Université du Québec
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Caractérisation des communautés des mares de fonte de l'Arctique canadien et de leurs stratégies de photoprotection

Mémoire présenté

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AVANT-PROPOS

Ce mémoire caractérise les communautés algales des mares de fonte dans l'Arctique canadien durant la saison estivale et leurs stratégies de photoprotection. Il est constitué d'une introduction générale, d'un chapitre central écrit sous la forme d'un article scientifique et d'une conclusion générale. Le chapitre central de ce mémoire sera soumis sous peu à une revue scientifique avec comité de lecture. Cette étude fut réalisée lors de la mission conjointe du réseau de centre d'excellence du Canada ArcticNet et du réseau NETCARE (Network on Climate and Aerosols: adressing Key Incertainties in Remote Canadian Environment) en 2014. Les résultats de cette recherche furent présentés à divers ateliers et congrès scientifiques. En novembre 2014, j'ai présenté les premiers résultats de cette étude sous forme de présentation orale lors de l'atelier de travail NETCARE, à Toronto (« Water masses, nutrients and algal production during the 2014 NETCARE/ArcticNet joint expedition »). En mai et juin 2015, les résultats préliminaires furent exposés sous forme de présentation orale ayant pour titre « The Changing Arctic Ocean: New environments conducive to algal blooms », lors des congrès de l'Association francophone pour le savoir (Acfas) à Rimouski et de la Société canadienne de météorologie et d'océanographie (SCMO) à Whistler. En novembre 2015, les résultats de mon projet de maîtrise furent présentés sous forme d'affiche, ayant pour titre « Spatial variability of microbial communities in Arctic melt ponds », lors de l'Assemblée générale annuelle de Québec-Océan, à Québec, et de l'atelier de travail de NETCARE, à Toronto. Finalement, en février 2016, j'ai eu la chance de présenter une affiche lors de l'*Ocean Science Meeting* à La Nouvelle-Orléans (« Dynamics of primary producers at a receding ice edge during early summer in the Canadian High Arctic »).

Je tiens à adresser mes plus sincères remerciements à mon directeur de recherche, le professeur Michel Gosselin, de l'Institut des sciences de la mer de Rimouski, et mon codirecteur de recherche, le professeur Maurice Levasseur, du Département de biologie de

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Finalement, je tiens à remercier les divers organismes ayant soutenus financièrement ce projet, soit, le Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG), ArcticNet, le Fonds de recherche du Québec - Nature et technologies (FRQNT) par l’entremise de Québec-Océan, le Musée canadien de la nature, le Ministère des Affaires indiennes et du Nord par le programme de formation scientifique dans le Nord, l'Institut des sciences de la mer de Rimouski (ISMER) et NETCARE. Je suis également extrêmement reconnaissante envers les officiers et l'équipage du NGCC Amundsen pour leur précieux soutien lors de l'expédition de 2014.

RÉSUMÉ

Les mares de fonte sont des environnements éphémères situés à la surface de la glace de mer, et dont les caractéristiques biologiques ont été peu étudiées. Le but de cette étude est de caractériser la communauté d'algues se développant dans les mares de fonte au début de l'été dans le Haut-Arctique canadien. Plus précisément, ce projet a permis de déterminer la production, la biomasse la composition taxonomique de la communauté algale des mares de fonte, et leurs stratégies de photoprotection, en plus d'identifier les facteurs environnementaux influençant cette communauté durant l'été 2014. Il est attendu que la production, la biomasse et la diversité taxonomique dans les mares de fonte seront faibles et principalement limitées par la salinité et la disponibilité en éléments nutritifs. De plus, il est attendu que la proportion de pigments photoprotecteurs soit plus élevée dans les mares qu'à la surface de l'eau et à la base de la glace. La production primaire et la biomasse chlorophyllienne furent mesurées par la méthode d'assimilation du ^{14}C et par fluorométrie, respectivement. La composition taxonomique de la communauté fut évaluée en microscopie inversée et la structure de taille de la communauté par cytométrie en flux. Finalement, les stratégies de photoprotection furent identifiées grâce à la signature pigmentaire et au spectre d'absorption particulaire de la communauté. Les 10 mares de fonte échantillonnées durant cette étude se sont avérées des environnements oligotrophes, ayant des valeurs de production primaire et de biomasse chlorophyllienne faibles. La composition taxonomique des mares de fonte variait d'une station à l'autre, et plusieurs facteurs environnementaux (éclairement incident, la profondeur de la mare, la salinité et la concentration en phosphate) exerçaient une influence significative sur cette composition. Les nanoalgues (2–20 µm) dominaient la communauté en termes d'abondance. Les algues présentes dans les mares de fonte possédaient une plus grande proportion de caroténoïdes photoprotecteurs que les eaux de surface et à la base de la glace de l'Arctique canadien. De plus, deux composés absorbant dans l'UV (vraisemblablement des acides aminés de type mycosporines) étaient présents dans les mares de fonte. La présence de ces stratégies de protoprotection pourrait expliquer en partie la bonne condition physiologique des algues présentes dans les mares de fonte en dépit des fortes intensités lumineuses. La flore des mares de fonte est donc bien adaptée aux conditions de cet environnement particulier.

Mots clés : mares de fonte, algues, production, communauté, pigments, photoprotection, Haut-Arctique canadien

ABSTRACT

Melt ponds are ephemeral environments located at sea ice surface. Only a few studies have examined the biological characteristics of melt ponds. The main objective of this study is to characterize melt pond algal community during early summer in the Canadian High Arctic. More precisely, we determined the production, biomass and taxonomic composition of the melt pond algal community and its photoprotection strategy, as well as environmental factors influencing this community during the summer of 2014. We expected that production, biomass and taxonomic diversity of melt ponds would be low and mainly limited by salinity and nutrient availability. Moreover, the proportion of photoprotective pigments should be higher in melt ponds, compared to surface water and bottom ice. Primary production and chlorophyll *a* biomass were estimated by the ^{14}C-assimilation method and by fluorometry, respectively. Community taxonomic composition and size structure were assessed by inverted microscopy and flow cytometry, respectively. Photoprotective strategies were detected from pigment signature and particle absorption spectra of the community. The 10 melt ponds sampled during this study were oligotrophic environments, with low primary production and biomass values. The taxonomic composition of melt ponds varied between stations and was influenced by many environmental factors (incident irradiance, melt pond depth, salinity and phosphate concentration). Nanoalgae (2–20 µm) dominated the algal community. Melt pond algae had a higher proportion of photoprotective carotenoids than surface water and bottom ice algae of the Canadian Arctic. Moreover, two UV-absorbing compounds (likely mycosporine-like amino acids) were found in melt ponds. Those photoprotective strategies could partially explain the good physiological condition of melt pond algae despite the high irradiance. Melt pond flora is then well adapted to this particular environment.

Keywords: Melt ponds, Algae, Production, Community, Pigments, Photoprotection, Canadian High Arctic

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CHAPITRE 1 Caractérisation des communautés des mares de fonte de l'Arctique canadien et de leurs stratégies de photoprotection

INTRODUCTION GÉNÉRALE

La glace de mer est un des plus grands biomes sur Terre (Post et al. 2013, Arrigo 2014). En effet, elle représente une superficie de 16×10^6 km² en Arctique et de 22×10^6 km^2 en Antarctique (Dieckmann et Hellmer 2010, Arrigo 2014). De plus, la glace de mer offre plusieurs habitats différents aux organismes, des bactéries aux mammifères (Fig. 1) (Post et al. 2013, Arrigo 2014). Plusieurs mammifères dépendent de la glace de mer pour se nourrir, comme les ours polaires qui l'utilisent pour chasser leur proie préférentielle, le phoque (Stirling et al. 2012, Post et al. 2013). D'autres mammifères, comme les phoques, utilisent la glace comme lieu de reproduction (Tynan et al. 2010, Post et al. 2013). Finalement, ours polaires, phoques et morses utilisent la glace comme plate-forme pour se reposer (Tynan et al. 2010, Post et al. 2013). Les organismes se trouvant à la base de la chaîne trophique, les producteurs primaires, peuvent également bénéficier de différentes caractéristiques de la glace de mer, qui leur offre par exemple un substrat sur lequel ils peuvent croître et s'accumuler (Arrigo 2014). Les algues de glace, également appelées algues sympagiques, sont les algues unicellulaires qui vivent en association avec la glace de mer. En Arctique, on retrouve les algues de glace à l'interface neige-glace, à l'intérieur de la glace et à l'interface glace-eau (Horner 1985, Cota et al. 1991, Horner et al. 1992, Arrigo 2014). Ces algues sont non seulement importantes pour les organismes des niveaux trophiques supérieurs vivants dans la glace de mer, mais également pour les organismes pélagiques et benthiques (Arrigo 2014, Leu et al. 2015). Les algues de glace jouent donc un rôle important dans l'écosystème arctique.

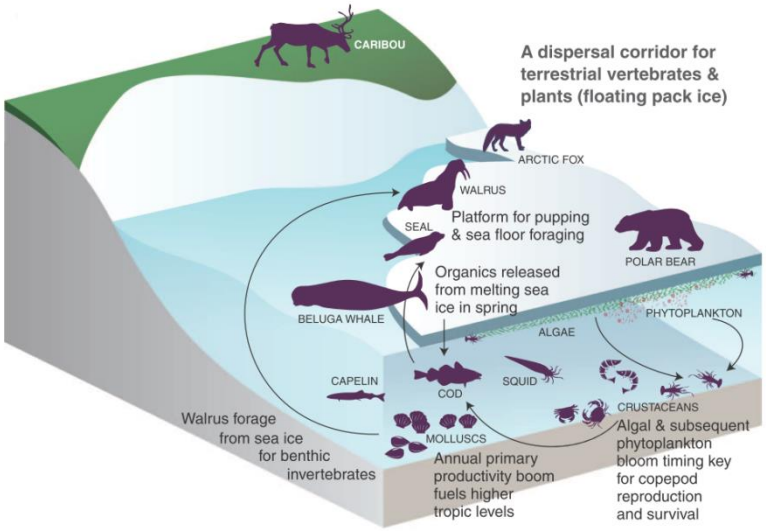

Fig. 1. Relations entre les différents organismes vivants en Arctique et la glace de mer (modifiée de Post et al. 2013)

LES ALGUES DE GLACE

Les trois principaux habitats associés à la glace sont illustrés à la Figure 2. Des communautés algales sont associées à chacun de ces habitats. L'interface neige-glace regroupe deux communautés, celle d'infiltration, et celle des mares de fonte (Cota et al. 1991, Arrigo 2014). La communauté d'infiltration se forme lorsque la neige atteint un poids suffisant pour faire renfoncer la glace sous le franc-bord, permettant l'infiltration de l'eau de mer entre la neige et la glace (Meguro 1962, Horner 1985, Ackley et Sullivan 1994, Fritsen et al. 1998). Elle est principalement retrouvée en Antarctique et peu fréquente en Arctique (Horner 1985, Buck et al. 1998). La communauté de mares de fonte est décrite en détail dans la section intitulée « Mare de fonte » de ce chapitre.

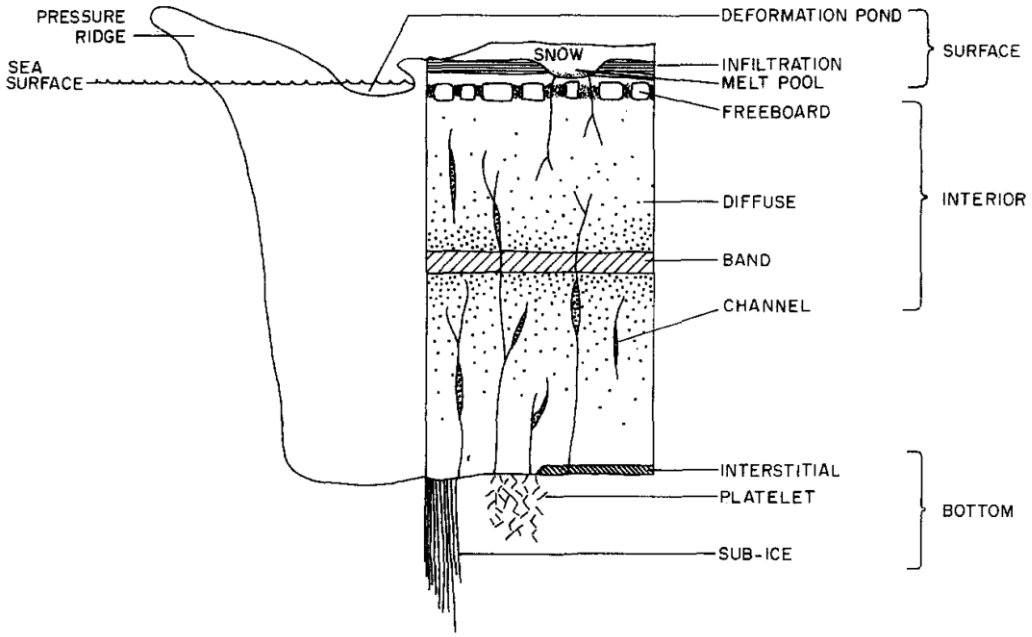

Fig. 2. Représentation schématique des différents habitats retrouvés dans la glace de mer (modifiée d'Horner et al. 1992)

Les canaux de saumures à l'intérieur de la glace abritent les micro-organismes de la communauté intérieure de la glace (Horner 1985, Cota et al. 1991, Horner et al. 1992, Arrigo 2014). La matrice de glace est résistante à l'incorporation des ions du sel de mer, ce qui mène à la formation de canaux de saumure dans la glace (Petrich et Eicken 2010). Cette saumure est majoritairement retournée dans l'océan par drainage, mais elle peut aussi rester dans des inclusions de la matrice solide de glace (Petrich et Eicken 2010). La croissance algale dans cet habitat est restreinte pendant l'hiver en raison de la forte salinité et la faible température de l'eau dans les canaux (Horner 1985, Arrigo et Sullivan 1992, Mundy et al. 2011). Toutefois, elle augmente au printemps, lorsque la salinité des canaux de saumure diminue, que leur volume augmente, et que les échanges d'éléments nutritifs soient possibles à l'intérieur de la glace (Arrigo et Sullivan 1992, Garrison et al. 2003, Mundy et al. 2011). La communauté de franc-bord est aussi une communauté qui se trouve à l'intérieur de la glace (Horner et al. 1992). Elle est formée lorsque la saumure des canaux

est drainée vers la surface de la glace en raison d'une augmentation de la température à la surface (Horner et al. 1992). Les communautés de bande se trouvent également à l'intérieur de la glace (Horner et al. 1992, Arrigo 2014). Ces communautés sont formées lorsque la glace multi-annuelle se forme, emprisonnant les algues se trouvant à la base de la glace de l'année précédente entre cette dernière et la nouvelle couche de glace (Hoshiai 1977, Ackley et al. 1979).

Les communautés d'algues se trouvant à la base de la glace sont celles qui sont les plus étudiées et qui accumulent, dans la glace, les plus fortes biomasses (Leu et al. 2015). Quatre différentes communautés sont présentes à la base de la glace, la communauté interstitielle et trois communautés sous-glaces (Cota et al. 1991). La communauté interstitielle se développe dans les derniers centimètres de l'horizon inférieur de la glace (Gosselin et al. 1986, 1997, Arrigo 2014). Cette communauté forme des blooms, principalement composés de diatomées pennales, au printemps, lorsqu'une quantité de lumière suffisante pénètre à travers la glace. Il s'agit de la communauté sympagique la plus productive (Horner 1985, Gosselin et al. 1986, 1997, Arrigo 2014).

La première des trois communautés sous-glace est aussi dominée par les diatomées pennales qui tapissent l'interface glace-eau (Gosselin et al. 1990, 1997). La deuxième communauté sous-glace est celle formée par une diatomée centrale, *Melosira arctica*, qui forme de longues agrégations mucilagineuses à la base de la glace, pouvant atteindre plusieurs mètres de longueur (Melnikov et Bondarchuk 1987, Arrigo 2014). La troisième, la communauté plaquettaire (en anglais, « platelet ice community »), se trouve dans la couche de glace du même nom et presque exclusivement en Antarctique (Arrigo 2014). Ces cristaux de glace qui se forment en profondeur près des barrières de glace, remontent en surface et s'accumulent sous la glace de congélation (Arrigo et al. 1995).

La glace peut également former des habitats différents lors de sa fonte. En effet, une communauté halocline est présente dans la colonne d'eau et distincte des autres communautés phytoplanctoniques qui y sont présentes (Apollonio 1985). Cette communauté confinée à l'halocline créée par la fonte de la glace, à environ 2 m de

profondeur, peut persister dans le système jusqu'à deux mois durant, et ce avec une concentration en chlorophylle *a* relativement constante (Apollonio 1985). Cette communauté serait composée principalement de chlorophytes et de chrysophytes (Apollonio 1985), tout comme la communauté des mares sous la glace décrite par Gradinger (1996). Cependant, les espèces et la biomasse de cette dernière communauté diffèrent de celle de la communauté halocline, ce qui en fait une communauté distincte (Eicken 1994, Gradinger 1996). La communauté des mares sous la glace fut également décrite par Mundy et al. (2011) dans la baie de Darnley pendant la période de fonte printanière.

LES MARES DE FONTE

Les mares de fonte sont des étangs composés d'eau de fonte situés à la surface de la glace de mer (Taylor et Feltham 2004, Polashenski et al. 2012, Rosel et Kaleschke 2012). L'eau composant ces mares provient principalement de la fonte de la neige, accumulée sur la glace durant la saison hivernale, mais également de la fonte de la partie supérieure de la glace de mer au printemps et à l'été (Taylor et Feltham 2004, Polashenski et al. 2012, Rosel et Kaleschke 2012). Les mares de fonte peuvent se former sur la glace de première année, comme sur la glace multi-annuelle (Polashenski et al. 2012). En raison des faibles reliefs topographiques de la glace de mer de première année, les mares de fonte sont plus étendues sur la glace de première année, mais elles y sont moins profondes que sur la glace multi-annuelle (Fetterer et Untersteiner 1998, Polashenski et al. 2012). Les mares de fonte peuvent couvrir jusqu'à 80–90 % de la glace de première année (Lüthje et al. 2006, Rosel et Kaleschke 2012).

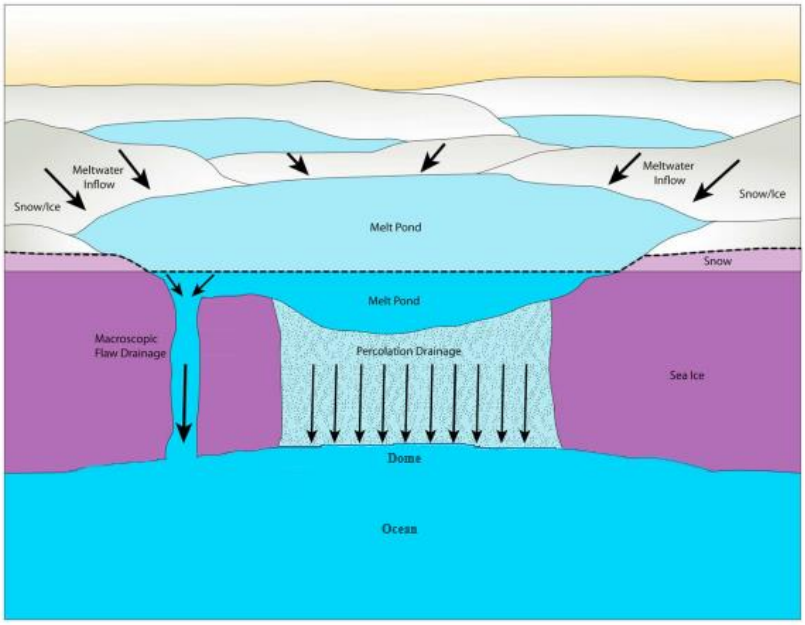

Figure 2. Idealized illustration of a melt pond, showing meltwater flux pathways.

Fig. 3. Représentation schématique des pertes et des gains d'eau des mares de fonte (modifiée de Polashenski et al. 2012).

FORMATION ET ÉVOLUTION DES MARES DE FONTE DURANT LA SAISON ESTIVALE

Les mares de fonte sont des environnements éphémères dans lesquels l'eau de fonte s'accumule, mais desquels elle s'écoule aussi, vers la colonne d'eau (Polashenski et al. 2012). La quantité d'eau s'accumulant dans la mare dépend du taux de fonte, des précipitations et de la grandeur du bassin versant de la mare (Polashenski et al. 2012). La quantité d'eau qui s'écoule de la mare vers la colonne d'eau dépend, quant à elle, de la charge hydraulique et de la présence de chemins permettant l'écoulement (Polashenski et al. 2012). L'écoulement peut se faire par percolation verticale, par des ouvertures de taille variable présentes dans la glace, allant de simples fissures, aux canaux de saumure ou encore aux trous percés par les phoques (Fig. 3), mais également horizontaux à travers la glace (Polashenski et al. 2012).

Quatre stades caractérisent l'évolution des mares de fonte durant la saison estivale (Fig. 4) (Eicken et al. 2002, Polashenski et al. 2012). Le premier stade est caractérisé par l'accumulation rapide d'eau de fonte pour former la mare (Eicken et al. 2002, Polashenski et al. 2012). À ce stade, la couverture des mares de fonte augmente rapidement puisque la glace, très peu perméable pendant cette période, ne laisse que peu percoler l'eau (Eicken et al. 2002, Polashenski et al. 2012). Les mares de fonte se trouvent alors bien au-dessus du niveau de la mer (Polashenski et al. 2012). La topographie de la glace, alors principalement façonnée par des processus survenus avant le début de la fonte (par exemple les déformations et la dérive de la neige), détermine les emplacements où s'accumulera l'eau (Fetterer et Untersteiner 1998, Eicken et al. 2002, Polashenski et al. 2012). Durant le deuxième stade, l'eau de fonte commence à percoler à travers la glace et s'école de plus en plus latéralement (Eicken et al. 2002, Scharien et Yackel 2005, Polashenski et al. 2012). L'augmentation de l'écoulement entraîne également la diminution de l'élévation des mares de fonte par rapport au niveau de la mer (Eicken et al. 2002, Polashenski et al. 2012). Ainsi, la couverture des mares de fonte diminue au cours de ce stade (Eicken et al. 2002, Polashenski et al. 2012).

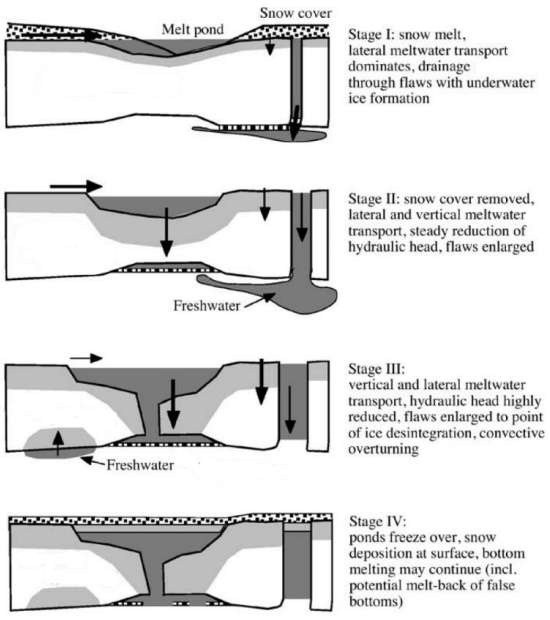

Fig. 4. Évolution temporelle des mares de fonte (modifiée d'Eicken et al. 2002)

Le troisième stade est caractérisé par l'augmentation régulière de la couverture des mares (Eicken et al. 2002, Polashenski et al. 2012). En effet, même si la glace est plus perméable, l'eau de fonte s'accumule à la hauteur du niveau de la mer, ce qui permet aux mares d'atteindre leur taille maximale saisonnière (Polashenski et al. 2012). Cependant, seule une légère pression hydraulique permet l'écoulement de l'eau vers l'océan (Eicken et al. 2002, Polashenski et al. 2012). Ainsi, certaines mares se vident complètement dans l'océan à ce stade, ce qui peut entraîner la désintégration de la glace (Polashenski et al. 2012). Finalement, le quatrième stade se manifeste par le regel des mares, ce qui peut se produire à tout moment durant la saison (Eicken et al. 2002, Polashenski et al. 2012). Ce regel est contrôlé par des forçages atmosphériques et peut arrêter momentanément les afflux et les écoulements d'eau.

Deux types de mares de fonte sont présents en Arctique : les mares fermées et les mares ouvertes (Fig. 4, stades I et II; Lee et al. 2011, 2012). Les mares fermées sont d'une couleur bleu pâle et ont une salinité faible, comparable à des environnements d'eau douce à saumâtre (Gradinger 2002, Lee et al. 2011). Les mares de fonte ouvertes sont quant à elles connectées à l'océan sous la glace, ce qui leur confère une salinité plus élevée, comparable à celle des eaux sous-jacentes, et une couleur bleu foncé (Gradinger 2002, Lee et al. 2011). La composition de la communauté algale pourrait également varier selon les types de mares de fonte (Gradinger 2002).

L'ALBÉDO ET LA LUMIÈRE

Puisque l'albédo de l'eau est plus faible que celui de la glace et de la neige (Sankelo et al. 2010), la formation de mares de fonte contribue au réchauffement de la glace et favorise la libération, dans la colonne d'eau, des algues à la base de la glace (Galindo et al. 2014). Ainsi, la formation de mares de fonte à la surface de la glace de mer permet d'augmenter la transmission de la lumière à travers la glace (Perovich et al. 2002, 2003, Grenfell et Perovich 2004, Sankelo et al. 2010, Ehn et al. 2011, Polashenski et al. 2012). Cette boucle de rétroaction positive de l'albédo de la glace de mer entraîne une

augmentation de l'énergie absorbée par le système, entraînant une diminution de l'étendue et de l'épaisseur de glace de mer, ce qui amplifie l'absorption de l'énergie (Curry et al. 1995).

Les mares sont des environnements aquatiques recevant de fortes doses de lumière, principalement en raison de leur faible profondeur (Rautio et al. 2011). Un excès de lumière, tant du rayonnement photosynthétiquement actif (RPA, 400-700 nm) que du rayonnement ultraviolet (UV, 280-400 nm), peut engendrer des effets néfastes chez les algues, comme la production de dérivés réactifs de l'oxygène (DRO, en anglais « reactive oxygen species », ROS) et la photoinhibition (Vincent et Roy 1993, Brunet et al. 2011). Les algues ont cependant développé des stratégies leur permettant d'éviter ces phénomènes (Vincent et Roy 1993, Serôdio et al. 2006, Goss et Jakob 2010, Rastogi et al. 2010, Brunet et al. 2011). Parmi ces stratégies certaines sont comportementales, comme les migrations, qui peuvent prendre place dans la colonne d'eau ou dans les sédiments (Vincent et Roy 1993, Serôdio et al. 2006), alors que d'autres sont physiologiques, comme le cycle des xanthophylles ainsi que l'accumulation d'acides aminés de type mycosporine (MAAs) et/ou de caroténoïdes photoprotecteurs (Vincent et Roy 1993, Rastogi et al. 2010, Brunet et al. 2011).

Le cycle des xanthophylles est un mécanisme de photoprotection à court terme (minutes à heures) qui implique la dé-époxidation de caroténoïdes afin de dissiper l'excès d'énergie captée par les algues lors d'une exposition à de forts rayons lumineux (Sakshaug et al. 1997, Dubinsky et Stambler 2009, Brunet et al. 2011). Un premier cycle implique la violaxanthine, l'anthéraxanthine et la zéaxanthine et est, entre autres, présent chez les chlorophytes et les chrysophytes (Goss et Jakob 2010, Brunet et al. 2011). Le deuxième cycle des xanthophylles est celui de la diadinoxanthine et la diatoxanthine, présents chez plusieurs groupes algaux, dont les bacillariophycées, les haptophytes et les dinophytes (Goss et Jakob 2010, Brunet et al. 2011). Les pigments dé-époxidés peuvent revenir sous leur forme oxydée lors d'exposition à de moins grandes intensités lumineuses (Brunet et al. 2011).

Les caroténoïdes photoprotecteurs (PPC) sont des pigments non-photosynthétiquement actifs, c'est-à-dire des pigments ne transférant pas l'énergie captée de la lumière du soleil vers le centre réactionnel du photosystème II (Brunet et al. 2011). Les pigments impliqués dans le cycle des xanthophylles, mentionnés ci-dessus ainsi que la lutéine et la β,β-carotène, composent les PPC. Ces pigments sont présents dans une proportion plus importante dans les cellules exposées à de fortes intensités lumineuses (Brunet et al. 2011).

Les MAAs jouent plusieurs rôles au sein de la cellule, dont ceux de protection contre les photodommages causés par les rayons UV, d'antioxydant, et d'osmorégulation (Carreto et al. 2011). Ces composés possèdent donc des absorptions maximales dans les longueurs d'onde des rayons UV, plus précisément entre 309 et 362 nm (Carreto et al. 2005, Carreto et Carignan 2011, Gao et Garcia-Pichel 2011). Des MAAs ont récemment été détectées dans plusieurs environnements associés à la glace de mer, dont les mares de fonte, dans lesquelles deux MAAs ont été mesurés, soit la shinorine et un autre MAA inconnu (Elliott et al. 2015).

LES CHANGEMENTS CLIMATIQUES

L'océan Arctique est en mutation. En effet, les changements globaux, qui opèrent partout dans le monde, ont des conséquences particulièrement importantes dans cette région du globe (Duarte et al. 2012, Jeffries et al. 2013). Depuis les années 1980, près de 14 % de l'étendue de glace et 28 % du volume de glace au minimum annuel de septembre ont été perdus par décennie en Arctique (Overland et Wang 2013). Le couvert de glace à son minimum, le 11 septembre 2015, était de $4{,}41 \times 10^6$ km² en Arctique (Vizcarra 2015). En raison du réchauffement, l'Arctique pourrait être libre de glace à l'été dès 2037 (Wang et Overland 2009). De plus, la glace de première année, plus mince, continuera à prendre une place grandissante par rapport à la glace multi-annuelle (Arrigo et al. 2008, Nicolaus et al. 2012, Post et al. 2013).

Les mares de fonte seront affectées par les changements climatiques puisqu'elles sont liées à la dynamique de la glace et de la neige sur la glace. Elles couvriront une plus grande surface de la glace de mer, mais avec la diminution de celle-ci, l'aire de recouvrement total des mares de fonte diminuera (Rösel et Kaleschke 2012). Les mares de fonte seront donc moins présentes, mais en plus grande proportion par rapport à la glace. Les mares de fonte ne seront pas seulement affectées par les changements climatiques, elles contribueront également à la modification du climat (Sudakov et al. 2015). Comme expliqué ci-haut, elles influencent l'albédo de la glace de mer, absorbant une plus grande quantité d'énergie et amplifiant la fonte de la glace de mer (Maslanik et al. 2007, Perovich et al. 2007, Nicolaus et al. 2010). Cependant, elles influencent également l'océan sous-jacent, modifiant son budget de sel et de chaleur (Eicken et al. 2002) ainsi que la dynamique de l'écologie estivale de l'Arctique (Gradinger 1996, Ferguson et al. 2000).

Les études traitant de la biologie des mares de glace sont peu nombreuses (par ex., von Quillfeldt et al. 1997, Melnikov et al. 2002, Gradinger et al. 2005, Elliott et al. 2015, Fernandez-Mendez et al. 2015) par rapport à celles s'intéressant à la physique de ces milieux éphémères. À notre connaissance, seulement trois études incluaient des mesures de production primaire dans les mares de fonte en Arctique (Lee et al. 2011, 2015, Fernandez-Mendez et al. 2015). Un peu plus d'études ont porté sur la composition taxonomique des algues dans les mares de fonte (von Quillfeldt et al. 1997, Melnikov et al. 2002, Gradinger et al. 2005, Mundy et al. 2011, Elliott et al. 2015, Lee et al. 2015). Cependant, ces études ne traitent pas ou peu des relations entre les facteurs abiotiques et la composition des communautés. Ainsi, on connaît peu les facteurs qui influencent la composition taxonomique de ces communautés. Une seule étude s'est intéressée aux stratégies de photoprotection des algues dans les mares de fonte, se concentrant exclusivement sur les acides aminés de type mycosporine (MAAs) (Elliott et al. 2015). Cette étude est la première à examiner les pigments photoprotecteurs chez ces communautés fortement exposées aux rayons UV.

OBJECTIFS ET HYPOTHÈSE

L'objectif principal de cette étude est de caractériser les communautés des algues et des bactéries photosynthétiques (cyanobactéries), qui se développent dans les mares de fonte au début de l'été dans l'archipel arctique canadien et la mer de Beaufort. Les objectifs spécifiques de cette étude sont : (1) de déterminer la production, la biomasse chlorophyllienne et la composition taxonomique des algues des mares de fonte ainsi que (2) d'identifier les conditions environnementales influençant cette communauté et (3) de déterminer si des adaptations pigmentaires sont présentes chez ces communautés exposées à de forts rayonnements solaires.

Les hypothèses de travail testées lors de cette étude sont (1) la production primaire, la biomasse chlorophyllienne et la diversité taxonomique dans les mares de fonte sont faibles, principalement limitées par la disponibilité des éléments nutritifs et la faible salinité et (2) les algues dans les mares de fonte présentent une quantité plus élevée de pigments photoprotecteurs que celles présentes dans la colonne d'eau en raison de leurs fortes expositions aux UV.

CHAPITRE 1
CARACTÉRISATION DES COMMUNAUTÉS DES MARES DE FONTE DE L'ARCTIQUE CANADIEN ET DE LEURS STRATÉGIES DE PHOTOPROTECTION

1.1 RÉSUMÉ EN FRANÇAIS

Seulement quelques études ont examiné les caractéristiques biologiques des mares de fonte en Arctique, un habitat éphémère situé à la surface de la glace de mer. Nous avons évalué la production, la biomasse et la composition taxonomique de la communauté algale des mares de fonte et leurs stratégies de photoprotection dans le Haut-Arctique canadien au cours l'été 2014. Les mares de fonte recouvraient de 25 à 80 % de la surface de la glace de mer lors de l'échantillonnage et n'étaient pas connectées directement à la colonne d'eau sous-jacente, comme l'indique leur faible salinité (0,2-8,5 psu). Les mares étaient oligotrophes, en ce qui concerne la concentration en éléments nutritifs (<0,01 à 0,12 µM de phosphate et 0,08 à 0,23 µM de nitrate plus nitrite), la biomasse chlorophyllienne (0,04 à 0,44 µg l^{-1}) et la production primaire (0,3 à 24 µg C l^{-1} j^{-1}). L'abondance totale des algues variait de 0,1 à 2 x 10^6 cellules l^{-1} et était dominée par les nanoeucaryotes (2-20 µm) (48 à 74 %). Les flagellés non identifiés étaient le groupe algal >2 µm dominant (46 à 87 %). Le deuxième groupe de flagellés le plus abondant était (1) les chlorophytes dans la mer de Beaufort et les prymnésiophytes dans le détroit de Barrow, associées avec de faibles salinités et concentrations en phosphate, (2) les chrysophytes dans le passage de Resolute et le détroit de Barrow, associées à des mares peu profondes et (3) les prasinophytes dans le Navy Board Inlet, associées avec des faibles éclairements incidents et concentrations en nitrate plus nitrite. Des ratios production : biomasse relativement élevés (18 à 61 µg C µg chl *a*$^{-1}$ j^{-1}) et de faibles proportions de pigments de dégradation (<5 % de la chlorophylle *a* totale) suggèrent que les communautés étaient en bonne condition

physiologique. Les stratégies de photoprotection des algues des mares de fonte implique la production de caroténoïdes photoprotecteurs (PPC) et de deux composés absorbant dans l'UV (vraisemblablement des acides aminés de type mycosporine (MAAs), la shinorine et un inconnu appelé U2). Les algues des mares de fonte possèdent des mécanismes de photoprotection efficaces pour prévenir les dommages causés par les rayons du soleil, mécanisme leur permettant de maintenir un taux de croissance élevé bien que la biomasse totale soit limitée par la disponibilité des éléments nutritifs.

J'ai corédigé cet article scientifique, portant le titre de « Spatial variability and photoprotection strategy of melt pond algae in the Canadian Arctic », avec les professeurs Michel Gosselin et Maurice Levasseur, ainsi que ma collègue Marjolaine Blais. Il sera soumis dans les prochaines semaines à la revue Marine Ecology Progress Series. Ma contribution, en tant que premier auteur de cet article a constitué en l'échantillonnage, les analyses en laboratoire, l'analyse et l'interprétation des données et la rédaction de l'article. Les professeurs Gosselin et Levasseur, second et troisième auteurs respectivement, ont révisé l'article, en plus d'assister lors de l'échantillonnage. Le professeur Gosselin a également aidé à l'interprétation des données. Marjolaine Blais, quatrième auteure, a collaboré, entre autres, aux analyses en cytométrie en flux et de carbone particulaire total ainsi qu'à la révision de l'article. Les résultats de cette étude furent présentés, entre autres, à l'Ocean Science Meeting à La Nouvelle-Orléans, en février 2016.

1.2 CARACTÉRISATION DES COMMUNAUTÉS DES MARES DE FONTE DE L'ARCTIQUE CANADIEN ET DE LEURS STRATÉGIES DE PHOTOPROTECTION

1.3 ABSTRACT

Only a few studies have examined the biological characteristics of melt ponds in the Arctic, an ephemeral habitat located at the surface of sea ice. We assessed the production, biomass and taxonomic composition of the melt pond algal community and its photoprotection strategy in the Canadian High Arctic during summer 2014. Melt ponds covered 25–80 % of the sea-ice surface during our sampling period and were not directly connected to the overlying water column, as indicated by their low salinity (0.2–8.5 psu). All melt ponds sampled were oligotrophic, i.e. characterized by low nutrient concentrations (<0.01–0.12 µM for phosphate and 0.08–0.23 µM for nitrate plus nitrite), low chlorophyll *a* (chl *a*) biomass (0.04–0.44 µg l^{-1}) and low primary production (0.3–24 µg C l^{-1} d^{-1}). Total abundance of algal cells ranged from ca. 0.1 to ca. 2 x 10^6 cells l^{-1}. Nanoeukaryotes (2–20 µm) dominated the community, making up 48–74 % of the total algal abundance. Unidentified flagellates were the dominant algal group >2 µm, accounting for 46–87 % of the total cell abundance. The second most abundant flagellate groups were (1) chlorophytes in Beaufort Sea and prymnesiophytes in Barrow Strait, associated with lower salinity and depleted phosphate, (2) chrysophytes in Resolute Passage and Barrow Strait, associated with shallow melt ponds, and (3) prasinophytes in Navy Board Inlet associated with lower incident irradiance and depleted nitrate plus nitrite. Relatively high primary production:biomass ratios (18–61 µg C µg chl a^{-1} d^{-1}) and low proportion of degradation pigments (<5 % of total chl *a*) suggest that the autotrophic community was in good physiological conditions. The photoprotection strategy of melt pond algae implies the production of photoprotective carotenoids (PPC), among which one-third was diatoxanthin and diadinoxanthin, and of two UV-absorbing compounds (likely mycosporine-like amino acids (MAAs), shinorine and one unknown, named U2). Hence, melt pond algae have efficient photoprotective mechanisms to prevent damage caused by sunlight, allowing them

to maintain a high productivity in an environment where nutrient availability limits their biomass.

1.4 INTRODUCTION

Sea ice, one of the biggest biomes in the world, plays a key role in polar regions for many organisms, from bacteria to mammals (Post et al. 2013, Arrigo 2014). Sea ice-associated algae represent an important early-season source of food for the microbial and herbivorous food webs in the sea ice, the water column and the benthos (Leu et al. 2015). At the ice surface, two types of ice algal communities can be observed: an infiltration community and a pool community (Cota et al. 1991, Horner et al. 1992). The infiltration community, which is more common in Antarctica, occurs primarily on pack ice with heavy snow cover, which has been flooded with seawater at the snow-ice interface (Ackley & Sullivan 1994, Fritsen et al. 1998), whereas surface pool community forms in melt ponds, tidal cracks and leads (Cota et al. 1991). During the melt period, the ponded sea ice is colonized by unicellular algae, such as flagellates and diatoms (Horner et al. 1992).

Melt ponds are ephemeral environments formed of snow and sea ice melted water (Taylor & Feltham 2004, Polashenski et al. 2012, Rösel & Kaleschke 2012). They can cover up to 75% or the ice pack in spring and summer in the Arctic (Scharien & Yackel 2005). Melt ponds are usually fresh or brackish environments (Gradinger 2002, Lee et al. 2011), but could also be saltier, with salinity slightly lower than the surrounding ocean (Lee et al. 2012, 2015). The low salinity of the melt ponds may expose to an osmotic stress algae acclimated to high salinity brines and to saline ocean. Melt pond algae are also submitted to light stress. Indeed, high irradiances were measured at the surface of those shallow environments (Mundy et al. 2011). Moreover, light attenuation by dissolved organic carbon (DOC) and the related compound, chromophoric dissolved organic matter (CDOM), may be lower in the melt ponds than in the underlying waters during the melt period (Logvinova et al. 2016). Under these high light conditions, several mechanisms may help algae to protect their photosystems against photo-damage or photo-inhibition, such as the

production of mycosporine-like amino acid (MAAs) or photoprotective carotenoids (PPC) (Brunet et al. 2011, Carreto et al. 2011). These physiological strategies were identified in bottom ice algae during the melt period (Alou-Font et al. 2013, Elliott et al. 2015) and they were likely used to protect cells from reactive oxygen species such as $^1O_2$ (Suh et al. 2003, Brunet et al. 2011). Algae thriving in melt ponds are known to produce MAAs for protection against UV radiation (Elliott et al. 2005). However, to our knowledge, there is no published data on the pigment signature of melt pond algae and their PPC concentration.

The rapid warming of the Arctic should result in an increase in the melt ponds coverage in the future. First, the melt season will be prolonged (Rösel & Kaleschke 2012) given more time for their development. Second, the decrease of ice volume and the increase of first-year sea ice proportion, will favor their presence. Until now, only a few studies have focused their attention on melt pond ecosystems in the Arctic (e.g. Lee et al. 2011, 2012, 2015, Mundy et al. 2011). These studies showed that melt pond community composition is variable, with diatoms sometimes present. These algae also show a high photosynthetic capacity (Fernandez-Mendez et al. 2015). It is thus imperative to acquire new knowledge on the structure and functioning of the melt pond communities and to understand their linkages with their environment in order to better assess their survival strategies in this high light-low salinity environment.

The main objective of this study was to characterize melt pond algal community, including prokaryotic cyanobacteria, during early summer in the Canadian High Arctic. More specifically, we (1) determine the primary production, chlorophyll *a* (chl *a*) biomass and taxonomic composition of the algae in ten melt ponds located in the eastern and western Canadian Arctic, (2) identify environmental conditions influencing the algal community composition and (3) assess the photoadaptative strategies of these algae which are exposed to high irradiance.

1.5 MATERIALS AND METHODS

1.5.1 Sampling

The sampling of surface melt ponds was conducted at four landfast first-year sea ice stations (named Ice 1 to Ice 4 in Fig. 1) located in Navy Board Inlet, Barrow Strait and Resolute Passage (18–23 July 2014) and one multi-year pack ice station (named Ice 5 in Fig. 1) in Beaufort Sea (29 August 2014), during the ArcticNet-NETCARE joint expedition on board the CCGS Amundsen (Fig. 1). At each station, melt pond coverage was estimated from shipboard visual observations, using the standard procedure described by Environment Canada (2005). The white ice thickness was measured with an ice thickness gauge (Kovacs Enterprise). Downwelling incident photosynthetically active radiation (PAR, 400–700 nm) was measured at 1 min intervals with a LI-COR cosine sensor located at ca. 14 m from the water surface on a tower at the bow of the ship, which was next to the melt pond during sampling. PAR values were integrated over a 24-h period before sampling.

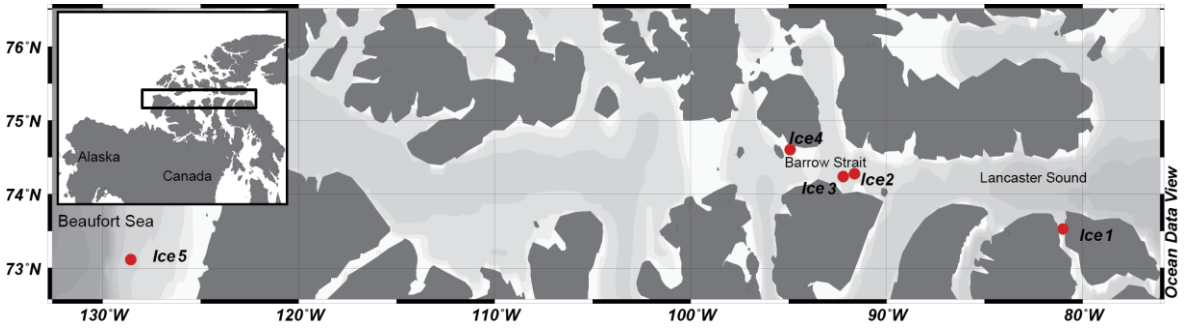

Fig. 1. Location of the sampling stations in the Canadian High Arctic during summer 2014

One to three melt ponds were sampled at each station within an area of ca. 0.01 km^2. For each melt pond, water depth was measured. Water temperature and salinity were measured with a handheld conductivity meter (Cond 330i, WTW). In each melt pond, 20 l of water was collected at 5 cm-depth with a battery-operated submersible pump (Rule IL200 In-Line Submersible Pump, 2.8 gpm, 12 V) for chemical and biological analyses.

At three stations (i.e. Ice 1, 3 and 4), water was collected at a depth of 0.5 m under the ice, with the same pump as the one used for the sampling of the melt ponds. Ice cores were also collected at these stations with a Mark II ice corer (9 cm internal diameter, Kovacs Enterprise). The bottom three centimeters were collected from three different ice cores and melted together in an isothermal container, with 0.2 µm filtered sea-water to minimize osmotic stress on the bottom ice algal community (Garrison & Buck 1986). These samples were analyzed for taxonomic composition.

Along the cruise, surface seawater was collected with a CTD-rosette (Sea-Bird Electronics SBE 911+) equipped with 24 12 l Niskin-type bottles (OceanTest Equipment). Subsamples for primary production, chl *a* as well as algal and bacterial abundances were transferred into acid-washed Nalgene bottles.

1.5.2 Laboratory analysis

Nutrients

Triplicate samples for dissolved inorganic nutrients were filtered through pre-rinsed 25 mm Whatman GF/F glass-fiber filters (nominal pore size of 0.7 µm), and the filtrate was collected in 15 ml acid-washed polyethylene tubes. Nutrient samples were rapidly analyzed on board the ship for nitrate plus nitrite (NO_3+NO_2), phosphate (PO_4) and silicic acid ($Si(OH)_4$) concentrations using a Bran-Luebbe 3 autoanalyzer (method adapted from Grasshoff et al. 1999). A simple linear correction for the effect of varying salinity was applied for phosphate and silicic acid concentrations, as recommended by Grasshoff et al. (1999).

Dissolved organic carbon and nitrogen

Duplicate subsamples were filtrated through pre-combusted (450°C for 5 h) 25 mm Whatman GF/F filters and the filtrates were collected in 9 ml Kimble Brand vials with Teflon-lined caps previously cleaned following the protocol of Burdige & Homstead (1994). Samples were then acidified with 100 µl of 2 N HCl and kept in the dark at 4°C

until analyzed by a Shimadzu TOC-VCPN analyzer coupled with a total nitrogen measuring unit (TNM-1), following the precautions given in Benner & Strom (1993). Potassium hydrogen phthalate and potassium nitrate were used to standardize dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) measurements. In addition, samples were systematically checked against low-carbon (1 µM) and low-nitrogen (0 µM) water and Florida Strait at 700 m reference water (ca. 44 µM C and 32 µM N) every seventh sample analysis. These seawater reference standards were produced by the Hansell's certified reference materials (CRM) program (http://yyy.rsmas.miami.edu/groups/biogeochem/CRM.html). The coefficient of variation for three replicate injections was typically <3 % for DOC and <10 % for TDN. Dissolved organic nitrogen (DON) was estimated as follows:

$$DON = TDN - (NO_3 + NO_2) \qquad \text{(Eq. 1).}$$

Total particulate carbon

For total particulate carbon (TPC) measurements, a 1000 ml subsample was filtered through pre-combusted 21 mm Whatman GF/F filter and then dried at 60°C for 24 h (Knap et al. 1996). The analysis was performed using a COSTECH 4010 elemental analyzer (Costech Analytical).

Primary production

Primary production was estimated by the ^{14}C-assimilation method (Knap et al. 1996, Ferland et al. 2011). Two light and one dark 500 ml Nalgene polycarbonate bottles were filled with melt pond water and then inoculated with 10 µCi of $NaH^{14}CO_3$. The dark bottle contained 250 µl of 0.02 M 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU; Legendre et al. 1983). Bottles were incubated for 24 h, generally starting in the morning (Mingelbier et al. 1994), in a Plexiglas deck incubator under simulated *in situ* conditions with running surface seawater. At the end of the incubation period, 250 ml were filtered onto Whatman GF/F filters and the remaining subsamples were filtered onto 5 µm Nuclepore polycarbonate membrane filters. The filters were then acidified with 100 µl of 0.5 N HCl

and left to evaporate for 6 to 12 h under a fume hood to remove inorganic ^{14}C (Lean & Burnison 1979). Subsequently, 10 ml of Ecolume scintillation cocktail was added to each vial. The activity of each sample was determined using a Packard Tri-Carb 2900 TR liquid scintillation counter. Production rates of particulate organic carbon were calculated according to Parsons et al. (1984), where the total dissolved inorganic carbon (TDIC) concentration (in mg C m^{-3}) at the beginning of the incubation was estimated from the salinity (S) following this equation (Geilfus et al. 2015):

$$TDIC = 0.082 \times S + 0.094 \quad \text{(Eq. 2).}$$

Algal biomass

For size-fractionated chl *a* measurement, a 500 ml subsample was filtrated onto a 25 mm Whatman GF/F filter and another one onto a 5 µm Nuclepore polycarbonate membrane filter. Another subsample (1 l) was filtrated onto a 20 µm silk mesh. Concentrations of chl *a* (hereafter denoted as Chl a_F) were measured on board the ship using a Turner Designs 10-AU fluorometer after 18 to 24 h of pigment extraction in 10 ml of 90 % acetone at 4 °C in the dark (acidification method of Parsons et al. 1984).

Pigments

For pigment signature analysis, a 4 l subsample was filtrated onto a 47 mm Whatman GF/F filter, frozen in liquid nitrogen and kept at -80 °C until analysis. Pigment extraction was done in 95 % MeOH and sonicated (Heat Systems XL2010), before being centrifuged 5 min at 3700 × g. Filtration onto 0.2 µm polytetrafluoroethylene (PTFE) Gellman Acrodisc filters was done to eliminate filter residues. The liquid was then placed in amber glass vials, gently sparged with argon and stored in the dark at 4 °C before analysis. Fifty µl of apo-carotene (trans-b-Apo-80-carotenal; 1.98 mg L^{-1}; Sigma-Aldrich) was added as internal standard in each sample and in blanks.

The method used for pigment analysis by high-performance liquid chromatography (HPLC) was that of Zapata et al. (2000), with solution A (MeOH:acetonitrile: aqueous

pyridine, 50:25:25, v/v), solution B (MeOH:acetonitrile:acetone, 20:60:20, v/v), and solution C (acetonitrile) at a flow rate of 3 ml min^{-1}. The HPLC Agilent Technologies 1200 Series system used is equipped with a quaternary pump (model G1311A), a Waters Symmetry C8 column (150 × 4.6 mm, 3.5 µm), an Agilent diode-array absorbance detector (model G1315P; 400–700 nm) and an Agilent fluorescence detector (model G1321A). Fifty µl of extract were injected for each sample. Calibrations were done with standards coming from DHI Water and Environment (Denmark). Limits of detection and quantification were estimated with the equations described in Bidigare et al. (2005). Pigment identification was done by comparing their retention time and spectral properties with those of pigment standards (Egeland et al. 2011).

Light microscopy analysis

A 200 ml subsample for the identification and enumeration of eukaryotic cells >2 µm was preserved in acidic Lugol's solution (0.4 % final concentration; Parsons et al. 1984) and stored in the dark at 4°C until analysis. Cells were identified to the lowest possible taxonomic rank using an inverted microscope (Zeiss Axiovert 10) according to Lund et al. (1958). For each sample, a minimum of 400 cells (accuracy ± 10 %) and three transects of 20 mm were counted at magnifications of 400 x. The main taxonomic references used to identify the eukaryotic cells were Tomas (1997), Bérard-Therriault et al. (1999) and Throndsen et al. (2007). The total richness (number of taxonomic entities), the mean richness (average of each sample) and the diversity index (Shannon 1948) were calculated for three habitats (melt ponds, under-ice surface water and bottom ice). We excluded cysts and spores from these calculations.

Flow cytometry analysis

The abundance of picoalgae (<2 µm), nanoalgae (2–20 µm) and bacteria was determined by flow cytometry. Duplicate 5 ml subsamples were fixed with 20 µl of 25 % glutaraldehyde Grade I (0.1 % final concentration; Sigma-Aldrich G5882), stored in liquid nitrogen, and kept frozen at -80 °C until analysis by flow cytometry (Marie et al. 2005).

Cyanobacteria were identified by orange fluorescence from phycoerythrin (575 ± 20 nm), while photosynthetic eukaryotes were identified by red fluorescence of chlorophyll (675 ± 10 nm). In each subsample, microspheres (1 µm and 2 µm, Fluoresbrite plain YG, Polysciences) were added as an internal standard and were used to verify that there was no degradation of the side scatter signal despite the relatively high flow rate used (Tremblay et al. 2009). Heterotrophic bacteria samples were stained with SYBR Green I and measured at 525 nm to detect low and high nucleic acid content (Belzile et al. 2008). Analyses were performed on an Epics Altra flow cytometer (Beckman Coulter), fitted with a 488 nm laser (15 mW output; blue), using Expo32 v1.2b software (Beckman Coulter). The injected volume was quantified by weighing a subsample before and after processing. Archaea could not be discriminated from bacteria using this protocol; therefore, bacterial abundances include both archaea and bacteria. Cyanobacteria abundance was lower than the limit of detection of the instrument (i.e. ca. 10×10^3 cells l^{-1}). Average coefficients of variation of duplicate samples were 9 % and 7 % for heterotrophic bacteria and eukaryotic algae abundances, respectively.

Cell abundances of heterotrophic bacteria and picoeukaryotic algae were converted to carbon biomass using factors of 9.1 fg C $cell^{-1}$ (Buitenhuis et al. 2012a) and 2590 fg C $cell^{-1}$ (Buitenhuis et al. 2012b), respectively.

Particle absorption

For particulate absorption analysis, 4 l subsamples were filtrated onto 25 mm Whatman GF/F filters and analyzed on board the ship, with a spectrophotometer, following the protocol described in Tassan & Ferrari (2002). This method allowed us to determine total, algal and non-algal particule absorption coefficients.

Statistical analyses

One-way analyses of variance (ANOVAs) were performed to seek significant differences in the mean value of richness and diversity between habitats (i.e. melt ponds, under-ice surface water and bottom ice) and of diversity between fresh (0.2–1.3 psu) and

brackish (4.1–8.5 psu) melt ponds. The ANOVA was completed by a multiple comparison test of means (Tukey's Honestly Significant Difference (HSD) test for unequal sample sizes). Prior to ANOVAs, the homogeneity of variance and the normality of distribution of each variable were verified using the Levine and Shapiro-Wilk tests, respectively. These analyses were performed using R statistical software (R Core Team 2016).

Two non-metric multidimensional scaling (MDS) ordinations of Bray-Curtis similarity matrices coupled with group-average cluster analyses were performed to identify melt ponds with similar taxonomic and pigment composition (Legendre & Legendre 2012), using R statistical software (R Core Team 2016) and MASS package for R (Venables & Ripley 2002). Taxonomic groups or pigments present in two melt ponds or less were excluded from the analysis (i.e. euglenophytes, and chl c_3, chlide *a*, pras, hex-fuco, croco and phytin *a*, respectively; see Table 3 for pigment abbreviations) to reduce double zeros in the matrix. The abundance of taxonomic groups and concentration of pigments were standardized by the total abundance of algae and the total concentration of pigments, respectively. An analysis of similarities (one-way ANOSIM) was conducted on the Bray-Curtis similarity matrix to test for significant differences between groups of samples identified from the taxonomic and pigment composition (Clarke 1993).

A redundancy analysis (RDA) was performed using R statistical software (R Core Team 2016) and Vegan package (Oksanen et al. 2016) to evaluate interactions of taxonomic groups of algae with environmental variables (Legendre & Legendre 2012). The relative abundance was used to perform this analysis, but no other transformation was done on the data. Missing environmental data were replaced using the mean value (Legendre & Legendre 2012). The variance inflation factor (VIF) was used to determine collinear variables. Water temperature and silicic acid concentration were eliminated from the analysis to avoid multicollinearity problems (VIF > 10) (Quinn & Keough 2002). A permutation test (ANOVA, n = 999 permutations) was performed to determine the environmental variables explaining the variation of taxonomic groups.

1.6 RESULTS

1.6.1 Environmental conditions

At the sampling stations, the sea-ice coverage varied between 70 and 100 % and melt ponds covered 25–80 % of the total sea-ice area (Table 1). Melt ponds were very shallow with depths ranging from 0.07 m to 0.3 m and exposed to relatively high incident PAR (16.1–27.8 mol photons m^{-2} d^{-1}). The thickness of the first-year white ice around the melt ponds in the eastern Canadian Arctic Archipelago (CAA) ranged from 1.10 to 1.27 m. In Beaufort Sea (BS), the thickness of the multi-year pack ice was 3.5 m. Melt pond water temperature varied between 0.21 and 1.82 °C in the eastern CAA and was higher in BS, with a value of 3.30 °C. Melt pond salinity values were low, with values varying between 0.2 and 8.5 psu. Melt pond nutrient concentrations were low, with silicic acid showing higher values (0.04–1.12 µM), followed by nitrate plus nitrite (0.08–0.23 µM) and phosphate (<0.02–0.12 µM). DOC and DON concentrations were also low, ranging from 11.3 to 56.5 µM and 0.2 to 5.0 µM, respectively (Table 1).

1.6.2 Primary production and chlorophyll *a* biomass

Total primary production and total chl a_F biomass varied, on average, between 1 and 25 µg C l^{-1} d^{-1} and between 0.04 and 0.44 µg l^{-1}, respectively (Fig. 2a, b). Minimum values of total primary production and total chl a_F biomass were observed at station Ice 5 and station Ice 3, respectively, while maximum values of both variables were found at station Ice 1. The small cells (0.7–5 µm) accounted for 63–85 % of the total primary production and for 40–80 % of the total chl a_F biomass. Chl a_F biomass was dominated by large cells (>5 µm) only at stations Ice 4 and 5 (Fig. 2b). Very large cells (>20 µm) represented less than 8 % of total chl a_F biomass. The mean production:biomass ratio ranged from 18.2 µg C µg chl a_F^{-1} d^{-1} at the BS station to 61.4 µg C µg chl a_F^{-1} d^{-1} at station Ice 2 in Barrow Strait (Fig. 2c).

Table 1. Physical and chemical characteristics of the melt ponds (MP) sampled in the Beaufort Sea (Ice 5) and the Eastern Canadian Arctic Archipelago (Ice 4 to Ice 1) during summer 2014. Ice thickness was measured in the vicinity of the sampled melt pond. MYI: multi-year sea ice; FYI: first-year sea ice; DOC: dissolved organic carbon; DON: dissolved organic nitrogen; NO_3+NO_2: nitrate + nitrite; PO_4: phosphate; $Si(OH)_4$: silicic acid; TPC: total particulate carbon; nd: not determined. For Ice station 5, total dissolved nitrogen (TDN) was measured instead of DON

Variable	**Ice 5**	**Ice 4**		**Ice 3**		**Ice 2**			**Ice 1**	
	MP1	**MP1**	**MP2**	**MP1**	**MP2**	**MP1**	**MP2**	**MP3**	**MP1**	**MP2**
Date	29 August	23 July		21 July		20 July			18 July	
Site	Beaufort Sea	Resolute Passage		Barrow Strait		Barrow Strait			Navy Board Inlet	
Latitude (N)	73°17’	74°36’		74°14’		74°17’			73°32’	
Longitude (W)	128°33’	94°55’		92°12’		91°38’			80°59’	
Incident PAR (mol photons m^{-2} d^{-1})	16.1	25.5		27.8		26.4			17.2	
Ice coverage (/10)	8	8		10		10			7	
Melt pond coverage (%)	25	25		70		70			80	
Ice type (FYI or MYI)	MYI	FYI		FYI		FYI			FYI	
Ice thickness (m)	3.5	1.27		1.10		nd			1.20	
Melt pond depth (m)	nd	0.12	0.13	0.07	0.10	0.30	0.19	0.11	0.18	0.18
Water temperature (°C)	3.30	0.80	0.80	0.21	0.21	0.42	0.31	0.23	1.86	1.82
Salinity	0.4	8.1	8.5	1.1	0.9	1.3	0.4	0.2	5.2	4.1
NO_3+NO_2 (µM)	nd	0.15	0.12	0.18	0.23	0.18	0.22	0.08	0.08	0.09
PO_4 (µM)	nd	0.10	0.12	0.01	<0.01	<0.01	<0.01	<0.01	0.02	0.03
$Si(OH)_4$ (µM)	nd	1.12	1.28	0.50	0.13	0.04	0.07	0.04	0.76	0.92
DON (µM)	0.1	1.84	2.05	0.47	0.37	0.20	0.50	0.37	5.72	2.55
DOC (µM)	11.3	36.7	39.5	22.1	18.0	20.3	23.4	19.2	56.5	47.5
TPC (µM)	2.4	8.2	5.4	2.7	2.8	2.3	4.1	3.4	15.1	13.9

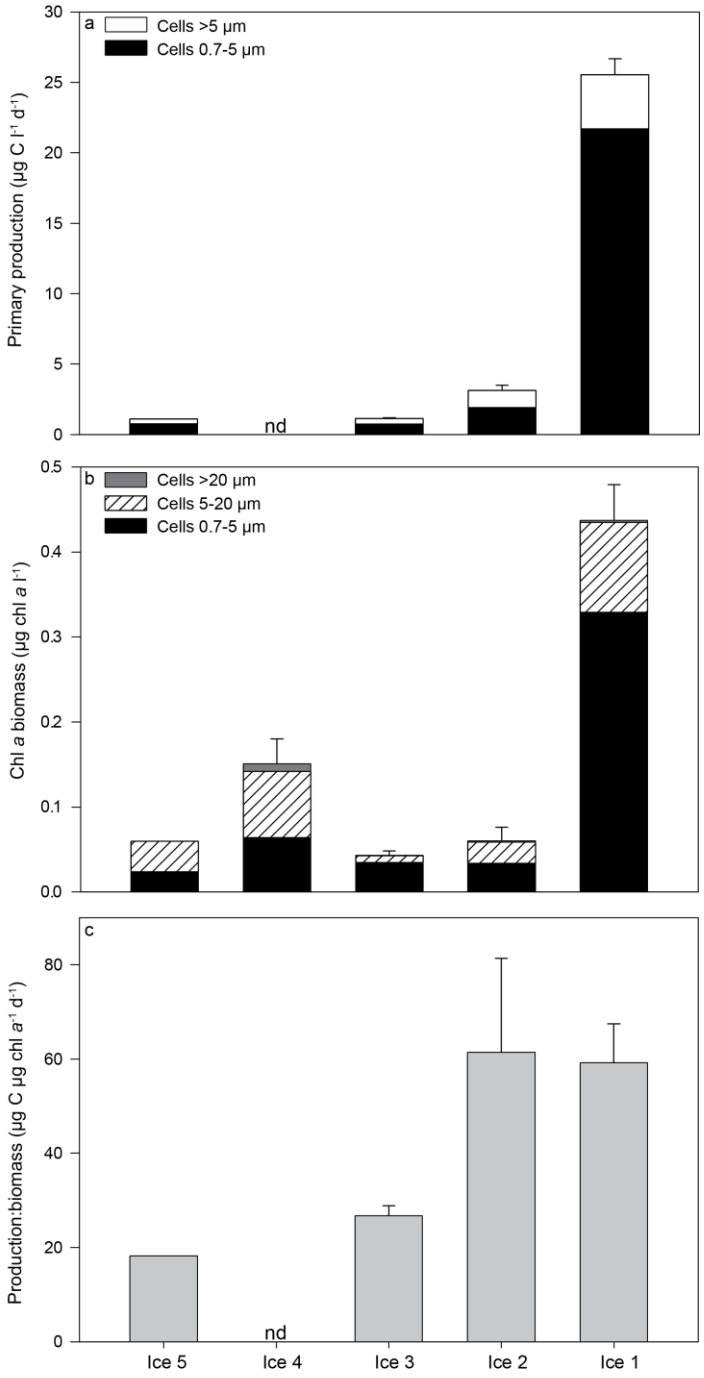

Fig. 2. Variations in (a) primary production for small (0.7-5 µm) and large (>5 µm) cells, (b) chlorophyll *a* (chl a_F) biomass for three size-fractions (0.7-5 µm, 5-20 µm, and >20 µm), and (c) ratio of total primary production to total chl a_F biomass in melt ponds during summer 2014. All stations are plotted from West to East. The vertical lines represent SE of mean total values. nd: not determined

1.6.3 Algal and bacterial abundance

The total abundance of algae varied between 0.1 x 10^6 cells l^{-1} at BS station and 2.0 x 10^6 cells l^{-1} at station Ice 1 in Navy Board Inlet (Fig. 3a). The community was numerically dominated by nanoeukaryotic algae (2–20 µm), which made up 48–74 % of the total algal cell abundance (Fig. 3a). Microeukaryotes represented a maximum of 5 % of the total algal abundance. Phycoerythrin-containing cyanobacteria were not detected in melt ponds. Bacterial abundance varied between 0.01 and 0.29 x 10^9 cells l^{-1} and was dominated by high nucleic acid bacteria, making up ≥55 % of the total bacterial abundance (Fig. 3b). Picoeukaryotes accounted, on average, for 1 % and 0.9 % and heterotrophic bacteria for 0.3 % and 9 % of the TPC in the eastern CAA and the BS, respectively.

1.6.4 Taxonomic composition of algal community

Unidentified flagellates dominated the algal community (>2 µm) at all sampling sites, representing between 46 and 87 % of the total algal abundance estimated by microscopy (Fig. 4a). This algal group was mainly composed of cells ranging from 2 to 5 µm (62–86 %). Pennate diatoms were the second major taxonomic group, accounting for ≥5 % of the total algal abundance in at least 5 melt pond samples. However, they were not detected at station Ice 5.

From West to East, the second most abundant group was chlorophytes at station Ice 5, pennate diatoms at stations Ice 4 and 2, chrysophytes at station Ice 3 and prasinophytes at station Ice 1 (Fig. 4a,b). At station Ice 5, chlorophytes, mainly *Chlamydomonas* spp. (10–20 µm), represented 20 % of the total community, while it represented less than 4 % at the other stations. At stations Ice 4 and 2, the pennate diatoms, mainly 10–20 µm pennates, made up 5–28 % of the total community. Chrysophytes were the third dominant group at station Ice 4 (13–16 % of the community) and the second at station Ice 3 (23–29 %), mostly due to *Chrysolykos* cf. *angulatu*s and Chrysophyceae spp. (10–20 µm), respectively.

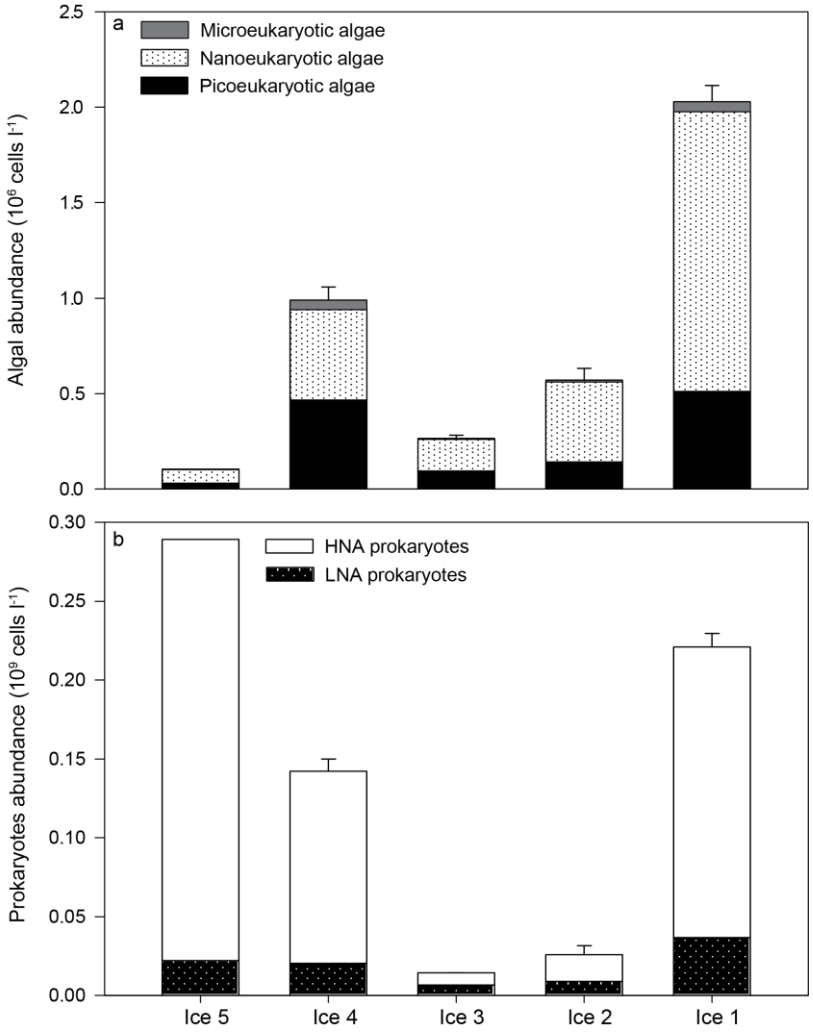

Fig. 3. Variations in the abundance of (a) picoeukaryotic (≤2 µm), nanoeukaryotic (2-20 µm) and microeukaryotic (>20 µm) algae, and (b) prokaryotes with low (LNA) and high (HNA) nucleic acid content in melt ponds during summer 2014. The abundance of microalgae was estimated by inverted microscopy. The vertical lines represent SE of mean total values

At station Ice 1, prasinophytes represented on average 25 % of the total community while they represented <2 % of the community at the other stations. This high proportion of prasinophytes at station Ice 1 was mostly due to the presence of *Pyramimonas* spp. (10–20 µm). Finally, prymnesiophytes were the third most abundant group at station Ice 2,

accounting for 5–11 % of the total community, while at the other stations, they represented less than 5 %. The main taxa were Prymnesiophyceae spp. (2–5 µm) and *Chrysochromulina* spp. (2–5 µm).

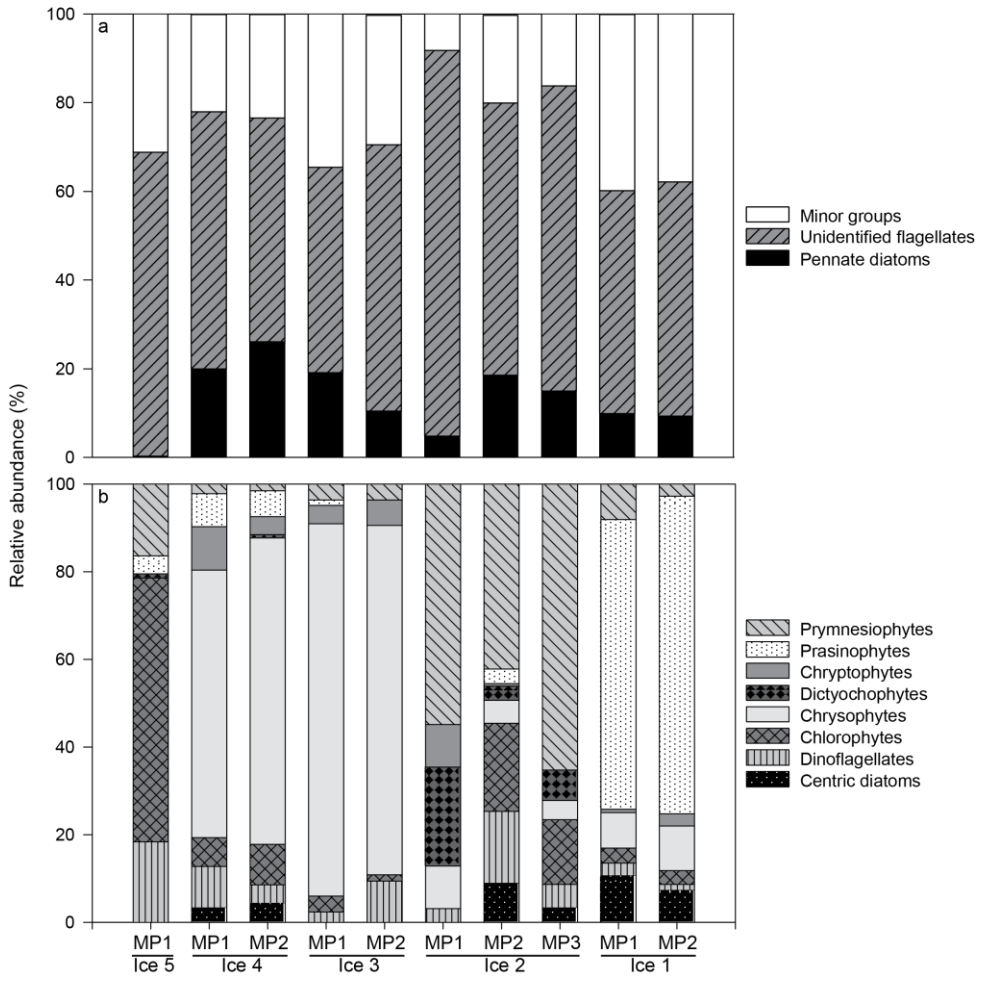

Fig. 4. Relative abundances of (a) major and (b) minor taxonomic groups in the melt ponds during summer 2014. A major taxonomic group was defined as a group accounting for ≥5 % of total protist abundance in at least five melt pond samples. The remaining groups were defined as minor taxonomic groups. In (b), abundances were divided by the total abundance of minor groups

Diatom resting spores as well as dinoflagellate and chrysophyte cysts were found in each melt pond. However, they were present in very low abundance, representing only between 1 and 3 % of the total algal cells. We also found a very large amount of empty

diatom frustules; they made up 58 % and 96 % of the total diatom frustules (i.e. empty frustules + chloroplast-containing frustules) at stations Ice 4 and 5, respectively. At the other stations, empty frustules accounted for 67–90 % of the total frustules (data not shown).

1.6.5 Taxa richness and diversity index

The total richness values of the melt ponds (75), bottom ice (76) and water column (79) were similar (Table 2). The mean average sample richness was not significantly different between the melt ponds (30 ± 4), the under-ice surface waters (45 ± 4) and the bottom ice (41 ± 6) ($p = 0.08$; Table 2). The Shannon-Weiner diversity index of taxa in melt ponds (0.84 ± 0.6; mean ± SE) was similar to the two other environments ($p = 0.06$; Table 2).

Table 2. Total and average sample richness and Shannon-Weiner diversity index for melt pond, water column and bottom ice samples during summer 2014. Average values ± SE are shown for average sample richness and diversity index

	Melt pond	Bottom ice	Water column
Total richness	75	76	79
Avg. sample richness	30 ± 4	41 ± 6	45 ± 4
Avg. sample diversity index	0.84 ± 0.06	1.2 ± 0.14	0.90 ± 0.11

1.6.6 Pigments

Abbreviations of the 25 pigments detected in the melt ponds by the HPLC method are listed in Table 3. During this study, divinyl chlorophyll *a*, chl *a* allomer and epimer, pheophorbide *a*, chlorophyllide *b*, divinyl chlorophyll *b*, and chlorophyll *b* allomer and epimer were not detected in any samples. Chl a_F concentration was regressed against Tchl *a* measured by HPLC (Fig. 5). Both measurements were performed on particles retained on Whatman GF/F filters. The slope of the regression was 1.02 ($F_{1,8} = 393.7$, $r^2_{adj} = 0.978$, $p < 0.001$) and the intercept was not significantly different from 0 (Student's *t*-test, $p = 0.357$).

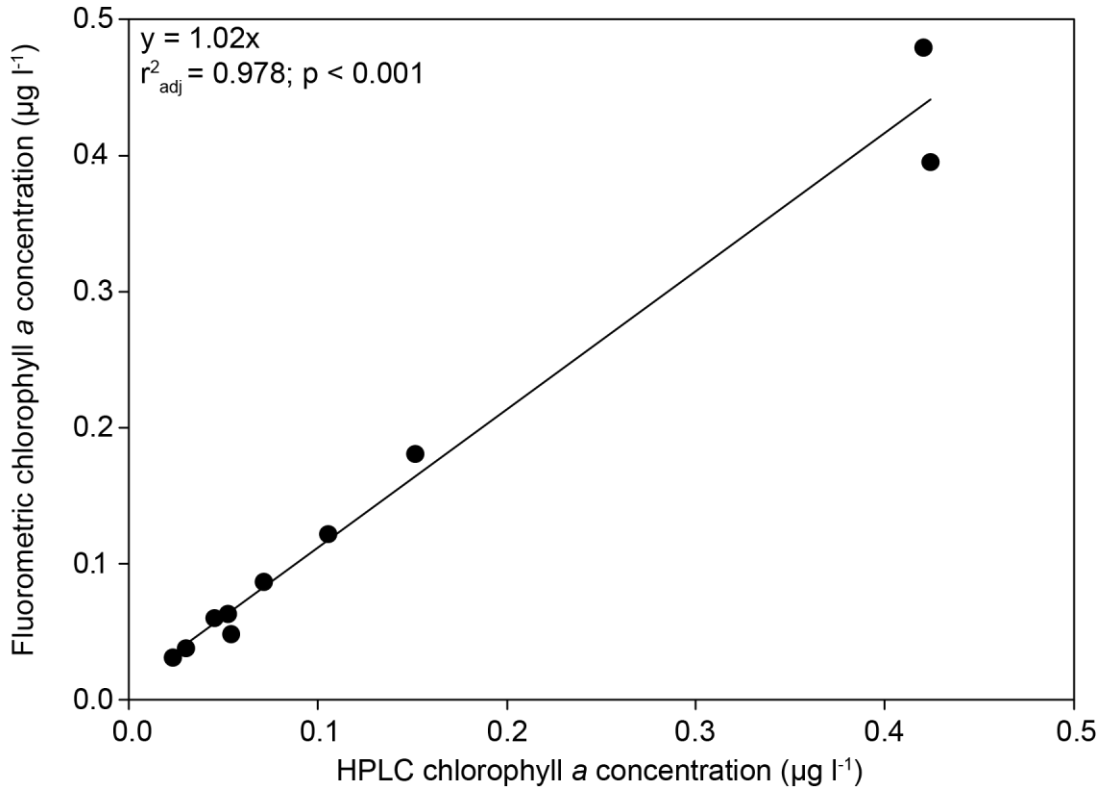

Fig. 5. Model I linear regression between chlorophyll a (chl a_F) measured by fluorometry and chlorophyll *a* (Tchl *a*) measured by HPLC in melt ponds during summer 2014

Table 3. Abbreviation of pigments detected in melt ponds during the 2014 summer and calculation of the sum of pigments. Lyco-like-2 was identified according to Zapata et al. (2012). MgDVP was not included in the calculation of Tchl *c* since it was clearly separated from chl c_2 in our chromatographs

Pigment	**Abbreviation**	**Calculation**
19'-Butanoyloxyfucixanthin	But-fuco	
19'-Hexanoyloxyfucoxanthin	Hex-fuco	
9'-cis-Neoxanthin	*c*-Neo	
Alloxanthin	Allo	
Antheraxanthin	Anthera	
Chlorophyll *a*	Chl *a*	
Chlorophyll *b*	Chl *b*	
Chlorophyll c_1	Chl c_1	
Chlorophyll c_2	Chl c_2	
Chlorophyll c_3	Chl c_3	
Chlorophyllide *a*	Chlide *a*	
Crocoxanthin	Croco	
Diadinoxanthin	Diadino	
Diatoxanthin	Diato	
Fucoxanthin	Fuco	
Lutein	Lut	
Lycopene-like*	Lyco-like-2	
Magnesium 2,4-divinylpheoporphyrin a_5 monomethyl ester	MgDVP	
Micromonal	Micral	
Peridinin	Peri	
Pheophythin *a*	Phytin *a*	
Prasinoxanthin	Pras	
Violaxanthin	Viola	
Zeaxanthin	Zea	
β,β-Carotene	ββ-caro	
Total chlorophyll *a*	Tchl *a*	Chl *a* + Chlide *a*
Total chlorophyll *b*	Tchl *b*	Chl *b* only
Total chlorophyll *c*	Tchl *c*	Chl c_1 + Chl c_2 + Chl c_3
Photosynthetic carotenoids	PSC	Allo + But-fuco + Fuco + *c*-Neo + Peri + Pras
Photoprotective carotenoids	PPC	Anthera + Diadino + Diato + Lut + Viola + Zea + ββ-caro

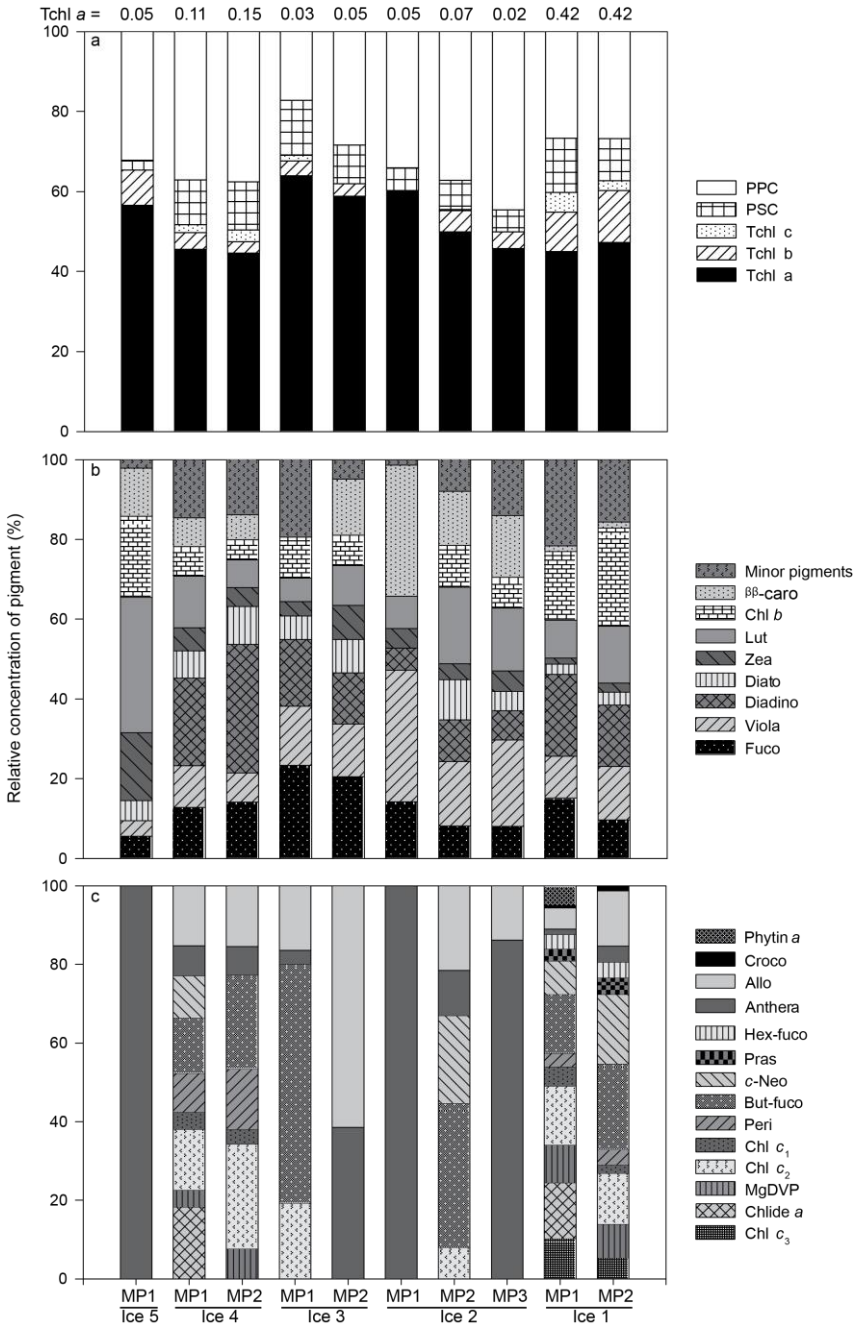

Fig. 6. Relative concentrations of (a) five pigment classes, (b) major pigments, and (c) minor pigments in the melt ponds sampled during summer 2014. A major pigment was defined as a pigment accounting for ≥5 % of Tchl *a* in at least five melt pond samples. The remaining pigments were defined as minor pigments. In (c), pigments were divided by the total concentration of minor pigments. Tchl *a* concentration (μg l^{-1}) at each sampling site is indicated on the top panel. Pigment abbreviations are defined in Table 3

The relative concentration of chlorophyll, PSC and PPC to total pigments in melt ponds is shown in Figure 6a. Tchl *a*, Tchl *b* and Tchl *c* made up, on average, 52 %, 6 % and 1 % of the total pigments, whereas PSC and PPC contributed, on average, for 9 % and 32 % of the total pigments, respectively. The chl a degradation products, chlide *a* and phytin *a*, were found in only two melt ponds (i.e. MP1 of stations Ice 4 and 1), contributing to <5 % of the chl *a* at these sites (Fig. 6c).

The relative concentrations of major and minor pigments are shown in Figure 6b and c. A major pigment was defined as a pigment accounting for more than 5 % of Tchl *a* in at least five melt pond samples. The remaining pigments were defined as minor pigments. Eight major pigments were present at each sampling site, except at stations Ice 5, 3 (MP1) and 2 (MP1) where Diadino, ββ-caro, and Diato and chl *b* were not detected, respectively (Fig. 6b). All major pigments, except Fuco and chl *b*, were PPC.

The 14 minor pigments contributed for 2–35 % of Tchl *a* (Fig. 6c). In contrast to major pigments, there were large differences in the relative concentration of minor pigments between melt ponds. Two different groups of stations could be distinguished: one with numerous pigments as for stations Ice 4 and 1, and one with only a few minor pigments as for stations Ice 5, 3 and 2 (Fig. 6c). Anthera was the only minor pigment present at stations Ice 5 and 2 (MP1) and it was associated with Allo at stations Ice 3 (MP2) and 2 (MP3).

The ratios of (diadino+diato):Tchl *a*, (viola+anthera+zea):Tchl *a* and (Lut+ββ-caro):Tchl *a* ranged from 0.04 to 0.45, 0.16 to 0.33 and 0.09 to 0.36 (wt:wt), respectively (Fig. 7). The total of PPC:Tchl *a* ratio varied between 0.40 and 0.84 (wt:wt). Maximum value of this ratio was found at station Ice 4. The PPC:PSC ratio varied between 2.1 and 13.2 (wt:wt), the maximum value being observed at station Ice 5.

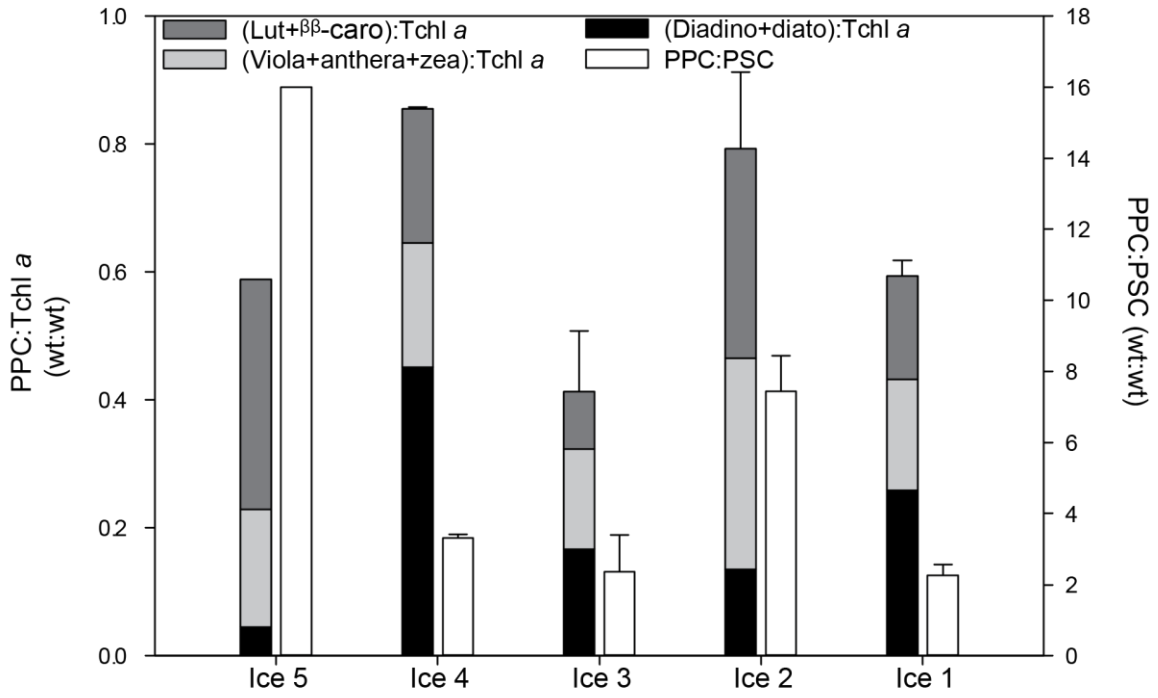

Fig. 7. Variations in the ratios of the photoprotective carotenoids to Tchl *a* (PPC:Tchl *a*) and to photosynthetic carotenoids (PPC:PSC) in melt ponds during summer 2014. PPC:Tchl *a* is composed of the diadino/diato cycle, the viola/anthera/zea cycle and the sum of lut and ββ-caro. The vertical lines represent SE of mean values

1.6.7 Algae light absorption spectra

Chl *a*-specific absorption coefficients of algae ($a_{\Phi}(\lambda)$/Tchl *a*) at selected melt ponds are shown in Figure 8. Absorption spectra clearly show the presence of two mycosporine-like amino acids (MAA) between 300 and 400 nm: the first one absorbing at around 332 nm (MAA 1) and the second one around 365 nm (MAA 2). MAA 1 and MAA 2 were more abundant at station Ice 3 and in MP1 of station Ice 4, respectively. Both MAAs were present in MP2 of station Ice 4. Station Ice 2 did not show the presence of any of the two MAAs.

In the PAR range (400–700 nm), all spectra showed strong absorbance peaks at ca. 450 and 670 nm. They also showed a strong absorbance shoulder centered at 490 nm, which matches peak absorption of many carotenoid pigments (Bricaud et al. 2004).

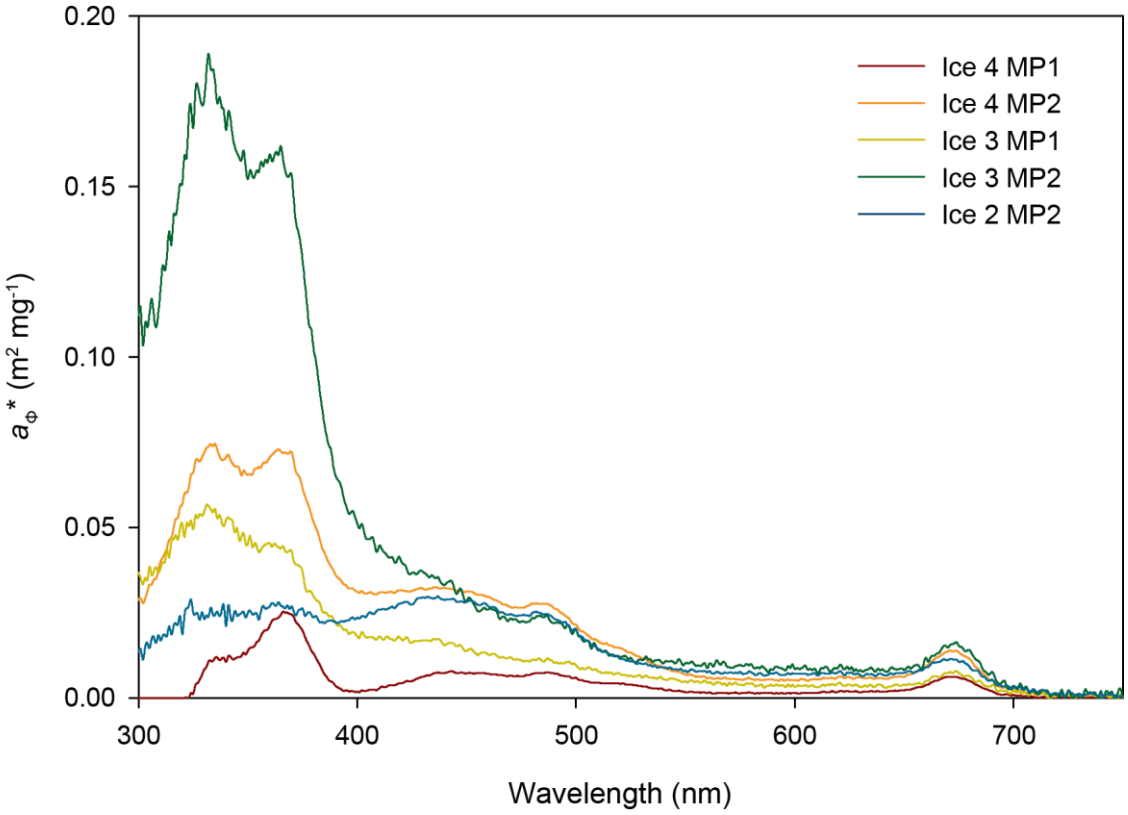

Fig. 8. Chlorophyll *a*-specific absorption spectra ($a_\Phi^*(\lambda) = a_\Phi$/Tchl *a*) measured in different melt ponds during summer 2014

1.6.8 Multivariate analysis

Five groups of melt ponds were identified based on the taxonomic composition of the community (ANOSIM, global R = 0.986, p < 0.001; Fig. 9a). Group I consisted of only one sample (Ice 5). It was composed of 68 % of unidentified flagellates and 19 % of chlorophytes and characterized by the absence of pennate and centric diatoms (Table A1). Group II also consisted of only one sample (Ice 2-MP1) and was characterized by the highest proportion of unidentified flagellates (87%) and a low proportion of pennate

diatoms (5 %). Group III was composed of unidentified flagellates at 65 %, pennate diatoms at 17 % and of prymnesiophytes at 9 %. Group IV is composed of 54 % of unidentified flagellates, 21 % of chrysophytes and 19 % of pennate diatoms. Finally, Group V is composed of 51 % of unidentified flagellates, 27 % of prasinophytes and 10 % of pennate diatoms.

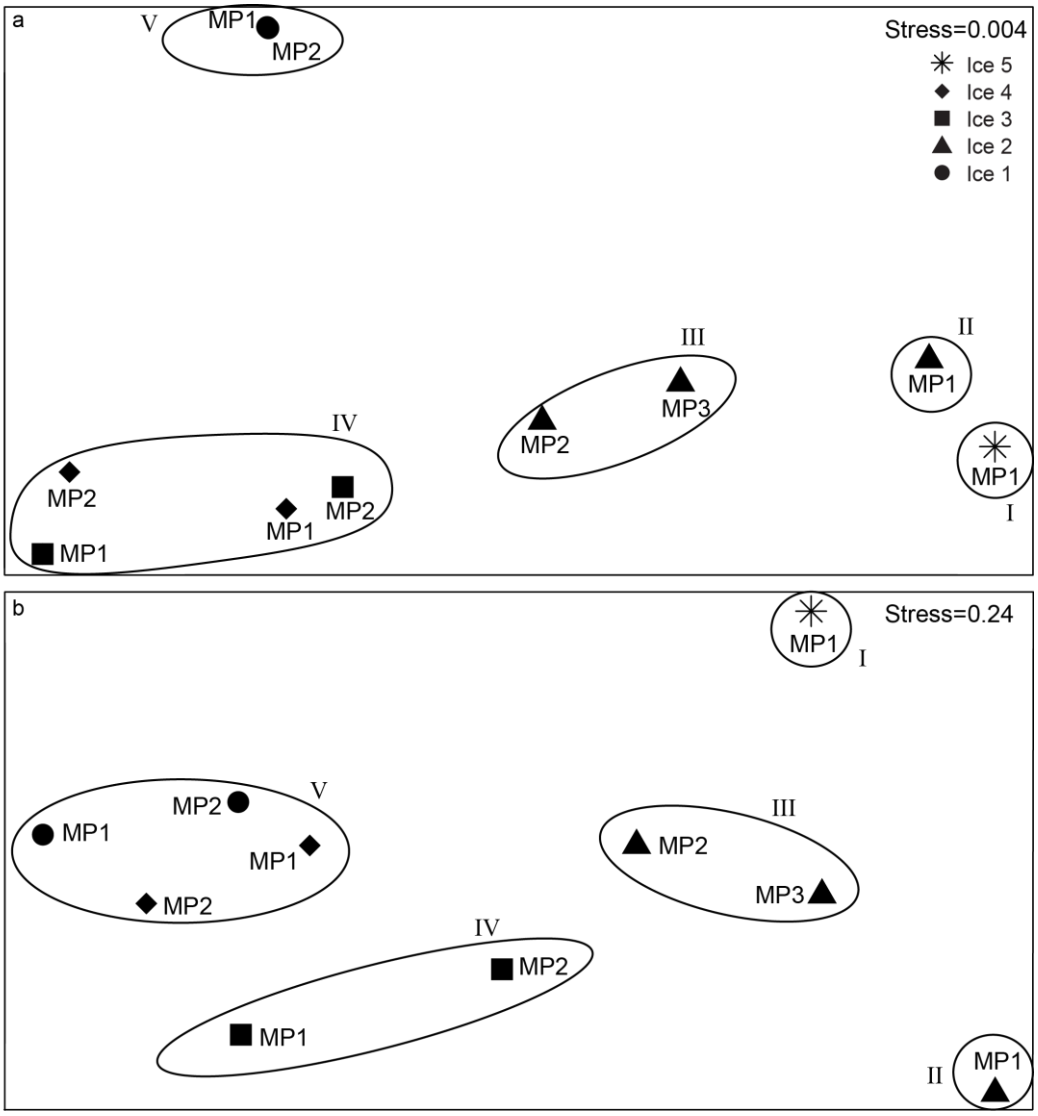

Fig. 9. Non-metric multidimensional scaling (MDS) based on (a) taxonomic composition and (b) pigment composition of 10 melt ponds sampled in the Arctic during summer 2014. The five groups of melt ponds with similar composition (determined with a group-average

clustering, at a similarity level of 80% and 70% for taxonomic and pigment composition, respectively) are superimposed on the MDS

Five groups of melt ponds were also identified based on the pigment composition (ANOSIM, global R = 0.885, $p < 0.001$; Fig. 9b). The main pigments contributing to those groups were: Group I: Lut, Chl *b*, and Zea (33, 22 and 18 %, respectively); Group II: β,β-caro and Viola (36 and 32 %, respectively); Group III: Lut, Viola, β,β-caro, Chl *b* (21, 19, 16 and 11 %, respectively); Group IV: Fuco, Diadino and Viola (28, 19 and 18 %, respectively); Group V: Diadino, Fuco, Viola and Lut (24, 15, 12 and 12 %, respectively) (Table A2). Those pigments represent at least 60% of the total pigments.

The RDA shows the influence of environmental variables on the taxonomic composition of melt pond algae (Fig. 10). It revealed four significant physico-chemical variables explaining 80 % of the distribution of the taxonomic groups; namely daily PAR, melt pond depth, salinity and phosphate concentration ($p < 0.01$ and $p < 0.05$ for the first two and last two variables, respectively). The first two RDA axes are significant ($p < 0.05$) and explain 32 and 23 % of the total variance. Melt pond depth, salinity and phosphate concentration show stronger correlation with the first RDA axis (r_p values of -0.63, 0.67 and 0.52, respectively) than to the second axis (r_p values of 0.34, 0.23 and -0.15, respectively). Daily PAR and NO_3+NO_2 concentration are correlated to the second RDA axis (r_p values of -0.67 and -0.75, respectively) than with the first axis (r_p values of 0.20 and 0.10, respectively). The distribution of pennate diatoms, cryptophytes and chrysophytes was more associated with the first axis and opposite to prymnesiophytes, dictyochophytes, unidentified flagellates and chlorophytes. The second axis was more associated with the distribution of prasinophytes and centric diatoms and opposite to dinoflagellates. Three combinations of melt ponds were found with the RDA. The first one included stations Ice 3 and 4, cryptophytes, chrysophytes and pennate diatoms, associated with shallower melt ponds and higher PO_4 concentration. The second one included station Ice 1, prasinophytes and centric diatoms and was associated with low nitrate plus nitrite concentration and low incident irradiance. Finally, the third association included stations Ice 2 and 5,

prymnesiophytes, dictyochophytes, unidentified flagellates and chlorophytes and was associated with saltier and deeper melt ponds.

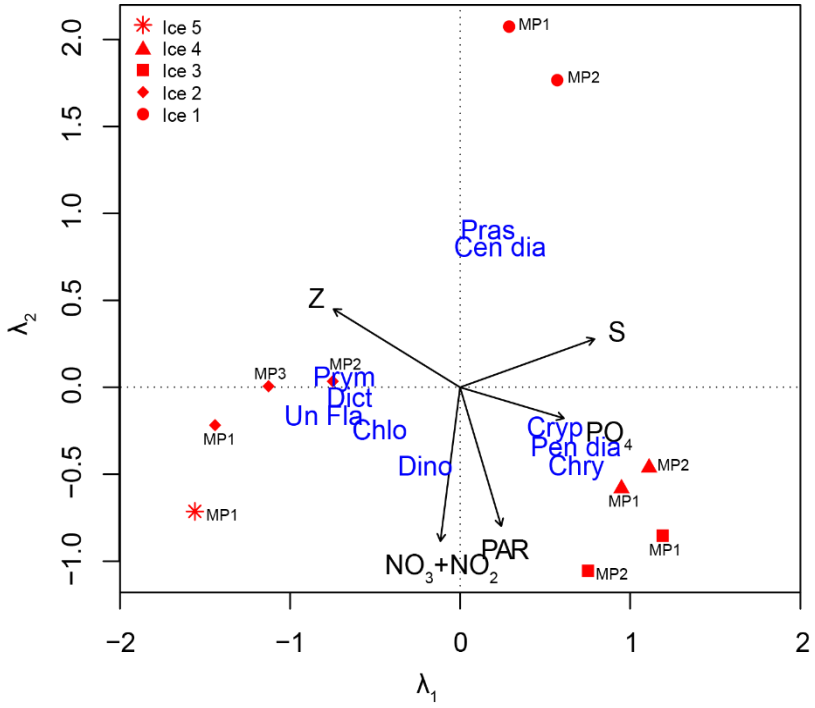

Fig. 10. Redundancy analysis (RDA) ordination plots of axes I and II showing taxonomic groups (blue) in relation to environmental (black arrows) variables for melt ponds (red) during summer 2014. Cen dia: centric diatoms; Chloro: chlorophytes; Chry: chrysophytes; Crypt: cryptophytes; Dict: dictyochophytes; Dino: dinoflagellates; Pen dia: pennate diatoms; Pras: prasinophytes; Prym: prymnesiophytes; Un fla: unidentified flagellates; PAR: daily incident irradiance; Z: melt pond depth; S: melt pond salinity; NO_3+NO_2: nitrate + nitrite; PO_4: phosphate

1.7 DISCUSSION

1.7.1 Algae

The melt ponds sampled in CAA and BS during our study were all oligotrophic environments, as shown by their low inorganic nutrient, DON and DOC concentrations, chl *a* biomass and primary production. Nutrient concentrations (nitrate, phosphate and silicic acid) in these melt ponds are similar to those measured in melt ponds from the

Canadian Basin (0−0.57, 0.03−0.52, 0.05−1.77 µM, respectively; Lee et al. 2012, 2015, Lin et al. 2016) and the central Arctic Ocean (0.06−0.8, 0−0.15, 0.01−1.6 µM, respectively; Fernandez-Mendez et al. 2015) during summer. For our sampling period, melt pond nutrient concentrations are generally lower than in surface water of CAA and southeastern BS (<0.8, 2−8, 0.42−1.44 µM; Tremblay et al. 2009). A recent study by Wentworth et al. (2016) showed that the atmosphere is an important source of ammonium for Arctic melt ponds. Melt pond DOC concentrations were 2−8 times lower than in surface water of eastern CAA and BS (68−92 µM). Wickhan & Carstens (1998) reported a DOC concentration <83 µM in a melt pond sampled on a drifting ice on the northeast coast of Greenland. To our knowledge, no DON value has been published for melt ponds. Melt pond DON concentrations were generally lower (0.2−5 µM) than in surface waters (3.7−6.1 µM). Hence, melt ponds are not a significant source of DOC and DON for the water column.

Our primary production rates were generally low and similar to those measured in melt ponds from the Canadian Basin (0.24−50 µg C l^{-1} d^{-1}: Lee et al. 2012, 2015) and the central Arctic Ocean (0.1−4 mg C m^{-2} d^{-1}: Fernandez-Mendez et al. 2015) during summer. In the eastern CAA, melt pond primary production was lower than in the under-ice and open surface water (5.5−37 µg C l^{-1} d^{-1}), except at station Ice 1 (25 µg C l^{-1} d^{-1}), which has a rate similar to surface water. In BS, melt pond primary production was at least 10 times lower than in surface waters (1.3−9.5 µg C l^{-1} d^{-1}). A lower primary production in melt ponds than in surface waters was also reported by Fernandez-Mendez et al. (2015). In both studies, nutrient concentrations were much lower in melt ponds than in under-ice surface water, suggesting that nutrients were limiting production in the melt ponds. However, Lee et al. (2011) found low primary production in both melt ponds and surface water likely due to nutrient limitation in both environments in late summer.

Even though our melt pond chl a_F biomass was low, other studies have reported similar values in Allen Bay (Cornwallis Island, Nunavut; <0.5 µg l^{-1}:Elliott et al. 2015) and central Arctic Ocean (0.1–0.3 µg l^{-1} in 2008: Lee et al. 2012; 0.1–1 µg l^{-1}:Fernandez-

Mendez et al. 2015; 0.06–1.28 µg l^{-1}: Lee et al. 2015). Higher range of chl *a* values was reported in Canada Basin (0.1–2.9 µg l^{-1}: Lee et al. 2012) and Beaufort Gyre (0.1–7.5 µg l^{-1}: Gradinger et al. 2005). A maximum value of 15.3 µg l^{-1} was reported in Canada Basin in a low salinity melt pond (0.2 psu: Lin et al. 2016). These differences in algal biomass may be also explained by differences in nutrient supply.

Total algal abundance (sum of pico-, nano- and microalgae) in melt ponds was also low compared to surface waters in the study area (varying from 2.5–19.4 x 10^6 cells l^{-1}) and elsewhere in surface water of the Canadian High Arctic (approximately 5–20 x 10^6 cells l^{-1}: Tremblay et al. 2009). Nanoeukaryotic algae were the most abundant algal size fraction in melt ponds. This is an interesting feature since oligotrophic systems are generally dominated in terms of abundance and biomass by picoalgae (Chisholm 1992, Agawin et al. 2000). Cold, nutrient-poor and well-lit waters may give a selective advantage to nanoalgae over picoalgae.

1.7.2 Prokaryotes

During this study, cyanobacteria were not detected in melt ponds. They were also not present in melt ponds sampled on the landfast first-year ice of Darley Bay (southeast Beaufort Sea; Mundy et al. 2011) and Allen Bay (Elliott et al. 2015) in late spring. These results are surprising since cyanobacteria are present in high abundance in Arctic lakes and ponds (Vincent 2000). In marine Arctic waters, they occurred in low abundance, except in river plumes and Atlantic-influenced waters (Not et al. 2005, Tremblay et al. 2009). Furthermore, heterotrophic bacteria abundance in melt ponds was very low, two-orders of magnitude lower than in the surface water of the study area (3.0–9.5 x 10^9 cells l^{-1}) and from the Resolute Passage (0.5–0.7 x 10^9 cells l^{-1}; Galindo et al. 2015). With a high DOC:DON molar ratio (range: 10–113; mean: 48) and a low concentration of dissolved inorganic nitrogen (Table 2), as measured during this study, bacteria should have had a competitive advantage over algae for nitrogen (Legendre & Rassoulzadegan 1995). This was not the case in our melt ponds where the low availability of DOC and PO_4 may have

limited the abundance of heterotrophic bacteria (Cotner et al. 2000, Pomeroy & Wiebe 2001). An alternative hypothesis is a high grazing pressure by bacterivorous nanoflagellates or an inhibition of their growth by UVR. More studies are needed to explain the low abundance of bacteria compared to algae in melt ponds.

1.7.3 Algal community

Melt pond algae may originate from the water column, the sea ice and the snow. Ice and snow are the two principal sources of water for melt ponds, so microorganisms living in those environments could easily be transferred into melt ponds. The water column can also provide organisms to melt ponds through sea ice brine channel, seal holes and from breaking waves along ice edge. Moreover, Horner et al. (1992) proposed that organisms living in melt ponds could origin from freshwater environments and be transported by birds or wind. The dominance of nanoalgae suggests a low proportion of atmospheric transport of freshwater algae to melt ponds. However, some taxa found in melt ponds are typically found in sea ice (*Nitzschia frigida*, Różańska et al. 2009), in the water column (*Chaetoceros* spp., Różańska et al. 2008), in snow (*Chlamydomonas* spp., Gradinger & Nurnberg 1996) (Table A3).

Melt ponds are submitted to extreme environmental conditions (i.e. low temperature, salinity and nutrient availability as well as high light exposure). This could suggest that only a few algal species or groups may be able to thrive in this particular environment. Microorganisms transported into melt ponds from sea ice or surface water are submitted to a high osmotic stress. They are originating from saline or hypersaline environments like brine channels, and have to acclimate to a fresh to brackish environment. Low salinity is not the only stress to which algae in melt ponds are submitted, they are also exposed to high PAR and UVR (see the next section for more details). As seen below, the diversity of algae was high in melt ponds sampled in spite of these stresses. The melt ponds were characterized by a relatively high algal richness despite the low total abundance of algae. The total number of taxa found in the melt ponds at the different stations (75) was similar

to those observed in under-ice surface water and at the ice bottom in the region studied (79 and 76, respectively). However, on average, a melt pond sample has a number of taxa lower than a water column or a bottom ice sample (30, 45 and 41, respectively). Hence, this indicates that melt ponds are more dissimilar in terms of species diversity from each other than two stations of the other surrounding environments. It is then possible to affirm that the species richness could be as much in melt ponds than at the bottom of the ice and in the surface water.

Melt ponds algal diversity was not significantly lower than in under-ice surface water and bottom ice, which is opposite to what Lee et al. (2011) found in the Canadian Basin. However, a higher diversity index (0.98 ± 0.03) has been found in saltier melt ponds (salinity of 4.1–8.5) compared to fresher (salinity of 0.2–1.3) melt ponds (0.75 ± 0.08), even within the small salinity range of the melt ponds sampled in the present study. This positive trend between salinity and algal diversity has been also reported by Lee et al. (2015).

Despite the high proportion of unidentified flagellates, it is possible to distinguish five groups of melt ponds based on the taxonomic composition of algal assemblages. All those groups are dominated by unidentified flagellates. Pennate diatoms are also one of the three most abundant taxonomic groups except at station Ice 5. The other taxonomic groups are composed of flagellates, notably by chlorophytes, chrysophytes, prymnesiophytes and prasinophytes. These results are consistent with those of Elliott et al. (2015) and Lee et al. (2011) which showed that unidentified flagellates (<20 µm) dominated the melt pond community (66 and 81 % of the total abundance, respectively) in Allen Bay and the Canadian Bassin, respectively. In low salinity ponds, Lee et al. (2015) also found a high proportion of unidentified flagellates, in terms of abundance. However, the same author noticed a higher proportion of diatoms in saltier ponds, a relationship we did not see in our study. This could result from the narrow salinity range of our samples (0.2 to 8.5 psu), compared to Lee et al. (2015) (0.0 to 28.3 psu). Nevertheless, even at a salinity of about 1 psu, pennate diatoms were representing up to 20 % of the community during our study, a

contribution much higher than in other studies in which diatoms represent less than 4 % of the community (Melnikov et al. 2002, Lee et al. 2015) or are absent (Lee et al. 2011). The fact that our study was conducted on landfast ice instead of pack ice may explain this difference.

Consistent with the dominance of chlorophytes at station Ice 5, Melnikov et al. (2002) found that the chlorophyte *Chlamydomonas nivalis* dominated their melt ponds, while Lin et al. (2016) found a dominance of the chlorophyte *Carteria lunzensis* in their blooming melt pond. Those results might indicate that chlorophytes are a dominant group in melt ponds during late summer.

Pigment signature is generally used to identify the taxonomic groups of small algae (typically flagellates <5 µm) that cannot be assessed with an inverted microscope. In this study, the grouping of the melt pond samples with nMDSs is not exactly the same using taxonomy and pigment data (Fig. 9a,b). Stations Ice 1 and 4 formed one group based on pigment signature, while they were different based on their taxonomic composition. These two stations had the highest Tchl *a* concentrations. Higher pigment concentration might have allowed us to identify more pigments. Moreover, the high proportion of PPC contained in our samples could have complicated pigment signature interpretation, since they could be taxonomically widespread (Jeffrey et al. 2011). Indeed, Coupel et al. (2015) had excluded those pigments from their chemotaxonomic analysis. Hence, the high concentration of PPC in our samples coupled with low pigment concentration may explain why we were not able to determine to which taxonomic classes belong the unidentified flagellates.

Finally, the high proportion of empty diatom frustules could indicate a high diatom mortality in the melt ponds. These empty cells could also have been introduced to the ponds during melting, since empty frustules are abundant in the top layer of the sea ice (unpublished data). Degradation pigments, such as pheopigments (pheide *a* and phytin *a*) and chlide *a* are found in senescent algae or in fecal pellets (Egeland et al. 2011), and their presence could then has been used to exclude the possibility that empty frustules came from

sea ice. However, as pigments could be rapidly photooxidated in high irradiance environments (SooHoo & Kiefer 1982, Roy et al. 2006), pigment signature did not allow us to determine the origin of the empty frustules in the ponds. Dinoflagellate cysts and diatom spores were also present in our melt ponds. This may indicate non-favorable environmental conditions for some species but these cells could also originate from the melting sea ice. More studies are needed to determine which process is taking place in the melt ponds.

1.7.4 Protection against excess irradiance

Melt ponds are subjected to high irradiance. This implies that light may be in excess and cause negative effects on melt pond organisms. In open waters, light is strongly absorbed by water molecules, colored dissolved organic matter (CDOM), algae and non-algal particulate (NAP) material (Kirk 2011). During this study, DOC concentrations were low, suggesting a low light absorption by CDOM in melt ponds (see Cooper et al. 2016). This idea is supported by the study of Logvinova et al. (2016) which showed that melting sea ice did not contribute to net CDOM in the Chukchi and Beaufort seas in early summer. In melt ponds, the contribution of non-algal material to the total particulate light absorption coefficient was, on average 90 %, at 443 nm (data not shown). These non-algal particles might help to attenuate light penetration in melt ponds to some extent. This idea is also supported by the results of Bélanger et al. (2013) showing that melt water from multi-year ice has a higher proportion of NAP than the upper water column during the growth season. Empty frustules, cysts and spores could contribute to this non-algal particle absorption and therefore, protect cells from photo-damage. However, even with a high quantity of particles in water, the shallow depth of melt ponds does not provide adequate protection against strong light. In order to grow in melt ponds, primary producers need to develop strategies to protect themselves from excess light. Among those photoprotection strategies, algae may synthetize mycosporine-like amino acids (MAAs) and photoprotective pigments.

MAAs play many roles in algal cells, and one of these is to protect them from damage induced by ultraviolet radiation (UVR) (Carreto et al. 2011). Elliott et al. (2015)

recently identified two MAAs in melt ponds from Allen Bay, close to the Resolute Passage, namely shinorine and an unknown MAA which they named U2. Particulate absorption spectra in our melt ponds show the presence of at least two UV-absorbing compounds, one absorbing at 332 nm that we designated MAA1 and another one at 363 nm named MAA2 (Fig. 8). Those two MAAs have the same λmax than those found by Elliott et al. (2015), which have been identified as shinorine and an unknown MAA called U2, respectively. In the study of Elliott et al. (2015), shinorine was correlated with the abundance of both total prasinophytes and the prymnesiophyte *Chrysochromulina* spp. (2–5 µm). However, these two taxa were in very low abundance where MAA1 was present in our samples. However, chrysophytes were relatively abundant in these samples (see Figs. 4b, 8 and 9; Table 1 in the appendix) suggesting that some species related to this algal group are able to produce MAA1.

Moreover, Elliott et al. (2015) suggested that the unknown MAA U2 comes from cyanobacteria, but they did not have cyanobacteria counts to confirm this assumption. MAA2 was present in four out of five melt ponds analyzed during our study. However, phycoerythrin-containing cyanobacteria were in very low abundance, if any, in our samples. Hence, U2 is probably not related to cyanobacteria.

Photoprotective carotenoids are non-photosynthetically active carotenoids. Following an exposition to high light, some algal groups could deepoxidate pigments in order to dissipate the excess of energy they accumulated. Pigments involved in the xanthophyll cycles could also be accumulated in algae photoacclimated to high light. Algae present in melt ponds thus present signs of photoacclimation, since photoprotective pigments are in high concentration in melt pond community.

The presence of photoprotective pigments was detected at a wavelength of 490 nm in the particulate absorption spectrum (Fig. 8). Such peak in absorption is not usual in low light acclimated phytoplankton cells (Brunelle et al. 2012). Photoprotective carotenoids represented, on average, 32 % of all pigments measured in melt ponds during our study. In comparison, Coupel et al. (2015) found that in surface BS water, photoprotective pigments

accounted for ca. 20 % of the total pigments. It is also interesting to note that diadino and diato accounted for one third of all PPC, while they accounted for two thirds of PPC in surface waters of BS (Alou-Font et al. 2016). This could be explained by the relatively low proportion of diatoms in our samples compared to the study of Alou-Font et al. (2016), as diatoms are one of the main groups using the diato and diadino cycle (Brunet et al. 2011). Therefore, pigments from other xanthophyll cycles (i.e. viola, anthera, and zea, as well as lut) showed a higher proportion of photoprotective pigments in melt ponds than in surface water and bottom ice. Moreover, the highest proportion of lut has been found at station Ice 5, the station with the highest proportion of chlorophytes, mainly *Chlamydomonas*, which is known to use the lutein xanthophyll cycle (Brunet et al. 2011). PPC:PSC and PPC:chl *a* ratios were higher in our melt ponds than in the bottom ice (Alou-Font et al. 2013) and open surface water (Alou-Font et al. 2016), which indicate that melt pond algae were photoacclimated to their high light environments.

Photoprotection strategies of melt pond algae seem to be efficient, as algae show a good physiological condition, as determined by the high primary production to biomass ratio measured during this study (18.2–61.4 µg C µg chl a_F^{-1} d^{-1}). As mentioned before, degradation pigments can be rapidly photooxydated in dead cells (SooHoo & Kiefer 1982, Roy et al. 2006). Consequently, these pigments characterize physiological state of living algae from our melt ponds and their absence or really low proportion (< 5 %) supports the argument that they are in good physiological state.

1.8 CONCLUSION

During the melt season, melt ponds are oligotrophic environments, as shown by their low nutrient concentrations, algal biomass and primary production. The algal community >2 µm was numerically dominated by flagellates, the main group being unidentified flagellates and the secondary groups were chlorophytes, chrysophytes, prymnesiophytes and prasinophytes depending of the melt ponds. Pennate diatoms were also present in melt

ponds at variable concentrations. Incident PAR, salinity, and melt pond depth influenced the community composition.

Microalgae thriving in melt ponds were acclimated to their high irradiance environment. PPC were found in high proportion compared to chl *a* and to PSC. Moreover, diadino and diato represent only one-third of the PPC. In addition to PPC, algae protected themselves against high light with at least two MAAs, likely shinorine, and one unknown MAA named U2 by Elliott et al. (2015). These photoprotection strategies of algal cells were efficient since production:biomass ratios were relatively high and a low proportion (<5 % of chl *a*) of degradation pigments (chlide *a* and phytin *a*) was found. In this environment, light absorption coefficients by non-algal particles were about 10 times higher than those by algae. This suggests that NAP, empty diatom frustules, cysts and spores suspended and floating in melt ponds may also protect the algae against UV light-damage. This study also shows the high variability in taxonomic and pigment composition in melt ponds during summer.

CONCLUSION GÉNÉRALE

Les changements climatiques entraînent une augmentation de la fonte de la glace de mer en Arctique (Overland et Wang 2013). Cette augmentation est, en outre, accentuée par l'apparition de mares de fonte à la surface de la glace. Ces étangs, formés d'eau provenant de la fonte de la glace de mer et de la neige s'étant accumulée à l'interface glace-atmosphère, permettent une plus grande pénétration de la lumière à travers la glace, en plus d'accélérer la fonte de cette dernière (Maslanik et al. 2007, Perovich et al. 2007, Nicolaus et al. 2010). Bien que très étudiées en ce qui concerne la physique, les mares de fonte sont très peu connues en ce qui concerne leur biologie. Cette étude tente donc d'améliorer les connaissances biologiques de ce milieu éphémère. Les objectifs de ce travail visaient à (1) déterminer la production, la biomasse chlorophyllienne et la composition taxonomique des algues des mares de fonte ainsi que (2) d'identifier les conditions environnementales influençant cette communauté et (3) de déterminer si des adaptations pigmentaires sont présentes chez ces communautés exposées à de forts rayonnements solaires.

Cette étude corrobore les informations selon lesquelles les mares de fonte sont des environnements oligotrophes (Brinkmeyer et al. 2004). En effet, les mares de fonte ont des valeurs de concentration en éléments nutritifs, de production primaire et de biomasse chlorophyllienne faibles, souvent moins élevées que les valeurs retrouvées à la surface de la colonne d'eau dans la même région (Tremblay et al. 2009).

Les mares de fonte sont cependant habitées par plusieurs producteurs primaires, principalement des flagellées. La petite taille de ces derniers ainsi que la fragilité de leurs flagelles les rendent difficiles à identifier par microscopie inversée, ce qui explique la dominance des flagellés non identifiés dans nos échantillons. Il est cependant possible de distinguer quatre groupes de flagellés, qui sont présents en relativement grande proportion à certaines stations, comme les chlorophytes, les chrysophytes, les prymnésiophytes et les

prasinophytes. La grande variabilité des groupes de flagellés présents aux différentes stations de mares de fonte permet d'expliquer la forte richesse en taxons de cet environnement, malgré une faible richesse moyenne, pour chaque échantillon. La diversité en taxons est également moins élevée dans les mares à faible salinité (0,2–1,3 usp) que dans les mares à eau saumâtre (4,1–8,5 usp) ainsi qu'à la base de la glace et la surface de la colonne d'eau. Des diatomées sont également présentes dans les mares de fonte, les diatomées pennales dominant largement les centrales, mais aucune relation avec la salinité ne fut observée pour ce groupe algal.

Bien que les éléments nutritifs ne soient présents qu'en faible concentration dans les mares de fonte, ces derniers n'influencent pas significativement la répartition des différents groupes d'algues dans les mares de fonte. Par contre, la salinité de l'eau et la profondeur des mares semblent jouer un rôle important en favorisant les chlorophytes et les prymnésiophytes ainsi que les chrysophytes, respectivement. Une température plus élevée ainsi qu'un rayonnement photosynthétiquement actif plus faible semblent quant à eux favoriser les prasinophytes.

Finalement, un effort fut fourni afin d'étudier deux mécanismes de photoprotection, l'un impliquant les acides aminés de type mycosporine (MAAs) et l'autre, les pigments photoprotecteurs (PPC). Deux MAAs furent retrouvées dans les mares de fonte, possiblement la shinorine et un MAA inconnu, concordant ainsi avec l'étude d'Elliott et al. (2015). Les PPC étaient également présents dans une grande proportion, composant de 20 à près de 40 % de tous les pigments retrouvés dans les mares. Ces valeurs sont plus élevées que celles mesurées par Coupel et al. (2015) dans les eaux de surface de la mer de Beaufort, où un maximum de 20 % des pigments était des PPC. Également, la diadinoxanthine et la diatoxanthine ne représentent que le tiers des PPC, ce qui est nettement inférieur aux valeurs de près de deux tiers trouvées dans les eaux de surface de la mer de Beaufort par Alou-Font et al. (2016). Il est également possible d'affirmer que les algues se trouvant dans les mares de fonte ont un ratio PPC:PSC beaucoup plus élevé que ceux des algues se trouvant à la surface de l'eau et à la base de la glace. Ces résultats suggèrent une plus

grande concentration en caroténoïdes photosynthétiques dans les mares de fonte que dans les autres environnements marins.

Malgré la présence de spores, de kystes et d'une proportion élevée de frustules vides, les microalgues semblaient être en bon état physiologique dans les mares de fonte échantillonnées. En effet, les ratios production primaire : biomasse étaient relativement élevé et les concentrations en pigments de dégradation étaient faible dans toutes les mares échantillonnées. Ces résultats suggèrent que les stratégies de photoprotection sont efficaces, et ce chez plusieurs groupes de flagellés.

Cette étude a permis de caractériser les communautés d'algues vivant dans les mares de fonte de l'Arctique canadien, en plus d'être la première étude à s'intéresser à plusieurs stratégies de photoprotection chez ces communautés d'algues. Les mares de fonte sont des environnements représentatifs des eaux de fonte, qui seront plus abondantes dans les années à venir en raison de l'augmentation de la fonte de la glace de mer. Il est donc impératif de continuer à étudier les communautés qui y vivent et les facteurs qui les influencent.

ANNEXE

Table A1. Average similarity and main taxonomic groups composing the taxonomic based groups of melt pond during summer 2014. Cont: average contribution to a total ≥ 80 %

Group I (st Ice 5)		Group II (st Ice 2 MP1)	
Average similarity : 100 (only one sample)	Cont (%)	Average similarity : 100 (only one sample)	Cont (%)
Unidentified flagellates	68	Unidentified flagellates	87
Chlorophytes	19	Pennate diatoms	5

Group III (st Ice 2 MP2 and MP3)		Group IV (st Ice 4)	
Average similarity : 90	Cont (%)	Average similarity : 85	Cont (%)
Unidentified flagellates	65	Unidentified flagellates	54
Pennate diatoms	17	Chrysophytes	21
Prymnesiophytes	9	Pennate diatoms	19

Group V (st Ice 1)	
Average similarity : 94	Cont (%)
Unidentified flagellates	51
Prasinophytes	27
Pennate diatoms	10

Table A2. Average similarity and main pigments composing the pigment based groups of melt pond during summer 2014. Cont: average contribution to a total ≥ 60 %

Group I (st Ice 5)		Group II (st Ice 2 MP1)	
Average similarity: 100 (only one sample)	Cont (%)	Average similarity: 100 (only one sample)	Cont (%)
Lut	33	β,β-caro	36
Chl *b*	22	Viola	32
Zea	18		
Group III (st Ice 2 MP2 and MP3)		**Group IV (st Ice 3)**	
Average similarity: 79	Cont (%)	Average similarity: 74	Cont (%)
Lut	21	Fuco	28
Viola	19	Diadino	19
β,β-caro	16	Viola	18
Chl *b*	11		
Group V (st Ice1 and Ice 4)			
Average similarity: 76	Cont (%)		
Diadino	24		
Fuco	15		
Viola	12		
Lut	12		

Table A3. Occurrence of eukaryotic cells in different melt ponds at each sampling site during summer 2014.

Eukaryotic cells	Ice 5	Ice 4		Ice 3			Ice 2		Ice 1	
	MP1	MP1	MP2	MP1	MP2	MP1	MP2	MP3	MP1	MP2
Centric diatoms										
Attheya septentrionalis (Østrup) Crawford		X	X						X	X
Attheya cf. *septentrionalis*[1] (Østrup) Crawford			X							
Chaetoceros fallax Prosckina-Lavrenko									X	X
C. furcillatus Bailey (spores)									X	
C. gelidus Chamnansinp, Li, Lundholm & Moestrup										X
C. gelidus Chamnansinp, Li, Lundholm & Moestrup (spores)	X						X	X	X	X
C. tenuissimus Meunier									X	
C. wighamii Brightwell							X			X
Chaetoceros (spores)		X					X			
Chaetoceros spp. ≤ 5 µm		X	X						X	X
Chaetoceros spp. 6-10 µm		X	X				X	X	X	X
Chaetoceros spp. 11-20 µm							X		X	X
Thalassiosira spp. 11-20 µm							X		X	
Thalassiosira spp. > 20µm		X					X		X	
Pennate diatoms										
Cylindrotheca closterium (Ehrenberg) Reimann & Lewin		X	X	X		X	X	X	X	X
Fragilariopsis cylindrus (Grunow ex Cleve) Frenguelli			X							X
Navicula gelida var. *radissonii* Poulin & Cardinal									X	
Navicula pelagica Cleve		X	X				X	X	X	
Nitzschia frigida Grunow		X	X	X				X		
Nitzschia spp. ≤ 50 µm		X	X			X	X		X	X

Nitzschia spp. > 50µm		X	X	X			X	X	X	X
Pseudo-nitzschia cf. *delicatissima* (Cleve) Heiden								X	X	
Stauroneis radissonii Poulin & Cardinal					X		X			
Synedropsis hyperborea (Grunow) Hasle, Medlin & Syvertsen		X	X				X			
Pennates ≤ 10 µm	X	X	X	X	X		X	X	X	X
Pennates 11-20 µm		X	X	X	X	X	X	X	X	X
Pennates 21-50 µm		X	X	X	X	X	X	X	X	X
Pennates ≥ 50 µm		X	X						X	X
Naked dinophyceae										
Amphidinium cf. *kesslitzii* Schiller				X	X	X	X	X	X	
Amphidinium spp.	X	X							X	X
Gymnodinium / *Gyrodinium* complex 10-20 µm		X	X						X	
Gymnodinium / *Gyrodinium* 21-50 µm		X	X		X					
Gyrodinium impudicum Fraga & Bravo (cysts)			X							
Thecate dinophyceae										
Gonyaulax spp.		X								
Heterocapsa arctica Horiguchi									X	X
Heterocapsa spp.		X								
Dinophyceae 10-20 µm		X	X	X	X		X		X	X
Dinophyceae 21-50 µm	X	X	X		X					
Dinophyceae > 50 µm				X						
Polarella glacialis Montresor, Procaccini & Stoecker (cysts)		X	X	X	X				X	
Dinophyceae 10-20 µm (cysts)		X								
Dinophyceae 21-50 µm (cysts)		X	X		X					

Chlorophyceae										
Chlamydomonas 10-20 µm	X	X	X	X	X		X	X	X	X
Chlamydomonas 21-50 µm							X	X		
Chlorophyceae 5-10 µm										X
Chlorophyceae 11-20 µm				X					X	X
Chlorophyceae > 20 µm		X								
Chrysophyceae										
Chrysolykos cf. *angulatus* (Willén) Nauwerck		X	X	X	X	X	X	X	X	X
Dinobryon balticum (Schütt) Lemmermann						X			X	X
Dinobryon faculiferum (Willén) Willén		X							X	X
Dinobryon spp.		X	X		X				X	X
Mallomonas spp.			X							
Chrysophyceae (stomatocysts)		X	X		X	X	X	X	X	X
Chrysophyceae ≤ 5 µm							X			
Chrysophyceae 6-10 µm				X	X		X	X		
Chrysophyceae 11-20 µm			X	X	X					
Dictyochophyceae										
Pseudopedinella / *Mesopedinella* spp. ≤ 5 µm			X			X	X	X		
Pseudopedinella / *Mesopedinella* spp. 6-10 µm	X									
Cryptophyceae										
Hemiselmis spp.		X				X				
Plagioselmis prolonga var. *nordica* Novarino, Lucas & Morrall										X
Cryptophyceae 5-10 µm		X	X	X	X				X	X
Cryptophyceae 11-20 µm		X	X	X	X		X		X	X
Euglenophyceae										
Eutreptiella 10-20 µm									X	
Prasinophyceae										

Pterosperma spp.		X	X						X	
Pyramimonas sp. 1									X	X
Pyramimonas ≤ 5 µm		X								
Pyramimonas 6-10 µm		X	X	X			X		X	X
Pyramimonas 11-20 µm		X	X	X					X	X
Prasinophyceae 5-10 µm	X		X				X		X	
Prasinophyceae 11-20 µm	X		X							X
Prymnesiophyceae										
Chrysochromulina ≤ 5 µm	X					X	X	X	X	
Chrysochromulina 6-10 µm	X				X		X	X	X	X
Chrysochromulina 11-20 µm							X			
Prymnesiophyceae ≤ 5 µm	X		X	X		X	X	X	X	X
Prymnesiophyceae 6-10 µm	X	X		X	X	X	X	X	X	X
Prymnesiophyceae 11-20 µm		X					X		X	
Unidentified flagellates										
Flagellates ≤ 5 µm	X	X	X	X	X	X	X	X	X	X
Flagellates 6-10 µm	X	X	X	X	X	X	X	X	X	X
Flagellates 11-20 µm	X	X	X	X	X	X	X	X	X	X
Flagellates > 20 µm	X	X	X	X						
Heterotrophic group										
Cryothecomonas sp.	X	X								
Ebria tripartita (Schumann) Lemmermann									X	
Leucocryptos marina (Braarud) Butcher		X								
Quadricilia rotundata (Skuja) Vørs							X			
Telonema subtile Griessmann								X	X	X
Telonema sp. 1	X	X		X	X		X	X	X	
Flagellate sp. A	X	X				X		X	X	
Ciliates										
Didinium spp.						X				
Ciliates 21-50 µm	X		X	X	X		X	X	X	

Ciliates > 50 µm		X	X	X	X	X				
Number of species	2	10	8	5	4	5	9	8	15	12
Number of taxa	20	45	40	28	24	19	38	26	51	39
Number of genera	11	14	15	13	12	10	15	12	15	14

[1]Setae short and straight

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