bloom*) is associated with increasing biomass in sea ice, and ends with the snow melt onset. The third phase (*ice algae collapse*) is a short transient period between snow melt onset and melt pond onset, associated with decreasing biomass in sea ice but increasing biomass in the water, and increasing PAR levels below sea ice. Finally, the fourth phase (*phytoplankton bloom*) is associated with high under-ice PAR levels, low biomass in ice (<1.5 mg Tchl*a* m^{-2} (2015) and <3.5 mg Tchl*a* m^{-2} (2016)) and increasing biomass in the water column. Note that we did not define a phytoplankton bloom decline as our time series does not capture the end of the bloom.

1.5.6 Protist assemblage

The sympagic community was numerically dominated by pennate diatoms throughout all phases of the phenology during 2015 and 2016 (Figure 13), with different genera dominating for each year. During 2015, *Entomoneis* spp. were dominating, mainly during the month of June. The community was also composed of *Nitzschia* spp. (mainly *N. frigida*) and of an assemblage of different chain-forming and single-cell pennate diatoms of the genera *Fragilariopsis*, *Navicula* and *Cylindrotheca*. During 2016, the community was dominated by *Nitzschia* spp. (mainly *N. frigida*), followed by a mixed assemblage of other pennate diatoms, comparable to that observed during 2015. For both years, the carbon estimates highlight the presence of chains or large pennate diatoms, as it can be seen from a higher relative abundance than that observed when looking at relative abundance based on cell count.

In the water column, during the pre-bloom and ice algae bloom, for both years, the community composition was alike that observed in sea ice, represented mainly by pennate diatoms. In fact, some chain forming (e.g. *Fragilariopsis* spp.) and single-cell pennate diatoms (e.g. *Navicula* spp., *Cylindrotheca* spp.) found in ice were also observed in the water column. The community composition was completed by small unknown protists ("Other phytoplankton"), dinoflagellates and to a lesser extent, flagellates and centric diatoms. While light intensities kept increasing with snow melt and melt pond formation, centric diatoms (mainly *Thalassiosira* spp. (2015) and *Chaetoceros* spp. (2016))

contributed more and more to the phytoplankton community, at the expense of pennate diatoms (Figure 13). Carbon estimates support the fact that the phytoplankton bloom was dominated by chain forming centric diatoms for both years, as their relative abundance based on carbon estimates was much larger than that based on cell count. Visual inspections of images also confirmed the presence of diatom chains. Other groups' (chlorophytes, prasinophytes, cryptophytes, dinoflagellates, ciliates, cyanophytes, euglenophytes, unidentified flagellates and unidentified phytoplankton) proportions decreased gradually over the sampling periods, but still did account for a significant proportion of the community (Figure 13). Both in 2015 and 2016, when the phytoplankton bloom was developed with high under-ice PAR levels and low nutrients in the surface layer (Figures 9 and 11), *Phaeocystis* spp. colonies were observed, with the exception of a few ice and water samples (<10) containing some *Phaeocystis* spp. cells at the end of April 2015. *Phaeocystis* spp. colonies contributed to a greater proportion of the community when considering the carbon estimates rather than the cell count. This is mostly due to the mucus produced by *Phaeocystis* spp., amounting to high biomass per image taken. Inversely, small phytoplankton cells ("Other phytoplankton") accounted for much less of the total biomass, despite high cell numbers.

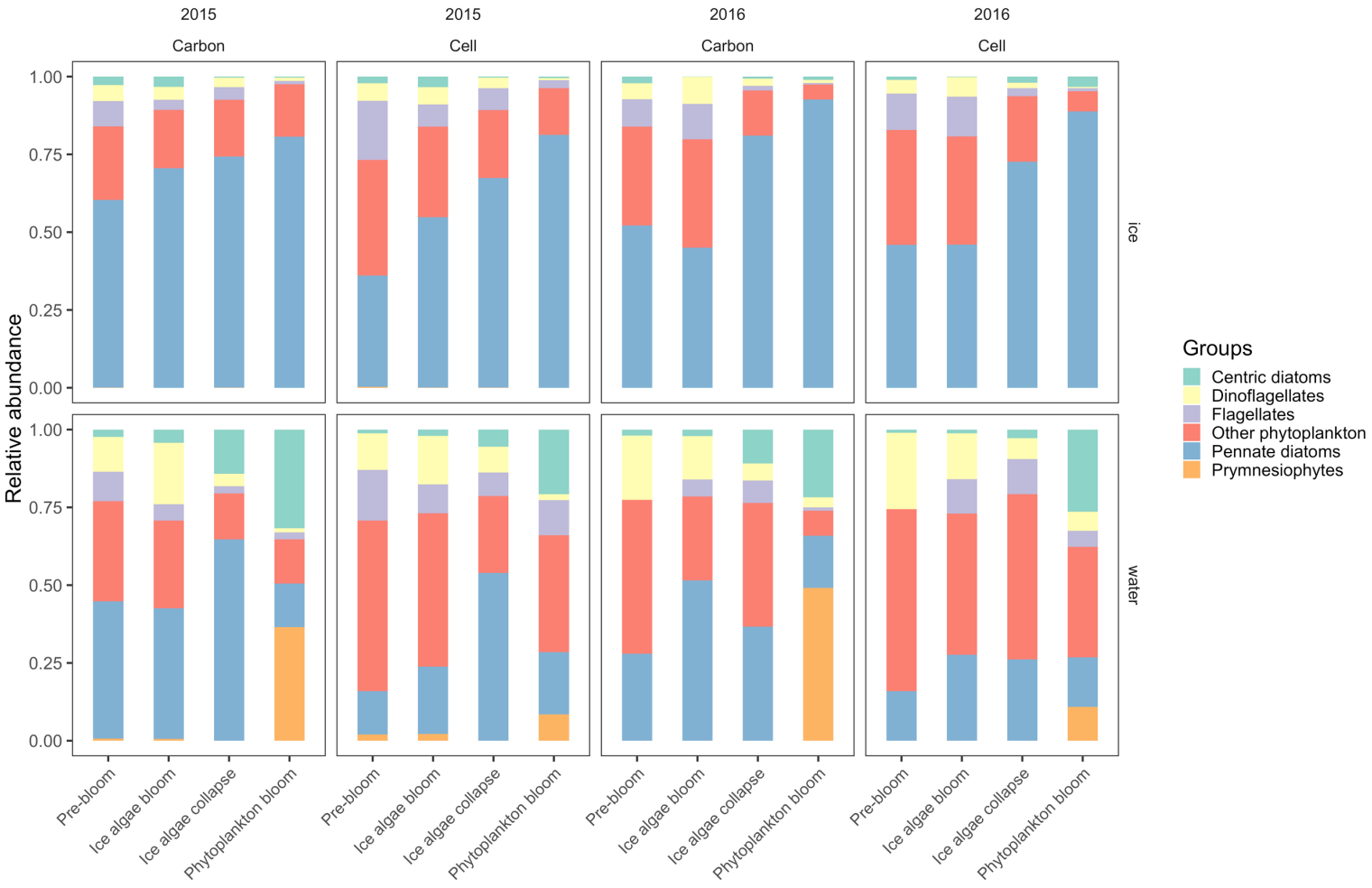

Figure 13. Relative abundance of protists (based on cell mL^{-1} and $mgC\ m^{-3}$) in the bottom 3 cm of sea ice (top panel) and the upper 60 m of the water column (bottom panel) for the different phases of the bloom phenology.

1.5.7 Pre-bloom

Our data suggests that the main limiting factor in 2015 and 2016, both in the bottom 3-cm of sea ice and in the water column during the pre-bloom, was light. Although some studies have shown that pennate diatoms can be acclimated to very low irradiances (Cota and Smith 1991), PAR <0.1 mol photons m^{-2} d^{-1} was most likely insufficient to support significant biomass accumulation. In fact, daily averaged instantaneous PAR values were lower than E_K (data not shown), suggesting that sympagic microalgae were light limited. Nutrients did not vary significantly during that phase.

The sympagic community was composed of 25-50% of pennate diatoms, the rest being mostly flagellates, dinoflagellates and other small phytoplanktonic cells. In water, <25% of the community was composed of pennate diatoms. However, genera observed were similar between sea ice and water samples. The similarity between both environments suggests that ice algae was released from the ice matrix and sank in the water column. Low under-ice PAR values and the absence of biomass accumulation in the water column suggests that sympagic algal cells were not actively growing and most likely sinking.

1.5.8 Ice algae bloom

The highest integrated biomass (Tchl*a*) values in the bottom 3-cm of sea ice were observed during the ice algae bloom in 2015 and 2016 (Figure 12A,B). In 2015, relative abundance of pennate diatoms increased both in numbers and in biomass (Figure 13). In 2016, while the Tchl*a* in sea ice slightly increased during the ice algae bloom, the relative contribution of pennate diatoms to the community merely changed from that observed during the pre-bloom. Early episodic melt events had most likely occurred before the sampling (Oziel *et al.* submitted), leading to early brine drainage and sloughing of ice algae (Mundy *et al.* 2005, Campbell *et al.* 2014). Hence, this could explain the lower biomass in the bottom 3-cm of sea ice observed in 2016 compared to 2015, and concurrently, the similarity in relative composition of the sympagic community between the two first phases of the bloom phenology.

A major difference in species composition between both years was the the dominance of *Entomoneis* spp. among pennate diatoms in the sympagic microalgal community in 2015, but its quasi absence in 2016. Our results suggest that species of the genus *Entomoneis* are growing preferentially in the interstitial layer at the bottom of the sea ice and that lower brine volume in 2016 might not have been favourable to this genus. Poulin *et al.* (2014) have also shown that *Entomoneis* spp. prefer to grow under low light intensities, which was the case in 2015 due to the snowfall event. This may have favoured this genus over others. The difference in community composition might also be due to taxa incorporated during ice formation in late fall the year before and to fall and winter ice dynamics (Niemi *et al.* 2011). Air temperature records at the Qikiqtarjuaq airport (data not shown) revealed a difference in the mean and minimum monthly temperatures between

both years, with fall 2014 being warmer than fall 2015, although winter 2015 was much colder than winter 2016. Unfortunately, no sample was collected at the time the ice formed in fall and winter, preventing us from investigating further that matter.

While there was a slight increase in the relative abundance of pennate diatoms in the water column during both years, the phytoplankton community was mostly represented by small cells (flagellates, dinoflagellates, small unidentified eukaryotes). Integrated Tchl*a* values in the bottom 3-cm of sea ice and the water column matched for both years (Figure 12A,B), except for the last two weeks of May 2015, where a snowfall event decreased the available under-ice PAR to <0.1 mol photons m^{-2} d^{-1} (Figure 9). Decreased biomass only in the water column at that time suggest PAR limitation due to attenuation from a thicker snow cover, where sinking sympagic and phytoplankton cells could not grow. In parallel, increasing Tchl*a* concentrations in the bottom 3-cm of sea ice suggest that ice algae were acclimated to very low light levels, and could actively grow despite increased PAR attenuation by snow.

In 2016, nitrate concentration in the bottom 3-cm of sea ice decreased throughout the ice algae bloom (Figure 11B), suggesting a possible limitation by nitrate over time. On the contrary, nitrate concentration was increasing along with biomass in 2015. As mentioned above, measured concentrations in 2015 are most likely reflecting intracellular pools released by algae during the melting of ice samples (Cota *et al.* 1990, Mundy *et al.* 2014). Algae having internal pools of nitrate as reserves could mean that even if low concentrations of nitrate are observed in the brines, nitrate is not necessarily a limiting factor for growth, at least in the short term. It is thus not possible to assess whether nitrate was actually a limiting factor in the bottom 3-cm of sea ice during this period of time in 2015. However, a rapid decrease to <1 µmol L^{-1} at the end of this phase, due to the drainage of melt water, and correlated with a decrease in ice algal biomass (Pearson's correlation, $r = 0.86$, p-value <0.001), suggest that nitrate could have become limiting at least at that moment.

1.5.9 Ice algae collapse

Both in 2015 and 2016, the integrated biomass (Tchl*a*) in the bottom 3-cm of the sea ice and in the upper 60 m of the water column were comparable until the snow melt

onset, but we then observed a decoupling of the values between sea ice and the water column (Figure 12AB). Air temperature >0˚C (Figure 5A), melting snow cover (Figure 6A) and decreasing brine salinity (Figure 7A) suggest that degradation of the ice habitat was responsible for the decline of the ice algae bloom, as observed in previous studies (Gosselin *et al.* 1986, Ralph *et al.* 2007). Our observations suggest that melt water from melting snow drained through the brine channels. This is supported by a decrease in the water salinity and an increase in water temperature in the top 3 meters below sea ice (Figure 8). This change in the physical environment mostly caused ice algae to be released into the water column. In fact, a sudden increase in biomass can be observed at the surface (Figure 12C,D) and species observed were mainly sympagic pennate diatoms and unidentified phytoplankton ("Other phytoplankton") in both habitats (Figure 13). This is further supported by a decrease in silicate in the surface water (mostly observed in 2015 due to higher biomass released from the sea ice), which was probably used by diatoms for their frustules (Figure 11E,F). A change in the currents direction and speed coinciding with the event might also have played a role in scraping off algae (L. Oziel, pers. comm.).

While there was an increase in under-ice PAR just below the surface (Figure 9), a delay of a few days was observed between the release of ice algae in the water column and the actual phytoplankton bloom developing (Figure 11C,D). Since there was no strong stratification of the water column, vertical mixing could have brought cells at greater depths (Oziel *et al.* submitted) where they have would been light limited. Our data suggest that a constant release of ice algae in the water column occurred, but that cells were most probably highly aggregated and sinking (Amiraux *et al.* 2017, Amiraux *et al.* submitted) and likely not contributing significantly to biomass by active growth in the water. The presence of chlorophyll *a* and low (or absence of) degradation pigments such as *chlorophyllide a* and *phaeophorbide* (Ras *et al.* 2008) suggests that phytoplankton cells were healthy, but light limited at greater depths. However, the good physiological condition of the cells have them potentially ready to grow once light becomes non limiting.

By the end of the ice algae collapse, increasing under-ice PAR intensities with advanced melting of the snow and ice, and apparition of melt ponds, might have favoured different taxonomic groups such as centric diatoms, associated with the water column blooms (Booth and Horner 1997). In order to further address the possible seeding of the

phytoplankton bloom in the water column by ice algae, primary production values between sea ice and water column samples would need to be compared. The rate at which sympagic algae are released and the magnitude of ice-associated blooms may also play a role in the possible seeding of phytoplankton bloom (Galindo *et al.* 2014, Selz *et al.* 2018).

This finding suggests that there is a potential for massive under ice phytoplankton blooms as soon as under-ice PAR intensities become non-limiting, and that the onset might be due to some ubiquitous sympagic microalgae being able to grow in water as well as in sea ice.

1.5.10 Phytoplankton bloom

With the apparition of the melt ponds, under-ice PAR intensities increased (Figure 9), allowing for active growth from phytoplankton cells. Within two to three weeks, the integrated biomass (Tchl*a*) increased by >10 fold, reaching maximum values of 151.35 mg chla m^{-2} in 2015 and 182.37 mg chla m^{-2} in 2016. The phytoplankton bloom initially developed in the first few meters of the water column and extended down to *ca*. 40 m in 2015 and *ca*. 60 m in 2016 by the end of July (Fig 11C,D). Stronger currents in 2016, without surface stratification, could explain the expansion of the bloom at greater depths than in 2015 (Oziel *et al.* submitted). As observed with sea ice algae, phytoplankton growth was most probably limited by light availability early in the season (Figures 9 and 11). Unlike previous phases of the phenology, the algae community in the water column during the phytoplankton bloom was different from that observed in sea ice (Figure 13). While sea ice was dominated by pennate diatoms with a decreasing total biomass over time (Figure 11), centric diatoms represented a bigger proportion of the community over pennate diatoms (Figure 13). Previous studies have shown that centric diatoms cope better than pennate diatoms with high light levels and that they can dissipate more efficiently excess energy to prevent photodamage (Campbell *et al.* 2018, A.C. Kvernvik, pers. comm.). Hence, increasing under-ice PAR intensities in the water column with snow and ice melt and melt pond formation seems to favour species being more efficient in such high-light conditions. Still, small unidentified phytoplankton cells were the main contributors (in numbers) to the community composition in the water column (Figure 13). The greater contribution of prymnesiophytes (>25%) in the water column for both years, in terms of

carbon estimates, is due to *Phaeocystis* spp. blooming at the end of our time series. Due to the extracellular polymeric substances (EPS) matrix produced by *Phaeocystis* spp. colonies, relative abundance based on carbon estimates is much larger than that based on the cell (image) count (Figure 13).

For both years, nutrient concentrations decreased concurrently with the phytoplankton biomass developing deeper (Figure 11A,B and 12C,D), suggesting microalgal consumption. Nitrate was identified to be the main potential limiting factor (RDA, p-value <0.001), and is negatively correlated with the biomass (Pearson's correlation, r = -0.81, p-value < 0.001). This is further supported by N:P and N:Si molar ratios with values under the Redfield ratios (respectively of 16 and 1) throughout the period of study (data not shown), thus it might have limited the expansion of the bloom in time and set its final yield (Tremblay *et al.* 2002). Although we did not capture the end of the under-ice phytoplankton spring bloom, light is likely to have become the limiting factor as the biomass got deeper. Species-specific physiological responses to the changing light conditions and nutrient affinity would be needed to further address interspecific capacities of the different groups, and therefore better explain environmental factors favouring one group over another.

1.6 Conclusion

The *Green Edge* campaigns were conducted at an ice camp in Baffin Bay from May to July 2015 and 2016 with the aim of studying the dynamics of sympagic algae and phytoplankton spring blooms.

Pennate diatoms dominated the sea ice community with different genera dominating each year. The phytoplankton community was initially alike that found in sea ice, suggesting a possible link between both communities. Light availability seemed to be the main controlling factor governing the onset of both sympagic and pelagic blooms, with a threshold value of about 0.1 mol photons m^{-2} d^{-1}. Increasing light intensities with snow melt and melt pond formation likely then favored centric diatoms, which dominated the pelagic protist assemblage during the phytoplankton bloom. At the same time, sea ice habitat degradation due to melting snow cover and sea ice likely caused the decline of the sympagic bloom. Actual nutrient limitation in ice was not clear because of the likely presence of large internal pools (reserves) in algae, while exhaustion of nitrate in the surface layer and the deepening biomass over time suggest that nitrate played a major role in the decline of the phytoplankton bloom.

With ongoing changes in the Arctic Ocean, thinner snow and ice covers are expected, allowing for more light, and earlier, to propagate into the sea ice and the underlying water column. Our results suggest that there is a potential for early and massive under ice blooms, which are light-limited early in the season. A shift in time of the blooms could lead to a mismatch with first order consumers, thus impacting the energy transfer to subsequent higher trophic levels. On top of changes in biomass and timing, a shift in species composition might influence the dynamics of ecosystems (Petrou *et al.*, 2016). As highlighted by Campbell *et al.* (2018), species-specific responses to growth conditions are needed to better understand how the expected changes will affect the marine ecosystems.

Conclusion

Les missions scientifiques *Green Edge* ont été réalisées à un camp de glace en baie de Baffin de mai à juillet 2015 et 2016. Elles avaient comme principal objectif d'améliorer notre compréhension des processus physiques et chimiques régissant la dynamique de la floraison printanière, et ultimement d'améliorer les prédictions concernant les impacts des changements climatiques sur les producteurs primaires.

Les communautés d'algues dans la glace de mer étaient principalement composées de diatomées pennées, différents genres dominants pour chaque année. De leur côté, les communautés phytoplanctoniques étaient semblables à celles observées dans la glace avant le début de la fonte printanière. Ceci suggère une possible interaction entre les deux communautés. L'utilisation d'un cytomètre en flux imageur submersible (Imaging FlowCytobot) a permis d'analyser un grand volume de données taxonomiques. Toutefois, la résolution des images n'est comparable à celle de la microscopie optique traditionnelle, limitant ainsi le détail de la classification taxonomique effectuée qu'aux grands groupes taxonomiques, avec quelques genres et espèces identifiées lorsque des caractéristiques morphologiques uniques le permettaient.

La disponibilité en lumière semble avoir été le facteur limitant principal contrôlant l'initiation des floraisons sympagiques et phytoplanctoniques, avec un seuil de 0.1 mol photons m^{-2} d^{-1}. L'intensité lumineuse augmentant avec la fonte de la neige et l'apparition de cuvettes d'eau de fonte semble avoir favorisé les diatomées centriques, ces dernières dominant les communautés pélagiques de protistes pendant les floraisons.

La fonte de la glace de mer, causant une dégradation de l'habitat pour les algues de glace, semble avoir causé le déclin de la floraison dans la glace. Une limitation en nutriments dans la glace n'a pas été clairement observée. Des réserves internes de nitrates chez les algues unicellulaires, tel qu'observés dans les échantillons de glace en 2015, pourraient leur permettre de conserver une croissance non-limitée alors que le milieu est appauvri en nitrates. Toutefois, un épuisement complet des nitrates dans la couche superficielle de l'océan et un approfondissement de la biomasse avec le temps suggèrent que les nitrates jouent un rôle prédominant dans le déclin de la floraison phytoplanctonique, suivi par une limitation en lumière lorsque la biomasse est trop profonde.

Avec les changements qui s'opèrent dans l'océan Arctique, un couvert de neige et de glace plus mince est attendu. Ceci permettra à de plus grandes intensités de lumière de se propager dans la glace et l'eau, et ce, plus tôt dans l'année. Nos résultats suggèrent qu'il y a un potentiel pour des floraisons importantes sous la glace, présentement limitées par la lumière. Une modification de la phénologie des floraisons pourrait causer un décalage temporel entre les producteurs primaires et les consommateurs de premier ordre, ce qui affecterait le transfert d'énergie et de matière vers les niveaux supérieurs de la chaîne alimentaire. Comme les différents groupes taxonomiques de producteurs primaires ne réagissent pas tous de la même façon et ont des stratégies différentes (Petrou *et al.* 2016), les réponses physiologiques aux conditions de croissance, par espèce, seraient requises afin de mieux prédire l'effet des changements environnementaux sur les écosystèmes marins (Campbell *et al.* 2018).

Références

Aminot, A. and KéRouel, R. (2007). Dosage automatique des nutriments dans les eaux marines: Méthodes en flux continu. Ifremer.

Amiraux, R., Belt, S. T., Vaultier, F., Galindo, V., Gosselin, M., Bonin, P., et al. (2017). "Monitoring photo-oxidative and salinity-induced bacterial stress in the canadian arctic using specific lipid tracers." Marine Chemistry **194**: 89-99.

Amiraux, R., Smik, L., Köseoğlu, D., Rontani, J.-F., Galindo, V., Grondin, P.-L., et al. (submitted). "Temporal evolution of ip25 and other highly branched isoprenoid lipids in sea ice and the underlying water column during an arctic melting season." Elementa-Science of the Anthropocene.

Ardyna, M., Babin, M., Gosselin, M., Devred, E., Rainville, L. and Tremblay, J. E. (2014). "Recent arctic ocean sea ice loss triggers novel fall phytoplankton blooms." Geophysical Research Letters **41**(17): 6207-6212.

Ardyna, M., Gosselin, M., Michel, C., Poulin, M. and Tremblay, J. E. (2011). "Environmental forcing of phytoplankton community structure and function in the canadian high arctic: Contrasting oligotrophic and eutrophic regions." Marine Ecology Progress Series **442**: 37-57.

Arrigo, K. R., Perovich, D. K., Pickart, R. S., Brown, Z. W., Van Dijken, G. L., Lowry, K. E., et al. (2012). "Massive phytoplankton blooms under arctic sea ice." Science **336**(6087): 1408-1408.

Arrigo, K. R., Perovich, D. K., Pickart, R. S., Brown, Z. W., Van Dijken, G. L., Lowry, K. E., et al. (2014). "Phytoplankton blooms beneath the sea ice in the chukchi sea." Deep-Sea Research Part Ii-Topical Studies in Oceanography **105**: 1-16.

Arrigo, K. R., Van Dijken, G. and Pabi, S. (2008). "Impact of a shrinking arctic ice cover on marine primary production." Geophysical Research Letters **35**(19).

Assmy, P., Fernandez-Mendez, M., Duarte, P., Meyer, A., Randelhoff, A., Mundy, C. J., et al. (2017). "Leads in arctic pack ice enable early phytoplankton blooms below snow-covered sea ice." Scientific Reports **7**: 9.

Babin, M., Morel, A. and Gagnon, R. (1994). "An incubator designed for extensive and sensitive measurements of phytoplankton photosynthetic parameters." Limnology and Oceanography **39**(3): 694-702.

Bacle, J., Carmack, E. C. and Ingram, R. G. (2002). "Water column structure and circulation under the north water during spring transition: April-july 1998." Deep-Sea Research Part Ii-Topical Studies in Oceanography **49**(22-23): 4907-4925.

Barber, D. G., Hop, H., Mundy, C. J., Else, B., Dmitrenko, I. A., Tremblay, J. E., et al. (2015). "Selected physical, biological and biogeochemical implications of a rapidly changing arctic marginal ice zone." Progress in Oceanography **139**: 122-150.

Bates, S. S. and Cota, G. F. (1986). "Fluorescence induction and photosynthetic responses of arctic ice algae to sample treatment and salinity." Journal of Phycology **22**(4): 421-429.

Baumann, M. E. M., Brandini, F. P. and Staubes, R. (1994). "The influence of light and temperature on carbon-specific dms release by cultures of phaeocystis-antarctica and 3 antarctic diatoms." Marine Chemistry **45**(1-2): 129-136.

Behrenfeld, M. J., Maranon, E., Siegel, D. A. and Hooker, S. B. (2002). "Photoacclimation and nutrient-based model of light-saturated photosynthesis for quantifying oceanic primary production." Marine Ecology Progress Series **228**: 103-117.

Belanger, S., Babin, M. and Tremblay, J. E. (2013). "Increasing cloudiness in arctic damps the increase in phytoplankton primary production due to sea ice receding." Biogeosciences **10**(6): 4087-4101.

Beszczynska-Moller, A., Woodgate, R. A., Lee, C., Melling, H. and Karcher, M. (2011). "A synthesis of exchanges through the main oceanic gateways to the arctic ocean." Oceanography **24**(3): 82-99.

Booth, B. C. and Horner, R. A. (1997). "Microalgae on the arctic ocean section, 1994: Species abundance and biomass." Deep-Sea Research Part II-Topical Studies in Oceanography **44**(8): 1607-1622.

Campbell, K., Mundy, C. J., Barber, D. G. and Gosselin, M. (2014). "Remote estimates of ice algae biomass and their response to environmental conditions during spring melt." Arctic **67**(3): 375-387.

Campbell, K., Mundy, C. J., Belzile, C., Delaforge, A. and Rysgaard, S. (2018). "Seasonal dynamics of algal and bacterial communities in arctic sea ice under variable snow cover." Polar Biology **41**(1): 41-58.

Campbell, K., Mundy, C. J., Gosselin, M., Landy, J. C., Delaforge, A. and Rysgaard, S. (2017). "Net community production in the bottom of first-year sea ice over the arctic spring bloom." Geophysical Research Letters **44**(17): 8971-8978.

Carmack, E., Barber, D., Christensen, J., Macdonald, R., Rudels, B. and Sakshaug, E. (2006). "Climate variability and physical forcing of the food webs and the carbon budget on panarctic shelves." Progress in Oceanography **71**(2-4): 145-181.

Carmack, E. and Chapman, D. C. (2003). "Wind-driven shelf/basin exchange on an arctic shelf: The joint roles of ice cover extent and shelf-break bathymetry." Geophysical Research Letters **30**(14): 4.

Carmack, E. and Wassmann, P. (2006). "Food webs and physical-biological coupling on pan-arctic shelves: Unifying concepts and comprehensive perspectives." Progress in Oceanography **71**(2-4): 446-477.

Carmack, E. C., Aagaard, K., Swift, J. H., Macdonald, R. W., Mclaughlin, F. A., Jones, E. P., et al. (1997). "Changes in temperature and tracer distributions within the arctic ocean: Results from the 1994 arctic ocean section." Deep-Sea Research Part II-Topical Studies in Oceanography **44**(8): 1487-1502.

Coachman, L. K. and Aagaard, K. (1974). Physical oceanography of arctic and subarctic seas. Marine geology
and oceanography of the arctic seas. New-York, Springer-Verlag**:** 1-72.

Comiso, J. C. (2012). "Large decadal decline of the arctic multiyear ice cover." Journal of Climate **25**(4): 1176-1193.

Comiso, J. C. and Hall, D. K. (2014). "Climate trends in the arctic as observed from space." Wiley Interdisciplinary Reviews-Climate Change **5**(3): 389-409.

Comiso, J. C., Parkinson, C. L., Gersten, R. and Stock, L. (2008). "Accelerated decline in the arctic sea ice cover." Geophysical Research Letters **35**(1).

Cota, G. F., Anning, J. L., Harris, L. R., Harrison, W. G. and Smith, R. E. H. (1990). "Impact of ice algae on inorganic nutrients in seawater and sea ice in barrow strait, nwt, canada, during spring." Canadian Journal of Fisheries and Aquatic Sciences **47**(7): 1402-1415.

Cota, G. F., Pomeroy, L. R., Harrison, W. G., Jones, E. P., Peters, F., Sheldon, W. M., et al. (1996). "Nutrients, primary production and microbial heterotrophy in the southeastern chukchi sea: Arctic summer nutrient depletion and heterotrophy." Marine Ecology Progress Series **135**(1-3): 247-258.

Cota, G. F. and Smith, R. E. H. (1991). "Ecology of bottom ice algae: Iii. Comparative physiology." Journal of Marine Systems **2**(3): 297-315.

Cox, G. F. N. and Weeks, W. F. (1983). "Equations for determining the gas and brine volumes in sea-ice samples." Journal of Glaciology **29**(102): 306-316.

Cullen, J. J. and Macintyre, J. G. (1998). Behavior, physiology and the niche of depth-regulating phytoplankton. The physiological ecology of harmful algal blooms. A. D. C. D. M. Anderson and G. M. Hallegraeff. Heidelberg, Springer-Verlag**:** 559-580.

Cunningham, A., Mckee, D., Craig, S., Tarran, G. and Widdicombe, C. (2003). "Fine-scale variability in phytoplankton community structure and inherent optical properties measured from an autonomous underwater vehicle." Journal of Marine Systems **43**(1-2): 51-59.

Davis, C. S., Gallager, S. M. and Solow, A. R. (1992). "Microaggregations of oceanic plankton observed by towed video microscopy." Science **257**(5067): 230-232.

Dugdale, R. C. (1967). "Nutrient limitation in sea - dynamics identification and significance." Limnology and Oceanography **12**(4): 685-&.

Falkowski, P. G. and Raven, J. A. (2007). Aquatic photosynthesis. New Jersey, Princeton University Press.

Fortier, M., Fortier, L., Michel, C. and Legendre, L. (2002). "Climatic and biological forcing of the vertical flux of biogenic particles under seasonal arctic sea ice." Marine Ecology Progress Series **225**: 1-16.

Galindo, V., Levasseur, M., Mundy, C. J., Gosselin, M., Scarratt, M., Papakyriakou, T., et al. (2016). "Contrasted sensitivity of dmsp production to high light exposure in two arctic under-ice blooms." Journal of Experimental Marine Biology and Ecology **475**: 38-48.

Galindo, V., Levasseur, M., Mundy, C. J., Gosselin, M., Tremblay, J. E., Scarratt, M., et al. (2014). "Biological and physical processes influencing sea ice, under-ice algae, and dimethylsulfoniopropionate during spring in the canadian arctic archipelago." Journal of Geophysical Research-Oceans **119**(6): 3746-3766.

Gallager, S. M., Davis, C. S., Epstein, A. W., Solow, A. and Beardsley, R. C. (1996). "High-resolution observations of plankton spatial distributions correlated with hydrography in the great south channel, georges bank." Deep-Sea Research Part II-Topical Studies in Oceanography **43**(7-8): 1627-1663.

Garrison, D. L. and Buck, K. R. (1986). "Organism losses during ice melting - a serious bias in sea ice community studies." Polar Biology **6**(4): 237-239.

Gosselin, M., Legendre, L., Therriault, J. C., Demers, S. and Rochet, M. (1986). "Physical control of the horizontal patchiness of sea-ice microalgae." Marine Ecology Progress Series **29**(3): 289-298.

Gosselin, M., Levasseur, M., Wheeler, P. A., Horner, R. A. and Booth, B. C. (1997). "New measurements of phytoplankton and ice algal production in the arctic ocean." Deep-Sea Research Part Ii-Topical Studies in Oceanography **44**(8): 1623-+.

Grebmeier, J. M., Cooper, L. W., Feder, H. M. and Sirenko, B. I. (2006). "Ecosystem dynamics of the pacific-influenced northern bering and chukchi seas in the amerasian arctic." Progress in Oceanography **71**(2-4): 331-361.

Hancke, K., Lund-Hansen, L. C., Lamare, M. L., Pedersen, S. H., King, M. D., Andersen, P., et al. (2018). "Extreme low light requirement for algae growth underneath sea ice: A case study from station nord, ne greenland." Journal of Geophysical Research-Oceans **123**(2): 985-1000.

Harrison, G. (1980). Nutrient regeneration and primary production in the sea. Primary production in the sea. P. G. Falkowski. New-York, Plenum**:** 433-460.

Hasle, G. R. and Heimdal, B. R. (1998). "The net phytoplankton in kongsfjorden, svalbard, july 1988, with general remarks on species composition of arctic phytoplankton." Polar Research **17**(1): 31-52.

Hill, V., Cota, G. and Stockwell, D. (2005). "Spring and summer phytoplankton communities in the chukchi and eastern beaufort seas." Deep-Sea Research Part II-Topical Studies in Oceanography **52**(24-26): 3369-3385.

Holte, J. and Talley, L. (2009). "A new algorithm for finding mixed layer depths with applications to argo data and subantarctic mode water formation." Journal of Atmospheric and Oceanic Technology **26**(9): 1920-1939.

Horner, R. and Schrader, G. C. (1982). "Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the beaufort sea." Arctic **35**(4): 485-503.

Horner, R. A. (1984). Phytoplankton abundance, chlorophyll *a* and primary production in the western beaufort sea. The alaskan beaufort sea. S. D. Barnes PW, Reimnitz E. New-York, Academic Press**:** 295-310.

Hsiao, S. I. C. (1992). "Dynamics of ice algae and phytoplankton in frobisher bay." Polar Biology **12**(6-7): 645-651.

Huller, R., Glossner, E., Schaub, S., Weingartner, J. and Kachel, V. (1994). "The macro flow planktometer - a new device for volume and fluorescence analysis of macro plankton including triggered video imaging in flow." Cytometry **17**(2): 109-118.

Ingram, R. G., Bacle, J., Barber, D. G., Gratton, Y. and Melling, H. (2002). "An overview of physical processes in the north water." Deep-Sea Research Part Ii-Topical Studies in Oceanography **49**(22-23): 4893-4906.

Kahru, M., Brotas, V., Manzano-Sarabia, M. and Mitchell, B. G. (2011). "Are phytoplankton blooms occurring earlier in the arctic?" Global Change Biology **17**(4): 1733-1739.

Kaleschke, L. and Tian-Kunze, X. (2016). Amsr2 asi 3.125 km sea ice concentration data. Germany. Available at ftp-projects.zmaw.de/seaice/.

Kattner, G. and Budeus, G. (1997). "Nutrient status of the northeast water polynya." Journal of Marine Systems **10**(1-4): 185-197.

Kirkwood, D. S. (1992). "Stability of solutions of nutrient salts during storage." Marine Chemistry **38**(3-4): 151-164.

Kirst, G. O. and Wiencke, C. (1995). "Ecophysiology of polar algae." Journal of Phycology **31**(2): 181-199.

Kristiansen, S., Farbrot, T. and Wheeler, P. A. (1994). "Nitrogen cycling in the barents sea - seasonal dynamics of new and regenerated production in the marginal ice-zone." Limnology and Oceanography **39**(7): 1630-1642.

Kristiansen, S. and Lund, B. A. (1989). "Nitrogen cycling in the barents sea .1. Uptake of nitrogen in the water column." Deep-Sea Research Part a-Oceanographic Research Papers **36**(2): 255-268.

Lacour, L., Claustre, H., Prieur, L. and D'ortenzio, F. (2015). "Phytoplankton biomass cycles in the north atlantic subpolar gyre: A similar mechanism for two different blooms in the labrador sea." Geophysical Research Letters **42**(13): 5403-5410.

Laliberte, J., Belanger, S. and Frouin, R. (2016). "Evaluation of satellite-based algorithms to estimate photosynthetically available radiation (par) reaching the ocean surface at high northern latitudes." Remote Sensing of Environment **184**: 199-211.

Laney, S. R. and Sosik, H. M. (2014). "Phytoplankton assemblage structure in and around a massive under-ice bloom in the chukchi sea." Deep Sea Research Part II: Topical Studies in Oceanography(0).

Le Fouest, V., Babin, M. and Tremblay, J. E. (2013). "The fate of riverine nutrients on arctic shelves." Biogeosciences **10**(6): 3661-3677.

Legendre, L., Martineau, M. J., Therriault, J. C. and Demers, S. (1992). "Chlorophyll-a biomass and growth of sea-ice microalgae along a salinity gradient (southeastern hudson-bay, canadian arctic)." Polar Biology **12**(3-4): 445-453.

Leu, E., Mundy, C. J., Assmy, P., Campbell, K., Gabrielsen, T. M., Gosselin, M., et al. (2015). "Arctic spring awakening - steering principles behind the phenology of vernal ice algal blooms." Progress in Oceanography **139**: 151-170.

Li, W. K. W., Mclaughlin, F. A., Lovejoy, C. and Carmack, E. C. (2009). "Smallest algae thrive as the arctic ocean freshens." Science **326**(5952): 539-539.

Maranon, E., Cermeno, P., Lopez-Sandoval, D. C., Rodriguez-Ramos, T., Sobrino, C., Huete-Ortega, M., et al. (2013). "Unimodal size scaling of phytoplankton growth and the size dependence of nutrient uptake and use." Ecology Letters **16**(3): 371-379.

Margalef, R. (1978). "Life-forms of phytoplankton as survival alternatives in an unstable environment." Oceanologica Acta **1**(4): 493-509.

Markus, T., Stroeve, J. C. and Miller, J. (2009). "Recent changes in arctic sea ice melt onset, freezeup, and melt season length." Journal of Geophysical Research-Oceans **114**.

Mccarthy, J. J. (1980). Nitrogen. The physiological ecology of phytoplankton. I. Morris. Oxford, UK, Blackwell**:** 195-233.

Menden-Deuer, S. and Lessard, E. J. (2000). "Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton." Limnology and Oceanography **45**(3): 569-579.

Moberg, E. A. and Sosik, H. M. (2012). "Distance maps to estimate cell volume from two-dimensional plankton images." Limnology and Oceanography-Methods **10**: 278-288.

Montegut, C. D., Madec, G., Fischer, A. S., Lazar, A. and Iudicone, D. (2004). "Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology." Journal of Geophysical Research-Oceans **109**(C12): 20.

Morata, N., Poulin, M. and Renaud, P. E. (2011). "A multiple biomarker approach to tracking the fate of an ice algal bloom to the sea floor." Polar Biology **34**(1): 101-112.

Mundy, C. J., Barber, D. G. and Michel, C. (2005). "Variability of snow and ice thermal, physical and optical properties pertinent to sea ice algae biomass during spring." Journal of Marine Systems **58**(3-4): 107-120.

Mundy, C. J., Gosselin, M., Ehn, J., Gratton, Y., Rossnagel, A., Barber, D. G., et al. (2009). "Contribution of under-ice primary production to an ice-edge upwelling phytoplankton bloom in the canadian beaufort sea." Geophysical Research Letters **36**: 5.

Mundy, C. J., Gosselin, M., Ehn, J. K., Belzile, C., Poulin, M., Alou, E., et al. (2011). "Characteristics of two distinct high-light acclimated algal communities during advanced stages of sea ice melt." Polar Biology **34**(12): 1869-1886.

Mundy, C. J., Gosselin, M., Gratton, Y., Brown, K., Galindo, V., Campbell, K., et al. (2014). "Role of environmental factors on phytoplankton bloom initiation under landfast sea ice in resolute passage, canada." Marine Ecology Progress Series **497**: 39-+.

Nahavandian Esfahani, S. (2014). Temporal and spatial evolution of the mixed layer in the southern beaufort sea and the amundsen gulf. Ph. D., Université du Québec
Institut National de la Recherche Scientifique Centre Eau Terre Environnement.

Nahavandian Esfahani, S., Prieur, L. and Gratton, Y. (2013). Impacts of surface fluxes on the mixed layer depth evolution in the southern beaufort sea and amundsen gulf. 12th Conference on Polar Meteorology and Oceanography. Seattle, WA.

Niemi, A., Michel, C., Hille, K. and Poulin, M. (2011). "Protist assemblages in winter sea ice: Setting the stage for the spring ice algal bloom." Polar Biology **34**(12): 1803-1817.

Olsen, A., Johannessen, T. and Rey, F. (2003). "On the nature of the factors that control spring bloom development at the entrance to the barents sea and their interannual variability." Sarsia **88**(6): 379-393.

Olson, R. J., Shalapyonok, A. and Sosik, H. M. (2003). "An automated submersible flow cytometer for analyzing pico- and nanophytoplankton: Flowcytobot." Deep-Sea Research Part I-Oceanographic Research Papers **50**(2): 301-315.

Olson, R. J. and Sosik, H. M. (2007). "A submersible imaging-in-flow instrument to analyze nano-and microplankton: Imaging flowcytobot." Limnology and Oceanography-Methods **5**: 195-203.

Oziel, L., Massicotte, P., Randelhoff, A., Ferland, J., Vladoiu, A., Lacour, L., et al. (submitted). "Environmental factors influencing the seasonal dynamics of under-ice spring blooms in baffin bay." Elementa-Science of the Anthropocene.

Pegau, W. S. and Paulson, C. A. (2001). "The albedo of arctic leads in summer." Annals of Glaciology **33**: 221-224.

Peralta-Ferriz, C. and Woodgate, R. A. (2015). "Seasonal and interannual variability of pan-arctic surface mixed layer properties from 1979 to 2012 from hydrographic data, and the dominance of stratification for multiyear mixed layer depth shoaling." Progress in Oceanography **134**: 19-53.

Perovich, D. K. (2011). "The changing arctic sea ice cover." Oceanography **24**(3): 162-173.

Perovich, D. K., Nghiem, S. V., Markus, T. and Schweiger, A. (2007). "Seasonal evolution and interannual variability of the local solar energy absorbed by the arctic sea ice-ocean system." Journal of Geophysical Research-Oceans **112**(C3): 13.

Perovich, D. K. and Polashenski, C. (2012). "Albedo evolution of seasonal arctic sea ice." Geophysical Research Letters **39**: 6.

Perovich, D. K. and Richter-Menge, J. A. (2009). "Loss of sea ice in the arctic." Annual Review of Marine Science **1**: 417-441.

Perovich, D. K., Richter-Menge, J. A., Jones, K. F. and Light, B. (2008). "Sunlight, water, and ice: Extreme arctic sea ice melt during the summer of 2007." Geophysical Research Letters **35**(11): 4.

Perrette, M., Yool, A., Quartly, G. D. and Popova, E. E. (2011). "Near-ubiquity of ice-edge blooms in the arctic." Biogeosciences **8**(2): 515-524.

Petrich, C. and Eicken, H. (2010). Growth, structure and properties of sea ice. Sea ice, Wiley-Blackwell**:** 23-77.

Petrou, K., Kranz, S. A., Trimborn, S., Hassler, C. S., Ameijeiras, S. B., Sackett, O., et al. (2016). "Southern ocean phytoplankton physiology in a changing climate." Journal of Plant Physiology **203**: 135-150.

Picheral, M., Colin, S. and Irisson, J.-O. (2017). Ecotaxa, a tool for the taxonomic classification of images Available at http://ecotaxa.obs-vlfr.fr.

Platt, T., Gallegos, C. L. and Harrison, W. G. (1980). "Photoinhibition of photosynthesis in natural assemblages of marine-phytoplankton." Journal of Marine Research **38**(4): 687-701.

Popova, E. E., Yool, A., Coward, A. C., Dupont, F., Deal, C., Elliott, S., et al. (2012). "What controls primary production in the arctic ocean? Results from an intercomparison of five general circulation models with biogeochemistry." Journal of Geophysical Research-Oceans **117**: 16.

Poulin, M., Daugbjerg, N., Gradinger, R., Ilyash, L., Ratkova, T. and Von Quillfeldt, C. (2011). "The pan-arctic biodiversity of marine pelagic and sea-ice unicellular eukaryotes: A first-attempt assessment." Marine Biodiversity **41**(1): 13-28.

Poulin, M., Underwood, G. J. C. and Michel, C. (2014). "Sub-ice colonial melosira arctica in arctic first-year ice." Diatom Research **29**(2): 213-221.

Ralph, P. J., Ryan, K. G., Martin, A. and Fenton, G. (2007). "Melting out of sea ice causes greater photosynthetic stress in algae than freezing in." Journal of Phycology **43**(5): 948-956.

Ras, J., Claustre, H. and Uitz, J. (2008). "Spatial variability of phytoplankton pigment distributions in the subtropical south pacific ocean: Comparison between in situ and predicted data." Biogeosciences **5**(2): 353-369.

Reigstad, M., Wassmann, P., Riser, C. W., Oygarden, S. and Rey, F. (2002). "Variations in hydrography, nutrients and chlorophyll a in the marginal ice-zone and the central barents sea." Journal of Marine Systems **38**(1-2): 9-29.

Reimnitz, E., Clayton, J. R., Kempema, E. W., Payne, J. R. and Weber, W. S. (1993). "Interaction of rising frazil with suspended particles - tank experiments with applications to nature." Cold Regions Science and Technology **21**(2): 117-135.

Reimnitz, E., Marincovich, L., Mccormick, M. and Briggs, W. M. (1992). "Suspension freezing of bottom sediment and biota in the northwest passage and implications for arctic-ocean sedimentation." Canadian Journal of Earth Sciences **29**(4): 693-703.

Ricchiazzi, P., Yang, S. R., Gautier, C. and Sowle, D. (1998). "Sbdart: A research and teaching software tool for plane-parallell radiative transfer in the earth's atmosphere." Bulletin of the American Meteorological Society **79**(10): 2101-2114.

Rozanska, M., Gosselin, M., Poulin, M., Wiktor, J. M. and Michel, C. (2009). "Influence of environmental factors on the development of bottom ice protist communities during the winter-spring transition." Marine Ecology Progress Series **386**: 43-59.

Rozanska, M., Poulin, M. and Gosselin, M. (2008). "Protist entrapment in newly formed sea ice in the coastal arctic ocean." Journal of Marine Systems **74**(3-4): 887-901.

Sakshaug, E. (2004). Primary and secondary production in the arctic seas. Organic carbon cycle in the arctic ocean. M. Stein R., R.W. Germany, Springer**:** 57-81.

Sakshaug, E. and Slagstad, D. (1991). "Light and productivity of phytoplankton in polar marine ecosystems - a physiological view." Polar Research **10**(1): 69-85.

Selz, V., Laney, S., Arnsten, A. E., Lewis, K. M., Lowry, K. E., Joy-Warren, H. L., et al. (2018). "Ice algal communities in the chukchi and beaufort seas in spring and early summer: Composition, distribution, and coupling with phytoplankton assemblages." Limnology and Oceanography **63**(3): 1109-1133.

Serreze, M. C., Holland, M. M. and Stroeve, J. (2007). "Perspectives on the arctic's shrinking sea-ice cover." Science **315**(5818): 1533-1536.

Sieracki, C. K., Sieracki, M. E. and Yentsch, C. S. (1998). "An imaging-in-flow system for automated analysis of marine microplankton." Marine Ecology Progress Series **168**: 285-296.

Simpson, K. G., Tremblay, J. E., Gratton, Y. and Price, N. M. (2008). "An annual study of inorganic and organic nitrogen and phosphorus and silicic acid in the southeastern beaufort sea." Journal of Geophysical Research-Oceans **113**(C7).

Soreide, J. E., Leu, E., Berge, J., Graeve, M. and Falk-Petersen, S. (2010). "Timing of blooms, algal food quality and calanus glacialis reproduction and growth in a changing arctic." Global Change Biology **16**(11): 3154-3163.

Sosik, H. M. and Olson, R. J. (2007). "Automated taxonomic classification of phytoplankton sampled with imaging-in-flow cytometry." Limnology and Oceanography-Methods **5**: 204-216.

Sosik, H. M., Olson, R. J., Neubert, M. G., Shalapyonok, A. and Solow, A. R. (2003). "Growth rates of coastal phytoplankton from time-series measurements with a submersible flow cytometer." Limnology and Oceanography **48**(5): 1756-1765.

Stroeve, J. and Notz, D. (2015). "Insights on past and future sea-ice evolution from combining observations and models." Global and Planetary Change **135**: 119-132.

Stroeve, J. C., Markus, T., Boisvert, L., Miller, J. and Barrett, A. (2014). "Changes in arctic melt season and implications for sea ice loss." Geophysical Research Letters **41**(4): 1216-1225.

Stroeve, J. C., Serreze, M. C., Holland, M. M., Kay, J. E., Malanik, J. and Barrett, A. P. (2012). "The arctic's rapidly shrinking sea ice cover: A research synthesis." Climatic Change **110**(3-4): 1005-1027.

Sukhanova, I. N., Maksimova, O. V. and Nezlin, N. P. (1999). Abundance and biomass of phytoplankton and chlorophyll concentration to eastern mediterranean in late summer period. Dordrecht, Springer.

Syvertsen, E. E. (1991). "Ice algae in the barents sea - types of assemblages, origin, fate and role in the ice-edge phytoplankton bloom." Polar Research **10**(1): 277-287.

Thingstad, T. F. and Sakshaug, E. (1990). "Control of phytoplankton growth in nutrient recycling ecosystems - theory and terminology." Marine Ecology Progress Series **63**(2-3): 261-272.

Thomson, R. E. and Fine, I. V. (2003). "Estimating mixed layer depth from oceanic profile data." Journal of Atmospheric and Oceanic Technology **20**(2): 319-329.

Thomson, R. E. and Fine, I. V. (2009). "A diagnostic model for mixed layer depth estimation with application to ocean station p in the northeast pacific." Journal of Physical Oceanography **39**(6): 1399-1415.

Thwaites, F. T., Gallager, S. M., Davis, C. S., Bradley, A. M., Girard, A., Paul, W., et al. (1998). A winch and cable for the autonomous vertically profiling plankton observatory. New York, Ieee.

Tozzi, S., Schofield, O. and Falkowski, P. (2004). "Historical climate change and ocean turbulence as selective agents for two key phytoplankton functional groups." Marine Ecology Progress Series **274**: 123-132.

Tremblay, J.-É. and Gagnon, J. (2009). The effects of irradiance and nutrient supply on the productivity of arctic waters: A perspective on climate change. Influence of climate change on the changing arctic and sub-arctic conditions. J. J. Nihoul and A. Kostianoy, Springer Netherlands**:** 73-93.

Tremblay, J. E., Gratton, Y., Carmack, E. C., Payne, C. D. and Price, N. M. (2002). "Impact of the large-scale arctic circulation and the north water polynya on nutrient inventories in baffin bay." Journal of Geophysical Research-Oceans **107**(C8): 15.

Tremblay, J. E., Michel, C., Hobson, K. A., Gosselin, M. and Price, N. M. (2006). "Bloom dynamics in early opening waters of the arctic ocean." Limnology and Oceanography **51**(2): 900-912.

Tremblay, J. E., Simpson, K. G., Martin, J., Miller, L., Gratton, Y., Barber, D., et al. (2008). "Vertical stability and the annual dynamics of nutrients and chlorophyll fluorescence in the coastal, southeast beaufort sea." Journal of Geophysical Research-Oceans **113**(C7): 14.

Turpin, D. H. and Harrison, P. J. (1979). "Limiting nutrient patchiness and its role in phytoplankton ecology." Journal of Experimental Marine Biology and Ecology **39**(2): 151-166.

Van Leeuwe, M. A., Tedesco, L., Arrigo, K. R., Assmy, P., Campbell, K., Meiners, K. M., et al. (2018). "Microalgal community structure and primary production in arctic and antarctic sea ice: A synthesis." Elementa-Science of the Anthropocene **6**: 25.

Wassmann, P., Duarte, C. M., Agusti, S. and Sejr, M. K. (2011). "Footprints of climate change in the arctic marine ecosystem." Global Change Biology **17**(2): 1235-1249.

Wassmann, P. and Reigstad, M. (2011). "Future arctic ocean seasonal ice zones and implications for pelagic-benthic coupling." Oceanography **24**(3): 220-231.

Weissenberger, J. and Grossmann, S. (1998). "Experimental formation of sea ice: Importance of water circulation and wave action for incorporation of phytoplankton and bacteria." Polar Biology **20**(3): 178-188.

Yamamoto-Kawai, M., Carmack, E. and Mclaughlin, F. (2006). "Nitrogen balance and arctic throughflow." Nature **443**(7107): 43-43.

Zingone, A., Chrétiennot-Dinet, M. J., Lange, M. and Medlin, L. (1999). "Morphological and genetic characterization of *phaeocystis cordata* and *p. Jahnii* (prymnesiophyceae), two new species from the mediterranean sea." Journal of Phycology **35**(6): 1322-1337.

Annexes

Table S1. Taxonomic categories and counts of IFCB images.

Categories	Count 2015	Count 2016
Anabaena	51	28
Attheya	78	1000
Centric diatoms	2504	300
Centric diatoms chains	169	31
Chaetoceros	595	3473
Ciliates	6	4
Cryptophytes	34	31
Cylindrotheca closterium	584	49
Cysts	6	1
Detritus	22992	3158
Dictyocha	1	1
Dinoflagellates	2533	740
Entomoneis	15025	395
Eucampia	1	2
Euglenozoa	916	148
Fecal pellets	6	21
Flagellates	1046	350
Fragilariopsis	16	NA
Gyro_Pleurosigma	384	42
Licmophora	1010	22
Melosira	60	20
Navicula	46	NA
Navicula pelagica	86	18
Navicula septentrionalis	2	NA
Neoceratium	1	NA
Nitzschia frigida	1470	1315
Other phytoplankton	19368	10239
Pennate diatoms	46393	33939
Pennate diatoms chains	7650	1045
Peridiniella catenata	37	2
Phaeocystis	67	189
Polarella glacialis	6	3
Porosira	7	NA
Pseudo-nitzschia	397	570
Rhizosolenia	2	NA
Rhodomonas	39	3
Thalassiosira	641	176
Thalassiosira nordenskioeldii	16	63
Zooplankton	2	NA
Mesodinium rubrum	NA	1
Porosira glacialis	NA	16
Synedropsis	NA	2
Total	**124,247**	**57,397**

Table S2. Description and dates of each phase of the bloom phenology

Phase number	Phase name	Physical parameter start	Physical parameter end	Start date		End date	
				2015	2016	2015	2016
1	Pre-bloom	Beginning of sampling period	First occurrence of $PAR_{1.3m}$ = 0.1 Eins m^{-2} d^{-1}	Apr. 1	Apr. 29	Apr. 26	May 17
2	Ice algae bloom	First occurrence of $PAR_{1.3m}$ = 0.1 Eins m^{-2} d^{-1}	Snow melt onset	Apr. 26	May 17	Jun. 8	Jun. 3
3	Ice algae collapse	Snow melt onset	Melt pond onset	Jun. 8	Jun. 3	Jun. 22	Jun. 15
4	Phytoplankton bloom	Melt pond onset	End of sampling period	Jun. 22	Jun. 15	Jul. 14	Jul. 22

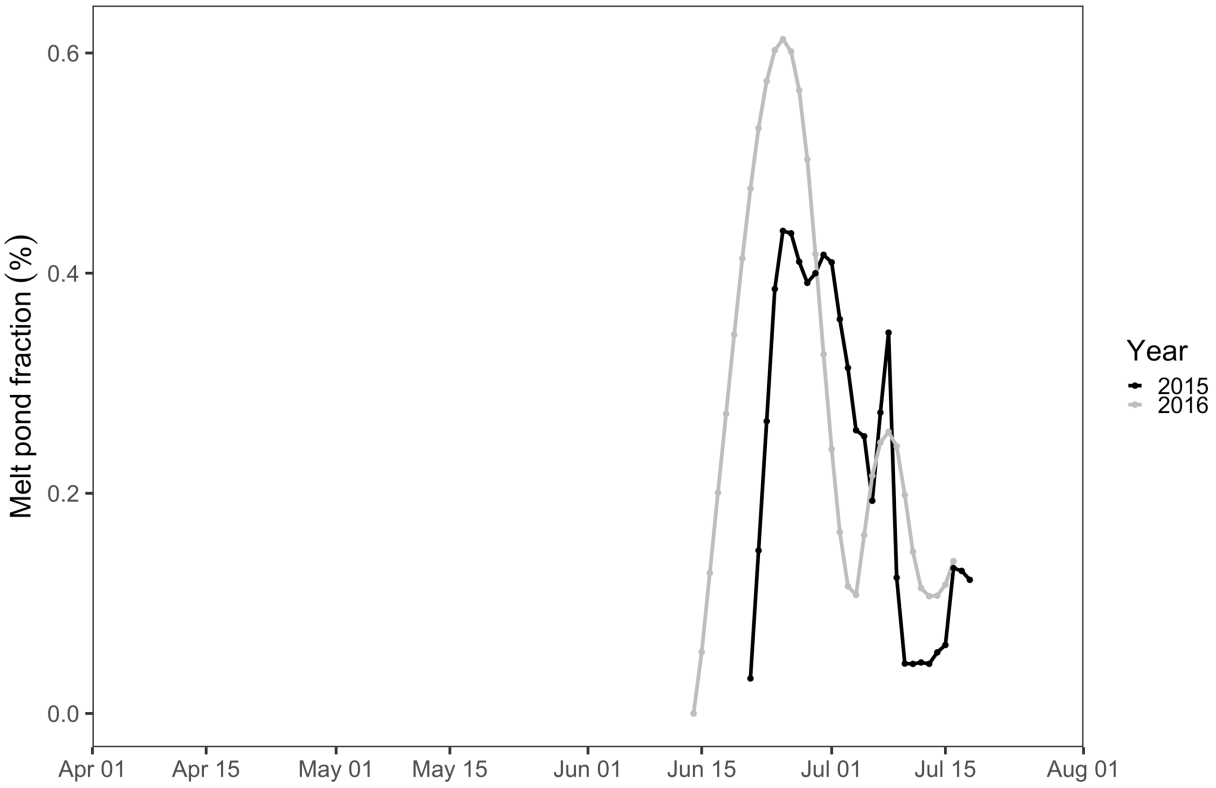

Figure S1. Melt pond fraction (%) observed in 2015 and 2016. No melt pond was observed earlier in the season for both years.