UNIVERSITÉ DU QUÉBEC À RIMOUSKI

INFLUENCE DES FACTEURS DU MILIEU SUR LA STRUCTURE ET LE FONCTIONNEMENT DES COMMUNAUTÉS PHYTOPLANCTONIQUES DU HAUT-ARCTIQUE CANADIEN :

DISTINCTION DES RÉGIONS OLIGOTROPHES ET EUTROPHES

Mémoire présenté

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PAR

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Dans les sciences, le chemin est plus important que le but.
Les sciences n'ont pas de fin.

Erwin Chargaff

La science ne sert guère qu'à donner une idée
de l'étendue de notre ignorance

Félicité de Lamennais

La science consiste à passer d'un étonnement à un autre

Aristote

AVANT-PROPOS

Ce mémoire traite de l'influence des variables du milieu sur la structure et la dynamique des communautés phytoplanctoniques du Haut-Arctique canadien. Il est composé d'une introduction générale, d'un chapitre central présenté sous la forme d'un article scientifique et d'une conclusion générale. Dans un proche avenir, cet article sera soumis à une revue scientifique avec comité de lecture. Cette étude porte sur cinq années consécutives d'échantillonnage dans le Haut-Arctique canadien lors de missions océanographiques menées par le Réseau des Centres d'excellence du Canada (RCE) ArcticNet de 2005 à 2010 et l'Étude du chenal de séparation circumpolaire / Circumpolar Flaw Lead (CFL) system study en 2007. Les résultats de cette étude ont été présentés à plusieurs ateliers et congrès scientifiques sous forme d'affiches (en 2008 : *Assemblée générale annuelle de Québec-Océan*, Rivière-du-Loup et *Arctic Change Conference*, Québec; en 2009 : *Assemblée générale annuelle de Québec-Océan*, Rimouski et *CFL All-Hands Meeting*, Winnipeg; en 2010 : *Malina Plenary Meeting*, Villefranche-sur-Mer, France, *International Polar Year-Oslo Science Conference*, Oslo, Norvège et le Symposium sur la biodiversité arctique, Ottawa, Canada) et de présentations orales (en 2009 : programme *School on board* à bord du NGCC *Amundsen*, *Symposium of Association of Polar Early Career Scientists* (APECS), Victoria et *Réunion scientifique annuelle ArcticNet*, Victoria; en 2010 : *Malina Plenary Meeting*, Villefranche-sur-Mer, France; en 2011 : *Arctic Frontiers*, Tromsø, Norvège). Les résultats de cette étude ont également été utilisés pour établir de nouveaux outils et techniques de vulgarisation et de communication pour une meilleure compréhension de la science par le grand public dans le cadre de l'Année polaire internationale (API). Ce travail, réalisé en collaboration avec le Dr David Carlson (Directeur de l'API et de l'Office des programmes internationaux), a fait l'objet d'une présentation orale durant l'*International Polar Year-Oslo Science Conference* en juin 2010 et d'un article à venir dans une revue scientifique avec comité de lecture.

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Pour conclure, l'acheminement à cette étape de mon parcours personnel et professionnel n'aurait jamais été possible sans le soutien inconditionnel de ma famille dans ma soif d'initiatives, de découvertes et de voyages.

RÉSUMÉ

Une étude biogéographique a été menée dans le Haut-Arctique canadien, afin d'examiner la dynamique phytoplanctonique en relation avec les facteurs du milieu. Lors de radiales de 3500 km couvrant la mer de Beaufort, l'archipel canadien et la baie de Baffin, un ensemble de variables environnementales (i.e. la structure hydrographique, et les conditions atmosphériques et celles du couvert de glace de mer) et biologiques ont été mesurées dans la zone euphotique pendant la fin de l'été en 2005, le début de l'automne en 2006 et l'automne en 2007. La production et la biomasse (chlorophylle (chl) *a*) phytoplanctonique ont été mesurées à sept profondeurs optiques et à la profondeur du maximum de fluorescence chlorophyllienne (Z_{DCM}). De plus, la composition taxinomique, l'abondance et la structure de taille du phytoplancton ont été caractérisées au Z_{DCM}. À l'aide d'analyses multidimensionnelles (i.e. analyses de redondance et analyses multidimensionnelles non métriques), les interactions entre la composition phytoplanctonique et les variables environnementales et biologiques ont été examinées. Deux régimes phytoplanctoniques distincts de par la production, la biomasse, l'abondance et la structure de taille des communautés, ont ainsi pu être mis en évidence : un système basé sur les flagellés situé au sud-ouest de la mer de Beaufort, dans le golfe Amundsen et la partie centrale de l'archipel canadien et un système basé sur les diatomées caractérisant la baie de Baffin, le détroit de Lancaster et le centre du golfe Amundsen. Les régions oligotrophes sont, d'une part, caractérisées par une faible production et une faible biomasse de cellules phytoplanctoniques de grande taille (> 5 µm) et, d'autre part, par une abondance relative élevée de picophytoplancton eucaryote (< 2 µm) et de nanoflagellés non identifiés (2 – 20 µm). En contraste, les régions eutrophes sont caractérisées par une forte production et une forte biomasse de cellules phytoplanctoniques de grande taille, en majeure partie des diatomées centrales surtout représentées par le genre *Chaetoceros*. Les différences entre ces deux régimes phytoplanctoniques sont expliquées, en grande partie par une faible stratification de la colonne d'eau et de fortes concentrations de nitrates au niveau du Z_{DCM} dans les régions eutrophes *versus* oligotrophes. Cette étude démontre le rôle clé du mélange vertical et des apports en nutriments sur le type de régime et de communautés phytoplanctoniques,

soulignant la diversité de régions biogéographiques pouvant être significativement perturbées par les changements en cours dans l'Arctique.

ABSTRACT

A large-scale biogeographic study was conducted to assess phytoplankton dynamics and its environmental control across the Canadian High Arctic. Repeated 3500 km transects across the Beaufort Sea, the Canadian Arctic Archipelago and Baffin Bay provided the opportunity to measure environmental (i.e. hydrographic structure, atmospheric and sea ice conditions) and biological variables measured in the upper water column during late summer 2005, early fall 2006 and fall 2007. Phytoplankton production and chlorophyll (chl) *a* biomass were measured at seven optical depths and at the depth of maximum chl *a* fluorescence (Z_{DCM}). In addition, phytoplankton taxonomic composition, abundance and size structure were determined at the Z_{DCM}. Redundancy analyses and non-metric multidimensional scaling were used to assess relationships between phytoplankton composition in relation to biological and environmental variables. Two distinct phytoplankton regimes were documented based on the production, biomass, abundance and size structure of phytoplankton communities: (1) a flagellate-based system extending over the eastern Beaufort Sea, the Amundsen Gulf and the central part of the Canadian Arctic Archipelago, and (2) a diatom-based system centered in Baffin Bay, Lancaster Sound and in central Amundsen Gulf. The oligotrophic regions were characterized by low production and biomass of large phytoplankton cells ($> 5\ \mu m$) and high relative abundance of eukaryotic picophytoplankton ($< 2\ \mu m$) and unidentified nanoflagellates ($2 - 20\ \mu m$). The eutrophic regions were characterized by high production and biomass of large cells and high relative abundance of centric diatoms, mainly *Chaetoceros* species. The differences between the two phytoplankton regimes were explained, in part, by differences in stratification of the water column and nitrate concentrations at the Z_{DCM}. This study demonstrates the key role of water column mixing and nutrient input on phytoplankton communities and regimes in the Canadian High Arctic, underpinning a diversity of biogeographic regions that may be significantly altered by ongoing Arctic changes.

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1. INTRODUCTION GÉNÉRALE

1.1 LA STRUCTURE DES RÉSEAUX TROPHIQUES PÉLAGIQUES

Les travaux fondamentaux de Margalef (1978, 1997), Margalef et al. (1979), Cushing (1989), Legendre & Le Fèvre (1989), Legendre & Rassoulzadegan (1995) et Legendre et al. (1993) ont contribué à établir les bases et les théories sur l'écologie du phytoplancton marin. Cette science requiert une approche pluridisciplinaire en associant différents domaines de l'océanographie : la physique, la chimie ainsi que la biologie afin de mieux comprendre les processus et les interactions entre les communautés phytoplanctoniques et le milieu ambiant. Plusieurs modèles ont mis en évidence des relations entre la turbulence, les teneurs en nutriments et les caractéristiques physiologiques adaptatives et écologiques du phytoplancton dans leur milieu naturel (Margalef et al. 1979, Levasseur et al. 1984, Legendre & Rassoulzadegan 1995, Cullen et al. 2002). L'un de ces modèles conceptuels est décrit à la Figure 1. Dans ce modèle, on distingue quatre types de régime phytoplanctonique ayant chacun des propriétés biologiques spécifiques et bien définies, entre autres, par la structure de taille, la biomasse, l'activité physiologique (e.g. taux de prise des nutriments, taux photosynthétique) et la composition taxinomique de la communauté phytoplanctonique. L'intensité de la stratification verticale détermine, en partie, le type de régime phytoplanctonique prédominant dans le milieu en contrôlant le renouvellement des nutriments dans la couche supérieure de la colonne d'eau. Le rapport surface:volume des cellules est l'un des éléments-clés de la réponse du phytoplancton aux apports en nutriments. Les milieux turbulents à fortes concentrations en nutriments favorisent la croissance et l'accumulation des grosses cellules algales au détriment des plus petites.

Au contraire, les milieux stratifiés et pauvres en nutriments favorisent le développement des petites cellules algales, en raison du rapport surface:volume élevé, permettant ainsi une meilleure accessibilité aux nutriments. Les régimes phytoplanctoniques sont donc fortement influencés par la turbulence et les teneurs en nutriments dans le milieu. Ainsi les milieux eutrophes et oligotrophes permettent le développement de deux régimes phytoplanctoniques distincts.

1.1.1 Milieu eutrophe : forte turbulence et forte teneur en nutriments

Margalef (1978) a démontré le rôle crucial de la turbulence permettant le renouvellement des éléments nutritifs dans la couche supérieure de la colonne d'eau en soutenant un régime phytoplanctonique composé de grandes cellules. Ce régime phytoplanctonique dominé par des diatomées est souvent caractérisé par une forte biomasse algale et une forte production primaire. Ce régime permet le développement d'un réseau alimentaire herbivore caractérisé par un transfert important de la production primaire vers les niveaux trophiques supérieurs comme les poissons et les mammifères marins (Michaels & Silver 1988, Legendre & Le Fèvre 1989, Kiørboe 1993) ainsi qu'une exportation relativement importante de la matière organique particulaire vers les profondeurs océaniques (Eppley & Peterson 1979, Michaels & Silver 1988).

1.1.2 Milieu oligotrophe : faible turbulence et faible teneur en nutriments

Les milieux aquatiques soumis à de faibles turbulences et à de faibles teneurs en nutriments sont régis principalement par de petites cellules algales, le picophytoplancton (0,2 – 2 µm; Waterbury et al. 1979, Chisholm et al. 1988), et par des bactéries hétérotrophes, d'où le concept de la boucle microbienne (Azam et al. 1983, Landry et al. 1997). Dans de tels systèmes, la production primaire est contrôlée par la régénération des nutriments (e.g. ammonium) permettant un fonctionnement autosuffisant (boucle *fermée*). Dans ces systèmes, une faible fraction de la production primaire est disponible pour les niveaux trophiques supérieurs et l'exportation en profondeur (Legendre & Le Fèvre 1989, Peinert et al. 1989, Kiørboe 1993).

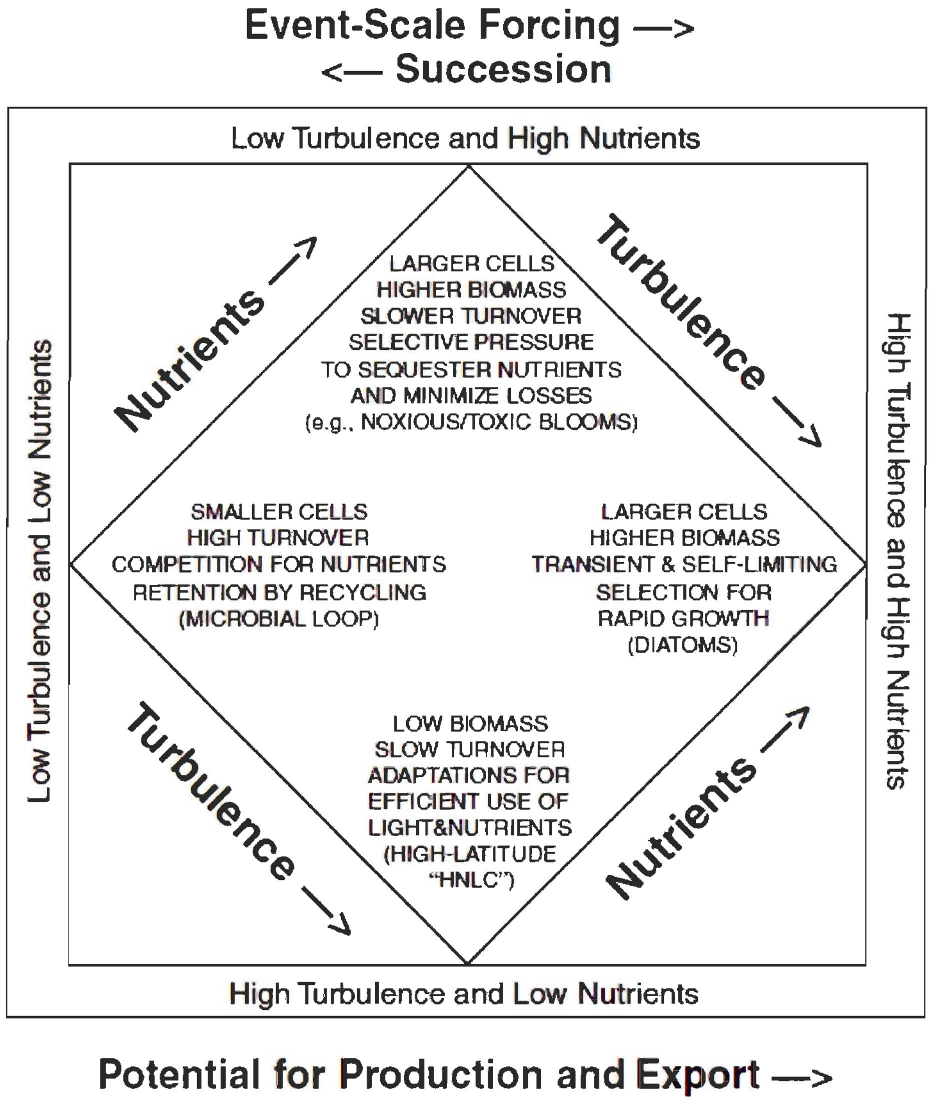

Fig. 1. Interactions entre la turbulence, les teneurs en nutriments et les caractéristiques du réseau trophique phytoplanctonique (Tirée de Cullen et al. (2002) d'après Margalef et al. (1979)).

1.2 LE CONCEPT DES OCEANS *ALPHA* (α) ET *BETA* (ß)

Dans cette même perspective de caractériser les régimes phytoplanctoniques selon la structure hydrographique, le concept des océans *alpha* (α) et *beta* (ß*)* pour les mers septentrionales de l'hémisphère Nord a été proposé à l'origine par Tully & Barber (1960) et récemment actualisé par Carmack & Wassmann (2006) (Fig. 2).

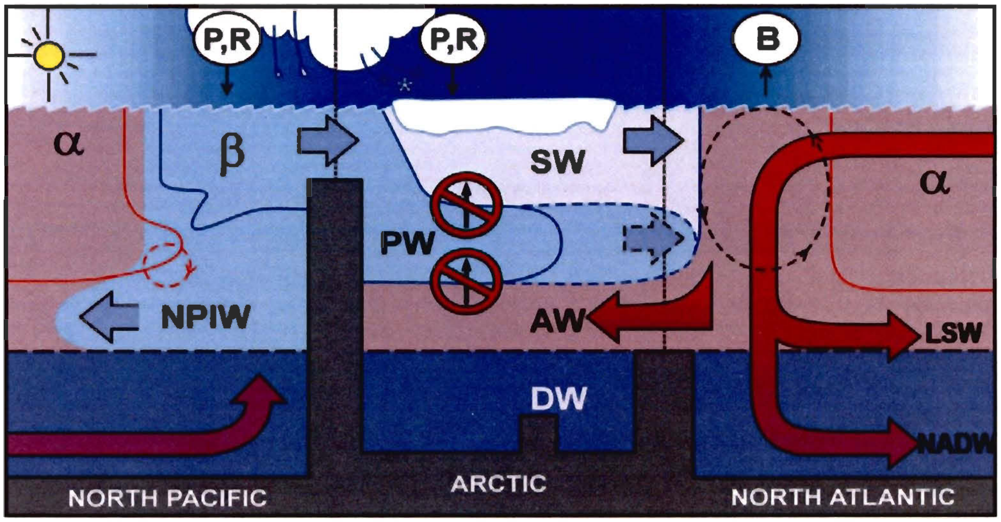

Fig. 2. Schéma de l'océanographie physique des océans Arctique, Pacifique Nord et Atlantique Nord, caractérisant les océans *alpha* (α) et *beta* (ß*)*. P = précipitation, R = apports terrestres en eau douce, B = turbulence, LSW = eau de la mer du Labrador (Labrador Sea water); NADW = eau profonde de l'Atlantique Nord (North Atlantic Deep water); NPIW = eau intermédiaire du Pacifique Nord (North Pacific Intermediate water); PW = eau pacifique (Pacific water); AW = eau atlantique (Atlantic water); SW = eau de surface (Surface water); DW = eau de fond (Deep water) (Tirée de Carmack & Wassmann 2006).

En accord avec les travaux fondamentaux présentés ci-dessus, la stratification verticale de la colonne d'eau est de nouveau décrite comme une variable importante des océans impliquée au niveau du climat et de la biologie (Carmack & Wassmann 2006, Carmack 2007). La structure verticale des océans *alpha* et *beta* est respectivement régie par la température et la salinité. Les océans *beta* sont caractérisés par une forte accumulation de la biomasse chlorophyllienne dans la zone euphotique lors des blooms phytoplanctoniques, mais aussi par une faible production primaire annuelle. Quant aux océans *alpha*, ils sont caractérisés par une faible accumulation de la biomasse chlorophyllienne et par une forte production primaire annuelle (Carmack & Wassmann 2006). Cette distinction entre les océans *alpha* et *beta* est une aide précieuse supplémentaire pour caractériser les régimes phytoplanctoniques à grande échelle.

Dans la présente section, l'accent a été mis sur la compréhension des régimes phytoplanctoniques et la particularité des zones de hautes latitudes (Carmack 2007). La stratification de la colonne d'eau est sans conteste un élément-clé agissant directement sur la disponibilité de la lumière et des nutriments pour les communautés phytoplanctoniques (Margalef 1978, Carmack 2007, Tremblay et al. 2009) et, par conséquent, la détermination du type de régime phytoplanctonique. Cependant, d'autres facteurs du milieu tels que la température (Agawin et al. 2000), les propriétés optiques de l'eau (Retamal et al. 2008) ou encore la qualité des sources azotées, en référence aux sources allochtone *versus* autochtone (Garneau et al. 2007), influencent aussi la production primaire. De plus, la présence de glace de mer aux hautes latitudes peut limiter la pénétration de la lumière nécessaire pour soutenir la production phytoplanctonique (Fortier et al. 2002). Dans l'océan Arctique, la saison productive couvre généralement une période de deux à quatre mois, entre mai et septembre, selon les dynamiques interannuelles de fonte et de formation des glaces de mer (Gosselin et al. 1997, Lovejoy et al. 2002a, Wassmann et al. 2006). La compréhension du rôle des facteurs du milieu apparaît ainsi comme une exigence incontournable pour caractériser les régimes phytoplanctoniques, surtout dans un contexte de réchauffement climatique.

1.3 CONTEXTE DE L'ÉTUDE

Des perturbations environnementales majeures, affectant plus spécifiquement l'équilibre fragile des réseaux trophiques arctiques, ont cours actuellement et vont vraisemblablement s'intensifier dans les prochaines décennies (e.g. ACIA 2005, IPCC 2007, Barber et al. 2008). La diminution accélérée de l'étendue des glaces de mer en période estivale est maintenant devenue une réalité dans l'hémisphère Nord (Stroeve et al. 2007, Comiso et al. 2008, Kwok et al. 2009). Wang & Overland (2009) prévoient des saisons estivales sans glace de mer dans l'océan Arctique d'ici 2037. L'étude menée par Ogi et al. (2010) sur les 31 dernières années démontre que 50% de la variabilité du minimum estival de la couverture de glace dans l'océan Arctique serait imputable à la combinaison des régimes de vents hivernaux et estivaux. De plus, l'augmentation de la fréquence et de l'intensité des tempêtes atmosphériques (McCabe et al. 2001, Zhang et al. 2004) aura pour effet d'amplifier les épisodes de mélange vertical de la colonne d'eau dans un océan ouvert libre de glace. D'importantes modifications dans le cycle hydrologique (Peterson et al. 2002, Serreze et al. 2006), telles que l'augmentation des précipitations aux hautes latitudes et la fonte de la glace de mer, contribuent à augmenter les apports d'eau douce (Peterson et al. 2006). Une réduction de la circulation thermohaline a été corrélée à une augmentation des apports d'eau douce dans l'Atlantique Nord, engendrée par des modifications de l'export et la fonte de glaces de mer provenant de l'archipel canadien et du détroit de Fram (Dickson et al. 2002, Curry & Mauritzen 2005, Serreze et al. 2006). D'autres conséquences importantes des changements climatiques se traduisent par un réchauffement global de l'océan Arctique (Polyakov et al. 2005) ainsi que par des changements majeurs dans la répartition des masses d'eau (Carmack et al. 1995). Les eaux de l'Atlantique se réchauffent et une nouvelle répartition des eaux de l'Atlantique et du Pacifique est observée dans l'océan Arctique (Carmack et al. 1995). Ces grands bouleversements seraient imputables à des changements dans la circulation atmosphérique (Proshutinsky & Johnson 1997) et à une augmentation des apports d'eau atlantique dans l'océan Arctique (Dickson et al. 2000). Les conséquences du réchauffement climatique sont telles qu'elles soumettent ainsi les écosystèmes arctiques marin et terrestre à de fortes pressions environnementales (Grebmeier et al. 2006, Moline et al. 2008, Post et al. 2009).

Une augmentation de l'étendue de la couverture des glaces de première année et la fonte accélérée des glaces pluriannuelles ont indéniablement des conséquences sur l'écosystème associé aux glaces de mer. Par exemple, Mel'nikov (2008) a rapporté une perte de la diversité des communautés de glace au cours des trente dernières années, vraisemblablement liée à la diminution du couvert de glace pluriannuelle. Cet auteur suggère d'ailleurs qu'en Arctique, les écosystèmes associés aux glaces sont en perte d'importance écologique au profit des systèmes pélagiques. De tels changements risquent d'entraîner des perturbations au niveau des interactions entre les écosystèmes sympagiques, pélagiques et benthiques (Arrigo et al. 2008, Tremblay & Gagnon 2009). Dans le détroit de Béring, Grebmeier et al. (2006) a montré des modifications fondamentales des réseaux trophiques occasionnées par la réduction du couvert de glace ainsi que par l'augmentation des températures atmosphériques et océaniques. Au cours des trois dernières décennies, les communautés benthiques et de mammifères marins, favorisées par les écosystèmes associés aux glaces, ont été remplacées par des populations de poissons pélagiques (Grebmeier et al. 2006). Cette restructuration écosystémique aurait entraîné également un déplacement des aires de répartition des mammifères marins (Grebmeier et al. 2006). Concernant la mer de Laptev, une étude récente indique plutôt une augmentation de l'exportation du carbone organique particulaire et une amplification du couplage entre les écosystèmes pélagiques et benthiques (Lalande et al. 2009). Malgré des conclusions parfois divergentes, différentes études s'accordent pour souligner le rôle primordial du broutage zooplanctonique sur l'efficacité de rétention du carbone dans la colonne d'eau, affectant directement l'intensité du couplage pélago-benthique (Wassmann et al. 2004, Sakshaug 2004, Lalande et al. 2009).

Outre des modifications de la couverture et des caractéristiques des glaces de mer dans l'océan Arctique, la dynamique de fonte et de formation de la banquise est également perturbée (Arrigo et al. 2008, Markus et al. 2009). Liés à ces modifications, des asynchronismes temporels et spatiaux importants se produisent à travers le réseau trophique provoquant des déséquilibres biologiques majeurs (Edwards & Richardson 2004). Par exemple, une étude en mer du Nord a démontré l'impact direct des changements dans la dynamique des glaces de mer sur les réponses écophysiologiques des producteurs primaires et secondaires (Edwards & Richardson 2004). Dans un océan en pleine transition, des phénomènes tels que les déplacements de niches écologiques, des bouleversements au niveau des interactions entre les écosystèmes sympagiques, pélagiques et benthiques risquent de s'amplifier.

1.4 PROBLÉMATIQUE : INCERTITUDES DES RÉPONSES DES COMMUNAUTÉS PHYTOPLANCTONIQUES DE L'ARCTIQUE AUX CHANGEMENTS CLIMATIQUES

Étant donné le rôle crucial de la lumière et de la stratification verticale de la colonne d'eau implicitement liée à la couverture de la glace de mer, une attention particulière doit être accordée à ces deux variables par rapport aux changements environnementaux en cours dans l'océan Arctique. La réduction de l'étendue et de l'épaisseur du couvert de glace de mer, ainsi que les changements dans la dynamique de la fonte et de la formation de la glace entraîneront une modification de la disponibilité de la lumière (ACIA 2005) pour le système pélagique en plus d'accroître la durée de la saison de production dans les mers arctiques (Arrigo et al. 2008, Kahru et al. 2010). Grâce à l'imagerie satellitaire, Arrigo et al. (2008) ont estimé une augmentation moyenne de la production annuelle dans l'océan Arctique de 27,5 Tg C a^{-1} entre 2003 et 2006 et de 35 Tg C a^{-1} entre 2006 et 2007. Trente pourcents de cette augmentation serait imputable à la réduction du minimum estival de l'étendue du couvert des glaces pluriannuelles et 70% à une saison de croissance prolongée. Pour leur part, Rysgaard et al. (1999) ont suggéré que l'augmentation de la production primaire annuelle dans les eaux arctiques était directement corrélée à la durée de la saison de production. Cependant, Tremblay & Gagnon (2009) ont proposé que la variabilité de la production primaire annuelle en océan libre de glace serait régulée par des forçages environnementaux contrôlant les apports en nutriments dans la partie supérieure de la colonne d'eau. Ainsi la stratification serait un facteur déterminant permettant de comprendre les possibles changements de la production primaire dans l'océan Arctique.

À l'aide de données historiques sur la transparence de l'eau et d'images satellitaires, Boyce et al. (2010) ont rapporté une baisse globale de 1% par année de la biomasse phytoplanctonique dans les 20 premiers mètres de la colonne d'eau entre 1899 et 2005. L'imagerie satellitaire a également montré une diminution globale de la production primaire de 190 Tg C a^{-1} entre 1999 et 2006 (Behrenfeld et al. 2006), ainsi qu'une augmentation de l'étendue des zones oligotrophes dans les océans méridionaux

(Polovina et al. 2008). De 1999 à 2004, une augmentation significative de la stratification des eaux de surface par le réchauffement solaire aurait réduit les apports en nutriments des eaux profondes dans la majeure partie des océans mondiaux (Behrenfeld et al. 2006). Une intensification de la stratification des eaux de surface a également été observée dans le Bassin canadien entre 2003 et 2008 (Li et al. 2009, Yamamoto-Kawai et al. 2009, McLaughlin & Carmack 2010). Dans cette région arctique, le réchauffement et l'adoucissement de la couche supérieure de la colonne d'eau ont entraîné un appauvrissement en nutriments des eaux de surface et le remplacement du phytoplancton de grande taille (2 – 20 µm) par des cellules algales de plus petite taille (< 2 µm) (Li et al. 2009). Des modifications de la stratification de la colonne d'eau reliées aux changements climatiques auront vraisemblablement des répercussions majeures sur la dynamique du phytoplancton dans l'océan Arctique. Toutefois, des incertitudes demeurent quant à la réponse des communautés phytoplanctoniques au réchauffement climatique. Le Haut-Arctique canadien apparaît ainsi comme une zone d'étude intéressante, vu sa complexité biogéographique et le manque de connaissance concernant les processus affectant les communautés phytoplanctoniques arctiques.

1.5 ZONE D'ÉTUDE

Cette étude a été réalisée dans le cadre du programme ArcticNet, un réseau de Centres d'excellence du Canada traitant des impacts du réchauffement climatique dans l'Arctique canadien côtier. Ce travail s'intègre aussi à l'Étude du chenal de séparation circumpolaire / Circumpolar Flaw Lead (CFL) system study, un projet canadien de l'Année polaire internationale, qui a pour but d'étudier l'effet des changements physiques sur les processus biologiques dans la zone du chenal de séparation du secteur canadien de la mer de Beaufort.

Le Haut-Arctique canadien est composé de trois régions biogéographiques aux propriétés physiques, chimiques et biologiques distinctes: (1) la mer de Beaufort, (2) l'archipel Arctique canadien et (3) la baie de Baffin (Fig. 3).

Dans cette étude, le secteur canadien de la mer de Beaufort comprend le plateau et le talus continental du Mackenzie ainsi que le golfe Amundsen. Le plateau continental est délimité par le canyon du Mackenzie à l'ouest, le talus continental du Mackenzie et le Bassin canadien au nord, le golfe Amundsen à l'ouest et le delta du Mackenzie au sud (Carmack et al. 2004). Le plateau continental est relativement plat, peu profond (0 – 80 m) et s'étend sur quelque 115 km vers le large avec la présence de deux canyons au niveau du talus continental : le canyon du Mackenzie au sud-ouest et le golfe Amundsen au nord-est (Williams & Carmack 2008). Le golfe Amundsen relie le sud-ouest de la mer de Beaufort à l'archipel Arctique canadien par le détroit de Dolphin et Union et il est relativement peu profond (moyenne de 150 m), sauf en son centre qui peut atteindre une profondeur d'environ 500 m. Il est aussi caractérisé par la polynie du cap Bathurst, un chenal de séparation qui se forme en hiver entre la banquise côtière et les glaces dérivantes. Globalement, le secteur canadien de la mer de Beaufort est peu productif dû à la stratification permanente des eaux de surface polaires qui limite les échanges avec les eaux intermédiaires du Pacifique riches en nutriments (Carmack et al. 2004, Tremblay et al. 2008, Brugel et al. 2009). La forte stratification des eaux de surface est liée à une combinaison de facteurs incluant les apports en eau douce provenant du fleuve Mackenzie et de la fonte de la glace de mer, et la présence d'un couvert de glace d'octobre à juin qui réduit le mélange de la colonne d'eau par le vent au cours de l'automne et de l'hiver (Barber & Hanesiak 2004, Carmack et al. 2004, Tremblay et al. 2008, Williams & Carmack 2008).

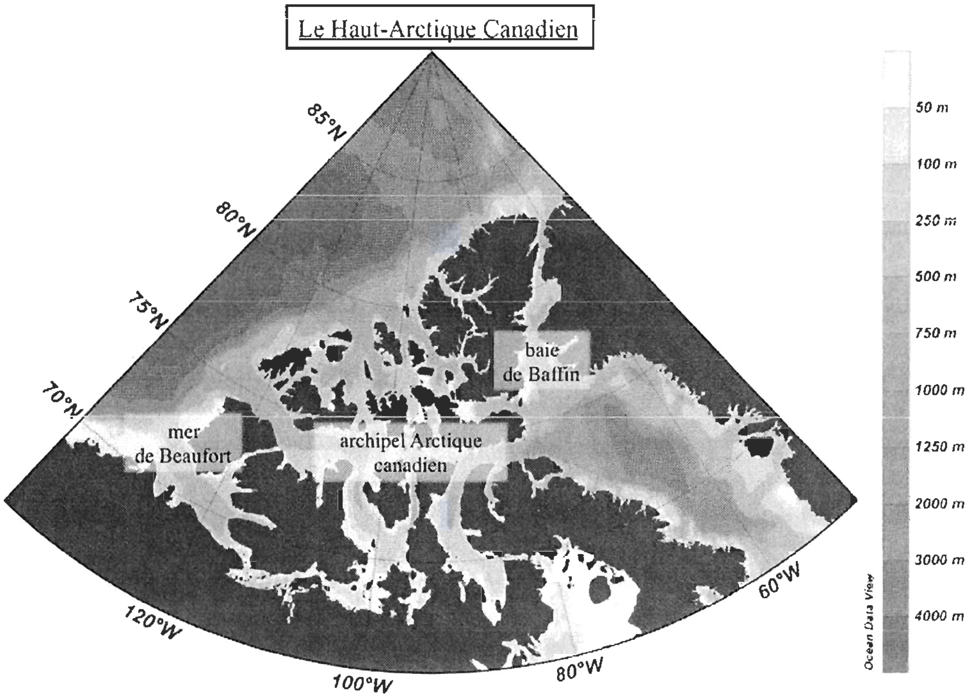

Fig. 3. Carte des différentes régions biogéographiques du Haut-Arctique canadien, avec une échelle bathymétrique en mètres.

L'archipel Arctique canadien est considéré comme une zone large et complexe du plateau continental de l'océan Arctique avec des canaux reliant des bassins océaniques séparés par des seuils (Michel et al. 2006). La topographie et les processus d'échange déterminent la circulation et le transport des masses d'eau (Melling et al. 2001). L'archipel est une zone primordiale pour les flux d'eau douce dans l'océan Arctique (Serreze et al. 2006). La dynamique et les caractéristiques des glaces de mer dans l'archipel demeurent encore aujourd'hui méconnues, s'expliquant en grande partie par sa complexité géographique (Howell et al. 2008). Les mécanismes en action dans le passage du Nord-Ouest, dont celui du drain à siphon, continueront d'y favoriser la présence continuelle de glace pluriannuelle pendant de nombreuses années (Howell et al. 2008). Le passage du Nord-Ouest constitue la voie principale de l'archipel reliant la mer de Beaufort à l'ouest à la baie de Baffin à l'est. En été, la répartition spatiale du phytoplancton est hétérogène dans le passage du Nord-Ouest; la communauté phytoplanctonique > 2 µm est dominée par des eucaryotes unicellulaires flagellés dans le secteur ouest de l'archipel et par des diatomées dans le détroit de Lancaster dans l'est de l'archipel (Tremblay et al. 2009).

Au nord de la baie de Baffin se situe la polynie des eaux du Nord, la plus grande polynie récurrente de l'Arctique (Smith & Rigby 1981, Stirling 1997, Barber & Massom 2007). Elle se forme généralement en avril et disparaît en juillet lorsque le pont de glace du bassin de Kane se brise et que la glace de mer au sud du 76^{e} parallèle se disloque (Ingram et al. 2002). L'ouverture et le maintien de la polynie des eaux du Nord dépendent d'une combinaison de mécanismes de chaleur latente et de chaleur sensible (Myzak & Huang 1992, Barber et al. 2001, Ingram et al. 2002). La polynie des eaux du Nord est considérée comme le système marin le plus productif au nord du cercle Arctique (Stirling 1997, Klein et al. 2002, Tremblay et al. 2002), ce qui s'explique par des remontées d'eau profonde intermittentes de nutriments soutenant des floraisons algales de longue durée (Lovejoy et al. 2002b, Tremblay et al. 2002). Cette région se caractérise par une première floraison intense de diatomées au printemps, suivie d'une seconde de moindre intensité à la fin de l'été (Mostajir et al. 2001, Booth et al. 2002, Klein et al. 2002, Caron et al. 2004, Garneau et al. 2007).

1.6 OBJECTIFS DE L'ÉTUDE

L'objectif général de cette étude est de documenter la variabilité spatiale du phytoplancton dans les principales régions biogéographiques du Haut-Arctique canadien à la fin des étés 2005, 2006 et 2007. Les objectifs spécifiques sont de: (1) caractériser la variabilité spatio-temporelle de la production, de la biomasse et de la structure de taille des communautés phytoplanctoniques, (2) déterminer l'influence des variables abiotiques et biologiques sur les caractéristiques des communautés phytoplanctoniques arctiques, et de (3) discuter dans le contexte du changement climatique, de l'impact potentiel des changements environnementaux sur les communautés et régimes phytoplanctoniques arctiques.

2. INFLUENCE OF ENVIRONMENTAL FACTORS ON THE STRUCTURE AND FUNCTION OF PHYTOPLANKTON COMMUNITIES IN THE CANADIAN HIGH ARCTIC:

DISTINCTION BETWEEN OLIGOTROPHIC AND EUTROPHIC REGIONS

2.1 INTRODUCTION

Polar regions are under severe environmental changes caused by global warming (ACIA 2005, IPCC 2007, Barber et al. 2008, Wassmann et al. 2010). The rapid decline of the sea ice cover in the Northern Hemisphere (Stroeve et al. 2007, Comiso et al. 2008, Kwok et al. 2009) has led to predictions of a sea ice free summer Arctic by the year 2037 (Wang & Overland 2009). Although the causes of the rapid decrease in sea ice extent are not fully elucidated yet, Ogi et al. (2010) recently showed that the combined effect of winter and summer wind forcing accounted for 50% of the variance in summer sea ice extent over the past three decades. Sea ice melt also contributes to significant freshwater input (Peterson et al. 2006, McPhee et al. 2009) which, combined with increased precipitation and an intensification of the hydrological cycle (Peterson et al. 2002, Serreze et al. 2006), increases the stratification of the water column (Behrenfeld et al. 2006, Yamamoto-Kawai et al. 2009). In addition, the dynamics of sea ice formation and melt is disturbed, affecting light availability (ACIA 2005) and the duration of the phytoplankton growing season (Arrigo et al. 2008, Kahru et al. 2010). Other changes taking place in the Arctic include: significant warming of the Arctic Ocean (Polyakov et al. 2005), changes in water mass characteristics and distribution (Shimada et al. 2006, Dmitrenko et al. 2008), and an increase in the frequency and intensity of storms (McCabe et al. 2001, Zhang et al. 2004), suggesting that episodes of vertical mixing will be more frequent in the future. Clearly, these alterations expose marine and terrestrial Arctic ecosystems, as well as their trophic structure, to high environmental pressures (Grebmeier et al. 2006, Moline et al. 2008, Post et al. 2009, Wassmann et al. 2010).

The balance between stratification and mixing, and the light regime, both implicitly linked to the sea ice cover, require special attention with respect to their control of phytoplankton production in the Arctic Ocean. Rysgaard et al. (1999) suggested that the annual primary production is correlated to the length of the growth season in the Arctic. Glud et al. (2007) later showed, with *in situ* experiments, that spring primary production was light limited in the Arctic. Recently, Tremblay & Gagnon (2009) showed that changes in annual primary production in ice-free waters of the Arctic are controlled by dissolved nitrogen supply rather than light availability. In line with fundamental ecological phytoplankton models (Margalef et al. 1979, Legendre & Rassoulzadegan 1995, Cullen et al. 2002), vertical stratification has been highlighted a key controlling factor of the productivity and structure of marine ecosystems of the Arctic Ocean (Carmack & Wassmann 2006, Carmack 2007). Vertical mixing determines, in part, the productivity regime and phytoplankton size structure (i.e. flagellate-based *versus* diatom-based systems), by favoring possible nutrient replenishment in the upper water column. Flagellate-based systems are typically supported by autochthonous (regenerated) nutrients, and are mainly characterized by picophytoplankton (< 2 µm), heterotrophic bacteria and heterotrophic nanoflagellates (Azam et al. 1983, Landry et al. 1997). In contrast, diatom-based systems are composed of large phytoplankton cells, taking up allochthonous (new) nutrients replenished by physical forcing events (Cushing et al. 1989). These two distinct phytoplankton regimes are present in the Arctic Ocean and adjacent seas (e.g. flagellate-based system: Legendre et al. 1993, Booth & Horner 1997, Tremblay et al. 2009, Li et al. 2009; diatom-based systems: Mostajir et al. 2001, Booth et al. 2002, Hill et al. 2005). These studies highlight the need to further investigate the large-scale distribution of phytoplankton regimes and its physical forcing in the Arctic Ocean.

There is evidence of a global decrease in phytoplankton biomass over the past century (Boyce et al. 2010), and an expansion of oligotrophic areas in the world's oceans (Polovina et al. 2008). From 1999 to 2004, a significant increase in vertical stratification in response to global warming has reduced the nutrient supply to the upper water column, reducing primary production in low-latitude oceans (Behrenfeld et al. 2006). In the Arctic Ocean, a remote sensing study of primary production showed an average increase of 27.5 Tg C y^{-1} between 2003 and 2006 and an increase of 35 Tg C y^{-1} between 2006 and 2007 (Arrigo et al. 2008). Thirty percent of the latter increase was attributable to the reduction in the minimum summer sea ice extent while the remaining 70% was attributable to a lengthening of the growing season. Recently, an increase in stratification associated with a warmer and fresher surface layer, has been observed in the Canada Basin (Yamamoto-Kawai et al. 2009), favoring the development of small phytoplankton cells (Li et al. 2009). In a rapidly changing Arctic, it is essential to understand and predict how phytoplankton regimes will respond to climate change.

The objectives of the present study were to (1) characterize marine phytoplankton regimes in the Canadian High Arctic in terms of phytoplankton production, biomass, cell-size structure and community composition and (2) assess the influence of biological and environmental factors on the structure and function of arctic phytoplankton communities in the context of current environmental changes. We addressed these objectives through a multi-year study covering three distinct biogeographic regions. In the west, the Beaufort Sea is characterized by nutrient-poor surface waters and low primary production due to the strong vertical stratification caused by freshwater input from the Mackenzie River (Carmack & Macdonald 2002). In the east, the North Water polynya in Baffin Bay is considered the most productive region in the Canadian Arctic due to enhanced vertical mixing (Klein et al. 2002, Tremblay et al. 2002). Baffin Bay is connected to the Beaufort Sea by the Canadian Arctic Archipelago, whose narrow channels and interconnected sounds form a complex and diverse shelf environment (Michel et al. 2006). A spatial gradient in phytoplankton size-structure was previously observed in this region, with a transition from picophytoplankton dominance in the west to greater nanophytoplankton abundance in the east (Tremblay et al. 2009).

2.2 MATERIAL AND METHODS

2.2.1 ***Study area and sampling design***

This study was carried out in the Canadian High Arctic onboard the CCGS *Amundsen* along transects from the Beaufort Sea to Baffin Bay through the Canadian Arctic Archipelago from 16 August to 13 September 2005, 7 September to 17 October 2006 and 29 September to 5 November 2007 (Fig. 1). A total of 18, 25 and 31 stations were visited in 2005, 2006 and 2007, respectively; hereafter referred to as late summer 2005, early fall 2006 and fall 2007 (Table 1, Appendix). Additional measurements of chlorophyll *a* concentrations were obtained from three ArcticNet expeditions in 2008 (9 – 24 September), 2009 (12 October – 7 November) and 2010 (28 September – 28 October) and were used only for the Figure 8. Water depth was > 200 m at 64%, 56% and 100% of the stations visited in the Beaufort Sea, Canadian Arctic Archipelago and Baffin Bay, respectively (Fig. 1).

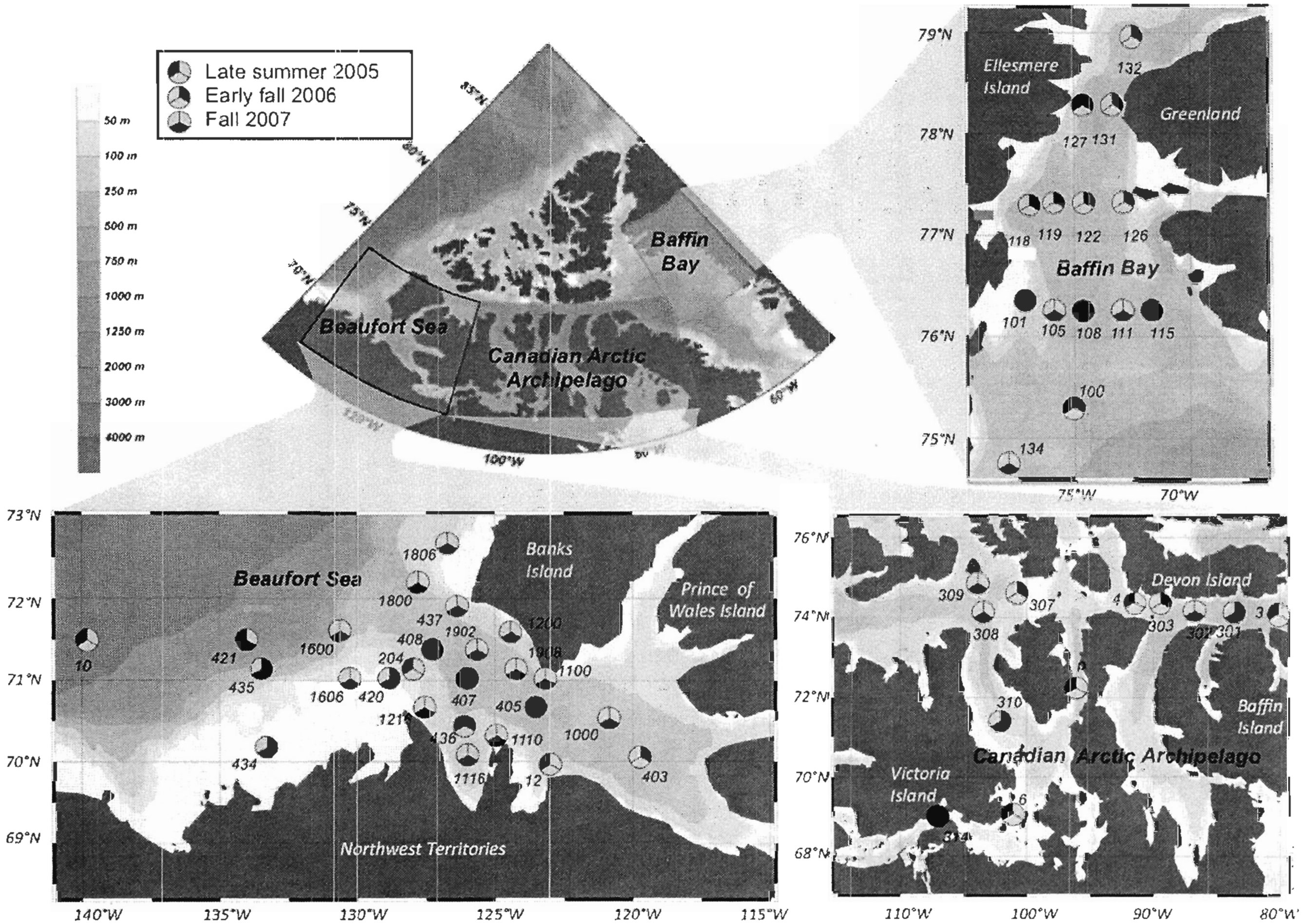

Fig. 1. Location of the sampling stations in the Canadian High Arctic during late summer 2005, early fall 2006 and fall 2007.

At each station, water samples were collected with a rosette sampler equipped with 12 l Niskin-type bottles (OceanTest Equipment), a Sea-Bird 911*plus* CTD probe for salinity and temperature measurements, a nitrate sensor (ISUS V2, Satlantic) and an chlorophyll fluorometer (SeaPoint). Water samples were collected at seven optical depths (100, 50, 30, 15, 5, 1 and 0.2% of surface irradiance) and at the depth of the maximum chlorophyll fluorescence (Z_{DCM}). Subsamples were transferred into acid-washed bottles and isothermal containers, and processed immediately after collection.

Downwelling incident photosynthetically active radiation (PAR, 400 to 700 nm) was measured at 10 min intervals with a LI-COR cosine sensor (LI-190SA) placed on foredeck in an area protected from shading. Underwater irradiance profiles were performed with a PNF-300 radiometer (Biospherical Instruments) and used to determine the depth of the euphotic zone (Z_{eu}, 0.2% of surface irradiance). Sea ice coverage (I_C) was estimated visually at each station.

2.2.2 *Nutrients, chlorophyll a and primary production*

Nutrient and chlorophyll (chl) *a* concentrations, and primary production rates were determined at all optical depths, including Z_{DCM}. Nitrate plus nitrite (NO_3+NO_2), phosphate (PO_4) and silicic acid ($Si(OH)_4$) concentrations were measured immediately after sampling using a Bran-Luebbe 3 autoanalyzer (adapted from Grasshoff et al. 1999). Nitrate data were used to post-calibrate the optical nitrate probe and generate high resolution vertical profiles, as in Martin et al. (2010).

Duplicate subsamples (500 ml) for chl *a* determination were filtered onto Whatman GF/F glass-fiber filters (referred to as total phytoplankton biomass: B_T, ≥ 0.7 μm) and onto 5 μm Nuclepore polycarbonate membrane filters (referred to as biomass of large phytoplankton cells: B_L, ≥ 5 μm). Chl *a* concentrations were measured using a Turner Designs 10-AU fluorometer, following a 24 h extraction in 90% acetone at 4°C in the dark without grinding (acidification method: Parsons et al. 1984).

At selected stations, primary production was estimated using the ^{14}C-uptake method (Knap et al. 1996, Gosselin et al. 1997). Two light and one dark 500 ml Nalgene polycarbonate bottles were filled with seawater from each light level and inoculated with 20 μCi of $NaH^{14}CO_3$. The dark bottle contained 0.5 ml of 0.02 M 3-(3,4-dichlorophenyl)-1,1-dimethyl urea (DCMU). Bottles containing the ^{14}C were incubated for 24 h, generally starting in the morning (Mingelbier et al. 1994), under simulated *in situ* conditions in a deck incubator with running surface seawater (see Garneau et al. 2007 for detail). At the end of the incubation period, 250 ml were filtered onto Whatman GF/F glass-fiber filters (referred to as total particulate phytoplankton production: P_T, ≥ 0.7 μm) and the remaining 250 ml were filtered onto 5 μm Nuclepore polycarbonate membrane filters (referred to as production of large phytoplankton cells: P_L, ≥ 5 μm). Each filter was then placed in a borosilicate scintillation vial, acidified with 0.2 ml of 0.5N HCl, and left to evaporate overnight under the fume hood to remove any ^{14}C that had not been incorporated (Lean & Burnison 1979). After this period, 10 ml of Ecolume (ICN) scintillation cocktail was added to each vial. The activity of each sample was determined using a Packard Tri-Carb 2900 TR liquid scintillation counter.

2.2.3 Cell abundances

Samples for the identification and enumeration of protists > 2 μm at Z_{DCM} were preserved in acidic Lugol's solution (Parsons et al. 1984) and stored in the dark at 4°C until analysis. Cell identification was carried out at the lowest possible taxonomic rank using an inverted microscope (Wild Herbrugg) according to Lund et al. (1958). A minimum of 400 cells (± 10% of accuracy) and three transects were counted at a magnification of 200× and 400×. The main taxonomic references used to identify the phytoplankton were Tomas (1997) and Bérard-Therriault et al. (1999).

Pico- (< 2 µm) and nanophytoplankton (2 – 20 µm) cell abundances were determined at each station at Z_{DCM}. Subsamples were fixed with glutaraldehyde Grade I (Sigma) to a final concentration of 0.1%, stored in liquid nitrogen onboard the ship and kept frozen at –80°C before analysis (Marie et al. 2005). Subsamples were pre-screened on 40 µm nylon cell strainer (Tremblay et al. 2009). Cells were counted using an EPICS ALTRA flow cytometer (Beckman Coulter) equipped with a 488 nm laser (15 mW output). Microspheres (1 µm, Fluoresbrite plain YG, Polysciences) were added to each sample as an internal standard. Picocyanobacteria and photosynthetic eukaryotes were distinguished from their differences in orange fluorescence from phycoerythrin (575 ± 20 nm) and red fluorescence from chlorophyll (675 ± 10 nm). Pico- and nanophytoplankton, counted by flow cytometry, were discriminated based on forward scatter calibration with known-size microspheres. Microphytoplankton (> 20 µm) abundances were determined from microscopic counts.

2.2.4 Calculations and statistical analyses

Daily incident downwelling irradiance (E_D) was calculated at each station. Water temperature and salinity were averaged over the euphotic zone and will hereafter be referred to as T_{eu} and S_{eu}, respectively. The surface mixed layer (Z_m) was defined as the depth where the density (sigma-t, σ_t) is > 0.03 kg m^{-3} than that at the shallowest measurement depth, according to Tremblay et al. (2009). The nitracline (Z_{Nit}) was determined from the second derivative of the nitrate concentration estimated with the Satlantic sensor with respect to depth according to Martinson & Iannuzzi (1998). The stratification index of the upper water column ($\Delta\sigma_t$) was estimated as the difference in σ_t values between 80 and 5 m, as in Tremblay et al. (2009). Nutrient concentrations were determined for Z_{DCM} and were integrated over Z_m and Z_{eu}, using trapezoidal integration (Knap et al. 1996). Small cell phytoplankton production (P_S, 0.7 – 5 μm) and biomass (B_S, 0.7 – 5 μm) was calculated by subtracting P_L from P_T and B_L from B_T, respectively. Chl *a* concentration and primary production values of the two size fractions were also integrated over Z_{eu}.

Prior to statistical analyses, all environmental and biological variables were tested for homoscedasticity and normality of distribution, using residual diagrams and Shapiro-Wilk test, respectively. When required, a logarithmic or square-root transformation was applied to the data. For each variable, two-way analysis of variance (ANOVA) was performed to assess significant differences between sampling years (i.e. 2005, 2006 and 2007) and biogeographic regions (i.e. Beaufort Sea, Canadian Arctic Archipelago and Baffin Bay) (Sokal & Rohlf 1995). The ANOVA test was completed by a *post hoc* test (Tukey's HSD test for unequal sample sizes). When the relationship between two variables was monotonic, Spearman's rank correlation (r_S) was computed (Sokal & Rohlf 1995). These statistical tests were carried out using JMP version 7.01 software.

A non-metric multidimensional scaling (MDS) ordination of a Bray-Curtis similarity matrix coupled with a group-average cluster analysis was performed to characterize groups of stations with similar taxonomic composition (Clarke & Warwick

2001), using the PRIMER v6 software (Clarke & Gorley 2006). Taxonomic groups (i.e. chlorophytes, choanoflagellates, dictyochophytes, euglenids, raphidophytes and ciliates), contributed < 2% of total protist abundance (determined from light microscopy) and were excluded from the analysis in order to reduce double zeros in the data matrix. The relative abundance of the remaining taxonomic groups (i.e. centric diatoms, pennate diatoms, dinoflagellates, chrysophytes, cryptophytes, prasinophytes, prymnesiophytes and unidentified flagellates) were used to calculate the similarity matrix.

An analysis of similarities (one-way ANOSIM) was performed on the Bray-Curtis similarity matrix to identify groups of stations with significantly different taxonomic composition (Clarke & Warwick 2001). A breakdown of species similarities (SIMPER) was performed to determine which taxonomic entry combination led to the resulting groups (Clarke 1993).

A redundancy analysis (RDA) was conducted to assess interactions between major taxonomic groups of protists and biological and environmental variables. Linear-based ordination was selected based on gradient lengths (expressed in standard deviation units) of the first axis being < 2. Each major taxonomic group was normalized using the Hellinger transformation (Legendre & Gallagher 2001, Sokal et al. 2008). The direct gradient technique of RDA was performed using forward selection (and Monte-Carlo permutation test, n = 9999 permutations) to determine a subset of significant environmental and biological variables explaining individually variation of taxonomic groups. Intraset Pearson's correlation (r_P) between environmental variables was determined by RDAs. Two ordination diagrams were produced to visualize interactions between various taxonomic groups of protists in relation to (1) biological and (2) environmental variables. Redundancy analysis was carried out using the CANOCO v. 4.5 software package (ter Braak & Šmilauer 2002).

2.3 RESULTS

2.3.1 Spatio-temporal variability of environmental factors in the Canadian High Arctic

The environmental and biological variables measured in the three biogeographic regions of the Canadian High Arctic (i.e. Beaufort Sea, Canadian Arctic Archipelago and Baffin Bay) during late summer 2005, early fall 2006 and fall 2007 are summarized in Tables 1 and 2. Two-way ANOVAs revealed significant regional and seasonal differences in the study area (Table 3).

During the three sampling periods, salinity averaged over the Z_{eu} (S_{eu}), Z_{DCM}:Z_{Nit}, and $(NO_3+NO_2):Si(OH)_4$ molar ratio at Z_{DCM} were significantly higher in Baffin Bay than in the other two biogeographic regions (Figs. 2b, d, e, Tables 1 & 3). Z_{DCM} was $< Z_{Nit}$ in the Beaufort Sea and $\geq Z_{Nit}$ in Baffin Bay. Z_{DCM} was $\geq Z_{Nit}$ in 2005 and 2006, and $< Z_{Nit}$ in 2007 in the Canadian Archipelago (Fig. 2e).

The $(NO_3+NO_2):Si(OH)_4$ and $(NO_3+NO_2):PO_4$ molar ratios at Z_{DCM} were generally lower than the Redfield's values (1 and 16 respectively, Redfield et al. 1963). Yet, the $(NO_3+NO_2):Si(OH)_4$ molar ratio were > 1 at 18% of the stations visited in Baffin Bay in early fall 2006, suggesting a possible shortage in $Si(OH)_4$ at Z_{DCM}.

Table 1. Environmental variables (average ± standard error) in the three biogeographic regions of the Canadian High Arctic during late summer 2005, early fall 2006 and fall 2007. T_{eu}: water temperature averaged over Z_{eu}; S_{eu}: salinity averaged over Z_{eu}; $\Delta\sigma_t$: stratification index; I_C: percent areal ice cover; E_d: daily incident irradiance; Z_{eu}: euphotic zone depth; Z_m: surface mixed layer depth; Z_{DCM}:Z_{Nit}: ratio of maximum chlorophyll fluorescence depth to nitracline depth; NO_3+NO_2: nitrate plus nitrite concentration at Z_{DCM}; $Si(OH)_4$: silicic acid concentration at Z_{DCM}; PO_4: phosphate concentration at Z_{DCM}. BS: Beaufort Sea; CA: Canadian Arctic Archipelago; BB: Baffin Bay.

	Environmental variable										
Biogeographic region	T_{eu} (°C)	S_{eu}	$\Delta\sigma_t$	Ice (%)	E_d (E m^{-2} d^{-1})	Z_{eu} (m)	Z_m (m)	Z_{DCM}:Z_{Nit} (m)	NO_3+NO_2 (µmol l^{-1})	$Si(OH)_4$ (µmol l^{-1})	PO_4 (µmol l^{-1})
Late summer 2005											
BS	0.4 ± 0.4	29.9 ± 0.5	5.0 ± 0.4	23 ± 6	15.8 ± 1.5	74.1 ± 9.5	8.1 ± 1.3	0.8 ± 0.1	1.7 ± 0.7	5.6 ± 0.8	0.88 ± 0.09
CA	0.6 ± 0.7	30.2 ± 1.3	3.8 ± 0.7	2 ± 2	12.8 ± 2.5	35.5 ± 7.2	8.0 ± 3.6	1.1 ± 0.1	3.3 ± 0.9	10.1 ± 0.8	1.00 ± 0.04
BB	0.6 ± 0.6	32.1 ± 0.4	1.7 ± 0.3	14 ± 15	19.5 ± 2.1	52.4 ± 8.1	16.4 ± 8.9	1.2 ± 0.5	2.6 ± 1.4	4.9 ± 1.3	0.70 ± 0.09
Early fall 2006											
BS	−0.2 ± 0.3	30.0 ± 0.4	3.5 ± 0.8	0	5.8 ± 1.0	51.6 ± 5.6	11.9 ± 1.3	0.8 ± 0.1	2.4 ± 0.7	8.0 ± 1.5	0.91 ± 0.11
CA	0.0 ± 0.4	29.2 ± 1.0	3.1 ± 0.7	10 ± 6	9.9 ± 1.7	49.0 ± 6.8	10.0 ± 3.1	1.0 ± 0.4	2.3 ± 1.3	6.1 ± 2.4	0.92 ± 0.13
BB	−0.3 ± 0.3	31.9 ± 0.3	1.0 ± 0.2	8 ± 3	10.2 ± 1.4	47.1 ± 2.8	22.4 ± 6.2	1.3 ± 0.2	3.2 ± 0.5	4.6 ± 0.7	0.65 ± 0.05
Fall 2007											
BS	−1.2 ± 0.1	31.6 ± 0.3	1.3 ± 0.5	41 ± 9	1.0 ± 0.2	60.0 ± 5.7	19.6 ± 2.6	0.5 ± 0.1	5.3 ± 1.5	10.8 ± 2.3	1.04 ± 0.08
CA	−0.8 ± 0.3	30.4 ± 0.7	2.3 ± 0.4	48 ± 14	3.3 ± 0.8	51.5 ± 6.9	19.0 ± 4.0	0.3 ± 0.1	0.39 ± 0.04	2.1 ± 0.3	0.67 ± 0.03
BB	−0.9 ± 0.2	32.1 ± 0.5	1.2 ± 0.2	28 ± 12	5.0	69.3 ± 9.6	18.2 ± 3.9	1.2 ± 0.3	2.2 ± 0.3	4.0 ± 0.7	0.76 ± 0.05

Table 2. Biological variables (average ± standard error) in the three oceanographic regions of the Canadian High Arctic during late summer 2005, early fall 2006 and fall 2007. B_T: total phytoplankton biomass; B_S: biomass of small phytoplankton (0.7 – 5 µm); B_L: biomass of large phytoplankton (≥ 5 µm); P_T: total phytoplankton production; P_S: production of small phytoplankton (0.7 – 5 µm); P_L: production of large phytoplankton (≥ 5 µm); Pico: picophytoplankton (< 2 µm) percent abundance; Nano: nanophytoplankton (2 – 20 µm) percent abundance; Micro: microphytoplankton (≥ 20 µm) percent abundance; Diat: diatoms; Flag: flagellates; Dino: dinoflagellates; Others: other protists > 2 µm. BS: Beaufort Sea; CA: Canadian Arctic Archipelago; BB: Baffin Bay; nd: no data available. Phytoplankton production and biomass were integrated over the euphotic zone. Community structure and composition were measured at Z_{DCM}.

	Biological variable												
Biogeographic region	Production (mg C m^{-2} d^{-1})			Biomass (mg chl *a* m^{-2})			Community structure (%)			Community composition (%)			
	P_T	P_S	P_L	B_T	B_S	B_L	Pico	Nano	Micro	Diat	Flag	Dino	Others
Late summer 2005													
BS	171.9 ± 97.3	97.0 ± 34.9	75.0 ± 63.5	23.2 ± 11.2	13.6 ± 4.0	9.6 ± 7.3	75.5 ± 7.2	23.4 ± 6.9	1.1 ± 0.6	11.3 ± 8.8	67.3 ± 6.6	3.8 ± 0.5	17.7 ± 4.7
CA	295.2 ± 149.1	171.9 ± 51.7	123.3 ± 100.7	38.3 ± 15.7	16.8 ± 4.7	21.5 ± 12.0	67.9 ± 13.7	30.6 ± 13.4	1.5 ± 0.9	29.8 ± 17.7	49.4 ± 11.8	1.7 ± 0.4	19.0 ± 9.1
BB	448.0 ± 152.5	314.2 ± 132.7	133.9 ± 31.1	56.8 ± 17.8	26.5 ± 10.4	30.4 ± 15.7	66.6 ± 10.6	32.6 ± 10.0	0.8 ± 0.6	25.2 ± 14.3	64.6 ± 14.5	3.3 ± 1.2	6.9 ± 2.5
Early fall 2006													
BS	64.1 ± 11.5	43.4 ± 8.1	20.7 ± 31.1	25.5 ± 15.7	12.6 ± 2.3	12.9 ± 3.9	55.4 ± 11.3	36.7 ± 8.5	7.9 ± 3.4	33.7 ± 10.5	54.7 ± 9.3	6.1 ± 1	5.5 ± 1.3
CA	121.7 ± 52.5	69.3 ± 26.5	52.4 ± 26.3	22.6 ± 7.7	7.3 ± 1.4	15.3 ± 6.8	46.6 ± 10.5	49.7 ± 9.9	3.7 ± 3.8	53.3 ± 6.6	40.4 ± 7.0	3.0 ± 0.9	3.3 ± 0.4
BB	310.0 ± 92.6	157.8 ± 53.6	152.4 ± 46.9	71.4 ± 10.7	18.1 ± 3.5	53.3 ± 7.7	34.5 ± 10.0	50.4 ± 9.9	15.1 ± 3.8	65.9 ± 5.9	25.6 ± 3.7	3.4 ± 1.1	5.1 ± 1.8
Fall 2007													
BS	nd	nd	nd	17.7 ± 3.0	8.3 ± 1.4	8.7 ± 2.4	70.3 ± 5.4	28.1 ± 5.3	1.6 ± 0.2	10.2 ± 6.4	75.2 ± 5.3	8.0 ± 1.5	6.6 ± 1.0
CA	49.3 ± 12.1	41.7 ± 8.8	7.6 ± 3.3	12.4 ± 1.0	9.9 ± 0.5	2.5 ± 0.6	88.1 ± 2	11.5 ± 1.8	0.4 ± 0.3	3.4 ± 1.0	82.0 ± 2.6	9.2 ± 1.3	5.4 ± 0.6
BB	137.1 ± 137.1	147.6 ± 62.2	178.0 ± 77.2	62.4 ± 20.1	19.8 ± 7.9	42.6 ± 16.1	51.3 ± 11.6	36.5 ± 8.2	12.2 ± 5.9	44.8 ± 10.9	40.7 ± 8.3	9.1 ± 3.5	5.5 ± 0.7

Table 3. Summary of two-way analysis of variance and Tukey test for environmental and biological variables in the three biogeographic regions of the Canadian High Arctic during late summer 2005, early fall 2006 and fall 2007. Total abund: total abundance of protists > 2 µm at Z_{DCM}. Other abbreviations are defined in Tables 1 and 2. ns: not significant. For *post hoc* Tukey tests: A > B > C.

Two-way analysis of variance				Tukey test ($\alpha \leq 0.05$)					
Environmental variable	Region	Season	Region × Season	BS	CA	BB	Late summer 2005	Early fall 2006	Fall 2007
T_{eu} (°C)	ns	< 0.001	ns				A	A	B
S_{eu}	< 0.001	ns	ns	B	B	A			
$\Delta\sigma_t$	< 0.001	< 0.001	ns	A	A,B	B	A	A,B	B
I_C (%)	ns	< 0.01	ns				B	B	A
E_d (E m^{-2} d^{-1})	< 0.01	< 0.001	ns	A	A,B	A	A	B	C
Z_{eu} (m)	ns	ns	ns						
Z_m (m)	ns	< 0.01	ns				B	A,B	A
Z_{DCM}:Z_{nit} (m:m)	< 0.001	ns	ns	B	B	A			
NO_3+NO_2 at Z_{DCM} (µmol l^{-1})	ns	ns							
$Si(OH)_4$ at Z_{DCM} (µmol l^{-1})	< 0.01	ns		A	A,B	B			
PO_4 at Z_{DCM} (µmol l^{-1})	< 0.01	ns		A	A,B	B			
(NO_3+NO_2):PO_4 (mol:mol)	ns	ns	ns						
(NO_3+NO_2):$Si(OH)_4$ (mol:mol)	< 0.01	ns	ns	B	B	A			
Biological variable									
B_T (mg chl *a* m^{-2})	< 0.001	ns	ns	B	B	A			
B_S (mg chl *a* m^{-2})	ns	ns	ns						
B_L (mg chl *a* m^{-2})	< 0.001	ns	ns	B	B	A			
P_T (mg C m^{-2} d^{-1})	< 0.01	ns	ns	B	A,B	A			
P_S (mg C m^{-2} d^{-1})	< 0.01	< 0.01	ns	B	A,B	A	A	B	
P_L (mg C m^{-2} d^{-1})	< 0.01	ns	ns	B	A,B	A			
Pico (%)	< 0.01	< 0.001	ns	A	A	B	A	B	A
Nano (%)	ns	< 0.01	ns	A	A	A	A,B	A	B
Micro (%)	< 0.001	< 0.001	ns	B	B	A	B	A	A,B
Diat (%)	< 0.001	< 0.001	ns	B	A,B	A	B	A	B
Flag (%)	< 0.01	< 0.001	ns	A	A,B	B	A	B	A
Dino (%)	ns	< 0.001	ns				B	B	A
Others (%)	ns	0.05	ns				A	B	A,B
Total protist abund. (10^6 cells l^{-1})	< 0.01	< 0.001	ns	B	B	A	A	A,B	B

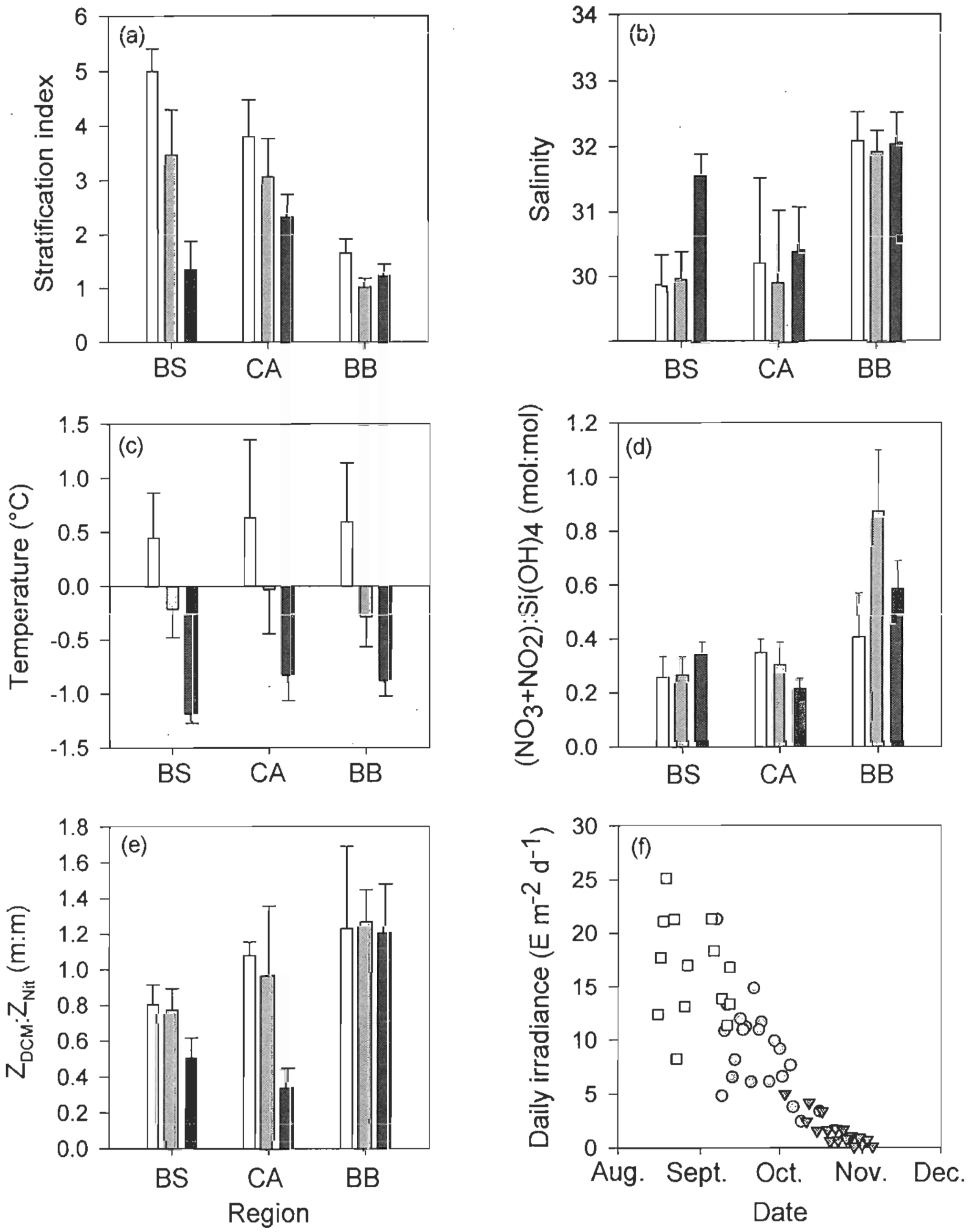

Fig. 2. Variations in (a) stratification index, (b) salinity averaged over the euphotic zone (Z_{eu}), (c) temperature averaged over Z_{eu}, (d) $(NO_3+NO_2):Si(OH)_4$ ratio at the depth of the maximum chlorophyll fluorescence, (e) $Z_{DCM}:Z_{Nit}$ ratio and (f) daily incident irradiance across the Canadian High Arctic during late summer 2005 (white), early fall 2006 (grey) and fall 2007 (black). In (a-e), bars and vertical lines represent average values and standard errors, respectively. BS: Beaufort Sea; CA: Canadian Arctic Archipelago; BB: Baffin Bay.

For each nutrient (NO_3+NO_2, $Si(OH)_4$ and PO_4), concentrations at Z_{DCM} were positively correlated with concentrations at Z_m and Z_{eu} ($p < 0.01$). The western part of the transect (> 95°W, Fig. 1) was characterized by higher $Si(OH)_4$ and PO_4 concentrations at Z_{DCM} than the eastern part (Table 3). NO_3+NO_2 concentrations did not show any significant regional nor seasonal differences (Table 3). NO_3+NO_2 concentrations were ca. one order of magnitude higher, whereas $Si(OH)_4$ concentrations were ca. twice higher, and PO_4 concentrations were similar at the Z_{DCM} compared to sea surface.

The daily incident irradiance was higher in Baffin Bay than in the Canadian Archipelago due to difference in sampling periods, but decreased gradually from late summer 2005 to fall 2007 (Fig. 2f, Table 3). The stratification index was significantly higher in the Beaufort Sea than in Baffin Bay and, for all regions, was significantly lower in fall 2007 than in late summer 2005 (Fig. 2a, Tables 1 & 3).

Water temperature averaged over the euphotic zone (T_{eu}; Fig. 2c) was lower, while percent sea ice coverage was higher, in fall 2007 than during the two previous sampling periods. The surface mixed layer (Z_m) was deeper in fall 2007 than in late summer 2005 (Tables 1 & 3). There was no significant regional or seasonal difference in the euphotic zone depth (Z_{eu}) nor (NO_3+NO_2):PO_4 ratio at Z_{DCM} during this study.

2.3.2 Spatio-temporal variability of biological variables in the Canadian High Arctic

During the three sampling periods, total (≥ 0.7 μm) and large (≥ 5 μm) phytoplankton chl *a* biomass integrated over the euphotic zone was significantly higher in Baffin Bay than in the other regions (Fig. 3a, c, e, Table 3). Phytoplankton biomass was generally dominated by large cells (≥ 5 μm) in Baffin Bay and by small cells (0.7 – 5 μm) in the Beaufort Sea and the Canadian Arctic Archipelago (Fig. 3a, c, e). Particulate phytoplankton production by large (≥ 5 μm) and small (0.7 – 5 μm) cells integrated over the euphotic zone was significantly higher in Baffin Bay than in the Beaufort Sea during the three sampling years (Fig. 3b, d, f, Table 3). Primary production was generally dominated by small cells, except in Baffin Bay in fall 2007 (Fig. 3b, d, f). There was no significant difference in chl *a* biomass between the three sampling periods (Table 3). However, primary production by small cells was significantly higher in late summer 2005 than in early fall 2006 (Fig. 3b, d, Table 3). Maximum chl *a* biomass and primary production were observed in early fall 2006 and late summer 2005, respectively (Fig. 3b, c). During the three sampling periods, the depth of maximum chl *a* fluorescence was at 26 ± 18 m in the Beaufort Sea, 24 ± 14 m in the Canadian Archipelago and 37 ± 25 m in Baffin Bay.

Except for the two westernmost stations where flagellates were numerically dominant, we observed a mixed protist community in late summer 2005 and a community generally dominated by diatoms in early fall 2006 and by flagellates in fall 2007 (Fig. 4). In contrast to the two previous years, dinoflagellates were consistently observed in fall 2007, making up 1 to 23.4% of the total protist abundance (Fig. 4c).

During the three sampling periods, the highest picophytoplankton relative abundance was observed in the Beaufort Sea and Canadian Archipelago whereas the highest relative abundance of microphytoplankton was observed in Baffin Bay (Fig. 5). Picophytoplankton numerically dominated the phytoplankton community throughout the sampling area during late summer 2005 and fall 2007 (Fig. 5a, c). The relative nanophytoplankton abundance was higher in early fall 2006 than in fall 2007 (Fig. 5b, c), whereas microphytoplankton showed a higher relative abundance in late summer 2005 than in early fall 2006 (Fig. 5a, b).

In the Beaufort Sea, some deep stations > 200 m (Fig. 1) located in the central Amundsen Gulf (i.e. Stn 405 in 2005 and 2006; Stn 407 in 2006 and 2007; Stn 408 in 2006 and 2007) consistently showed higher chl *a* biomass (≥ 40 mg m^{-2}) than surrounding stations (Fig. 3a, c, e) that were associated with high relative abundance of nanophytoplankton (Fig. 4) mainly diatoms (Fig. 5). Hereafter, this particular sector is referred to as the Amundsen Gulf hotspot.

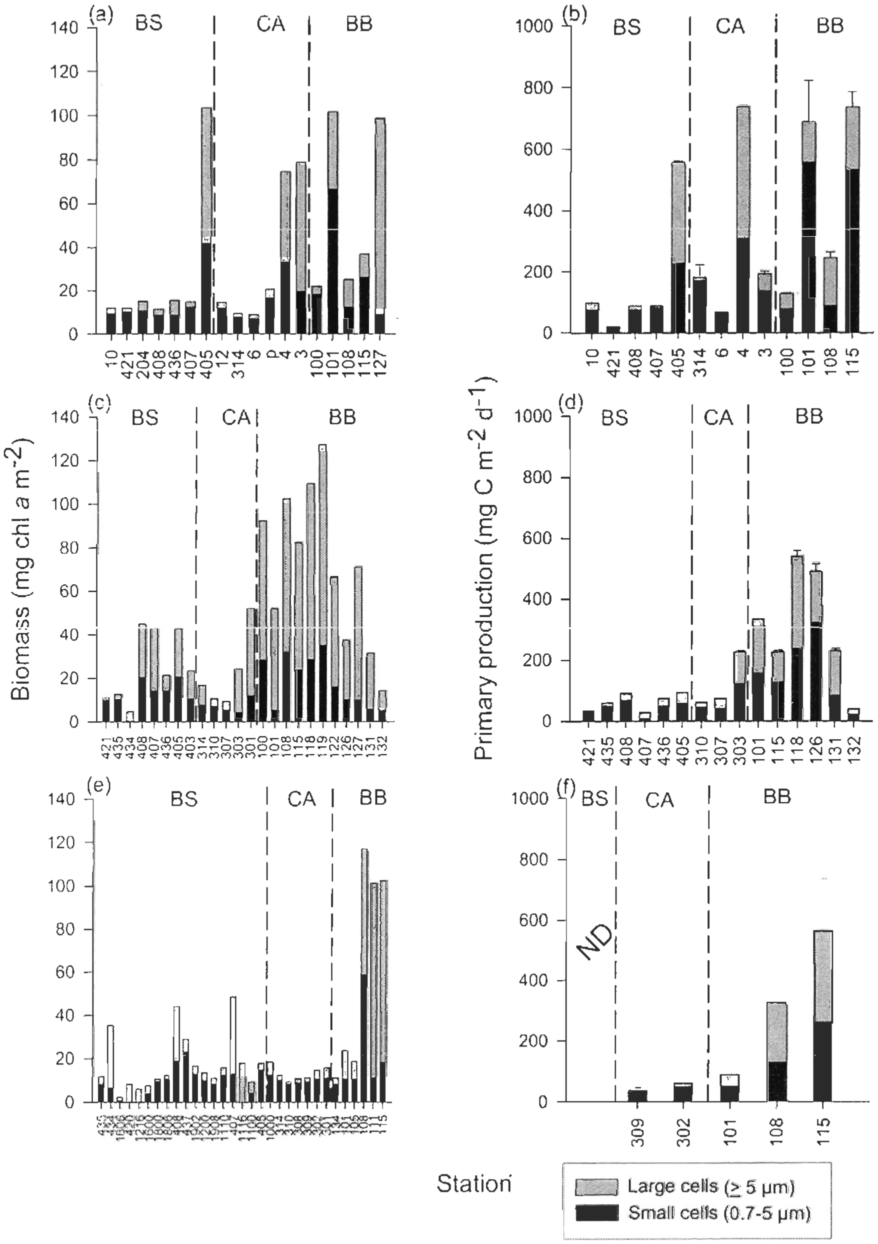

Fig. 3. Variations in phytoplankton (a, c, e) chlorophyll *a* (chl *a*) biomass and (b, d, f) production for small (0.7 – 5 μm) and large (≥ 5 μm) cells integrated over the euphotic zone of stations across the Canadian High Arctic during (a, b) late summer 2005, (c, d) early fall 2006 and (e, f) fall 2007. In (b, d, f), vertical lines represent standard deviations of estimated rates. BS: Beaufort Sea; CA: Canadian Arctic Archipelago; BB: Baffin Bay; ND: no data available.

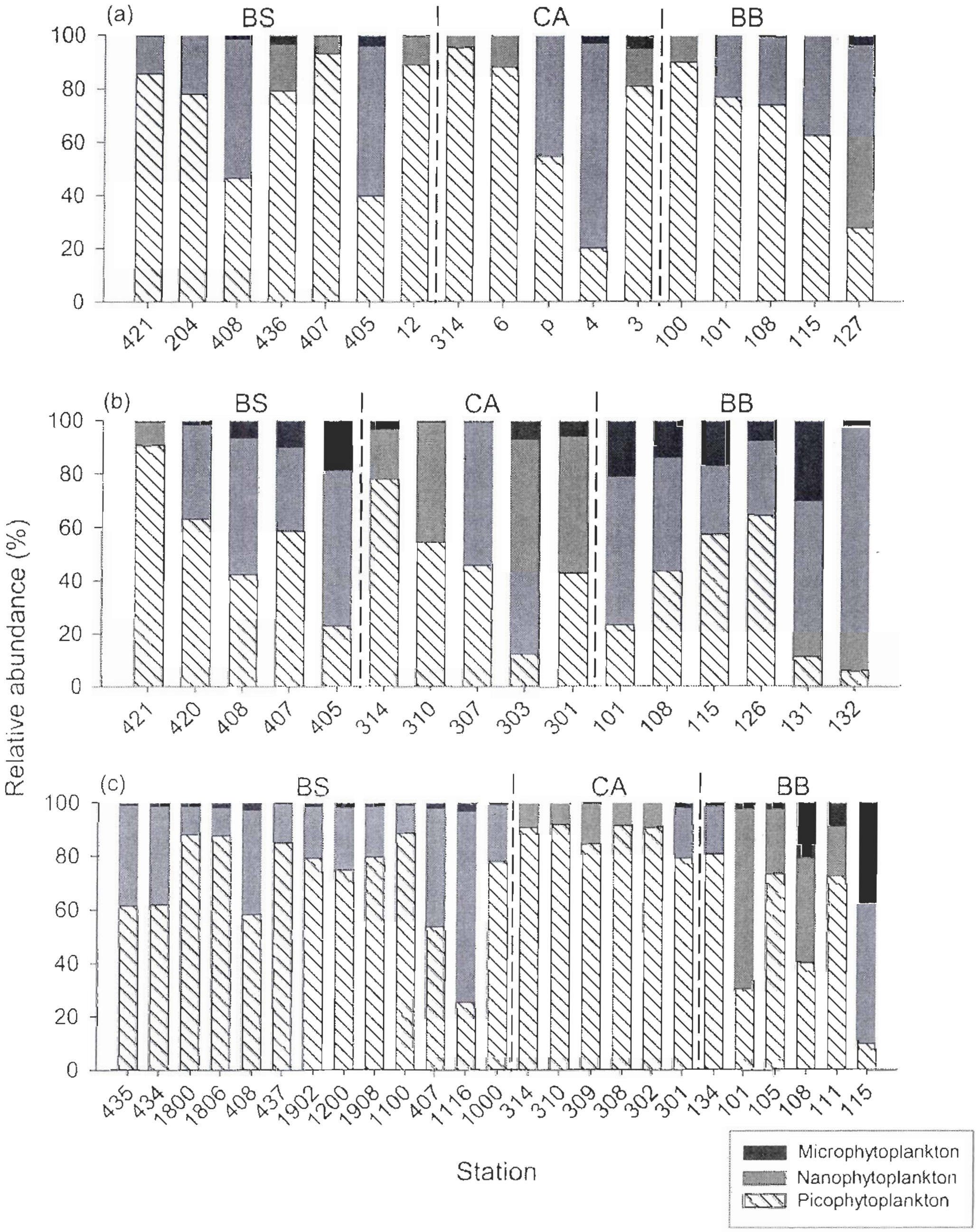

Fig. 4. Variations in relative abundance of four protist (> 2 μm) groups (diatoms, dinoflagellates, flagellates and other protists > 2 μm) at the depth of the maximum chlorophyll fluorescence at stations across the Canadian High Arctic in (a) late summer 2005, (b) early fall 2006 and (c) fall 2007. Other protists comprise choanoflagellates, ciliates and unidentified flagellates. BS: Beaufort Sea; CA: Canadian Arctic Archipelago; BB: Baffin Bay.

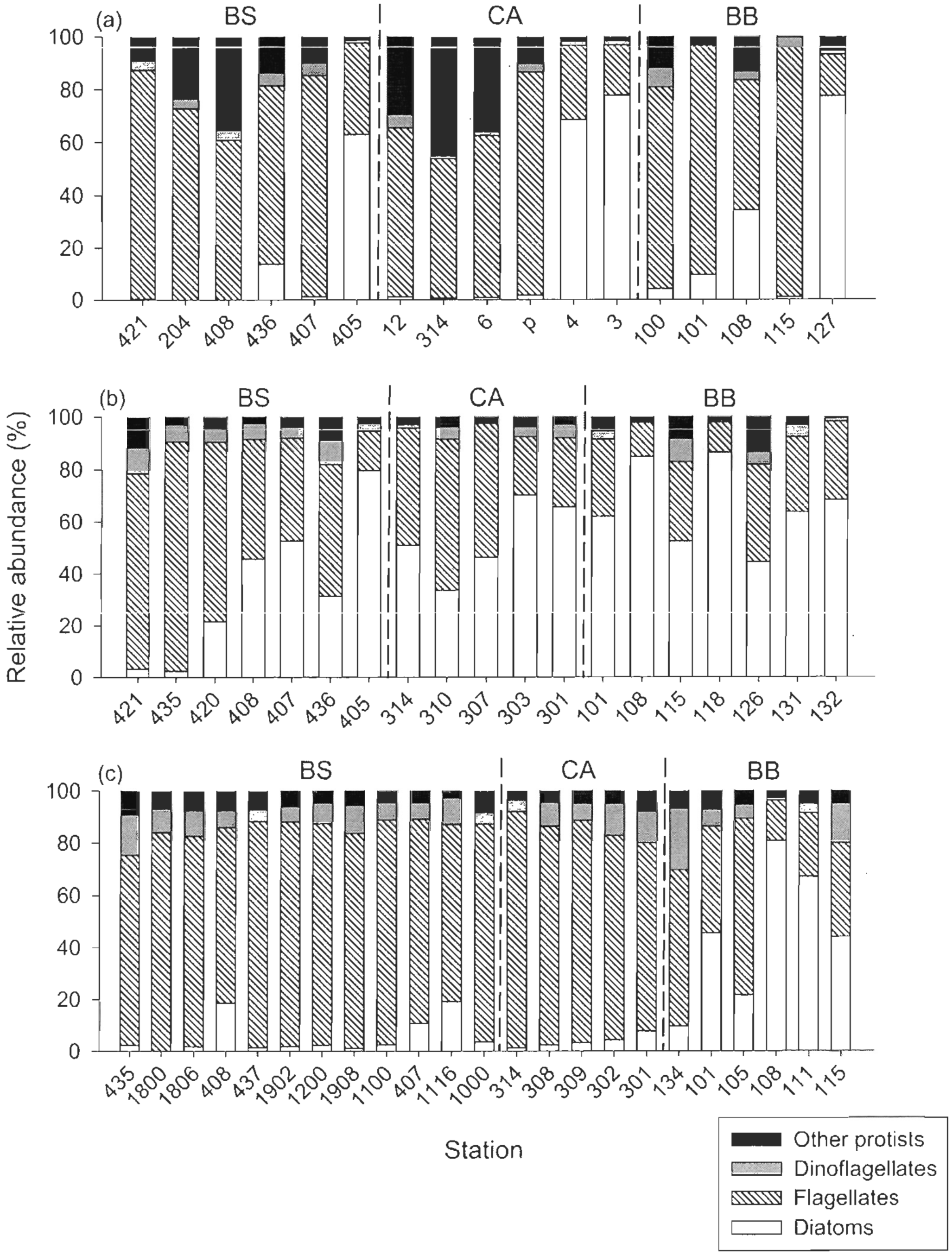

Fig. 5. Variations in relative abundance of pico- (< 2 µm), nano- (2 – 20 µm) and microphytoplankton (≥ 20 µm) at the depth of the maximum chlorophyll fluorescence at stations across the Canadian High Arctic during (a) late summer 2005, (b) early fall 2006 and (c) fall 2007.

2.3.3 Multivariate analyses

The cluster analysis identified five groups of taxonomically similar protist (> 2 μm) communities during the three-year sampling period in the Canadian High Arctic (ANOSIM, global $R = 0.921$, $p \leq 0.001$; Fig. 6, Table 4). Group I was largely dominated by unidentified flagellates (91%) and comprised most of the stations in the eastern Beaufort Sea (89%), Amundsen Gulf (62%) and the central part of the Canadian Arctic Archipelago (67%). Group II was mainly characterized by unidentified flagellates (65%) followed by centric diatoms (26%), and was composed of stations located outside (39%) and inside (25%) the Amundsen Gulf hotspot. Group III consisted of only one station (Stn 101) in Baffin Bay visited in 2005 and was characterized by a distinct taxonomic composition, with unidentified flagellates (53%), prymnesiophytes (22%) and chrysophytes (14%). Group IV consisted of centric diatoms (58%) and unidentified flagellates (35%), with stations mostly from the Amundsen Gulf hotspot (50%) and Baffin Bay (41%). Group V was dominated by centric diatoms (76%) followed by unidentified flagellates (17%) and comprised stations in Lancaster Sound (50%), Baffin Bay (35%) and the hotspot in Amundsen Gulf (25%).

In order to investigate protist distribution patterns in relation to biological and environmental variables in the Canadian High Arctic during late summer 2005, early fall 2006 and fall 2007, two constrained RDAs were conducted using the relative abundance (%) of major taxonomic groups of protists. Constrained RDAs revealed five significant biological variables explaining 33.7% of the protist distribution throughout the Canadian High Arctic (Fig. 7a, Table 5).

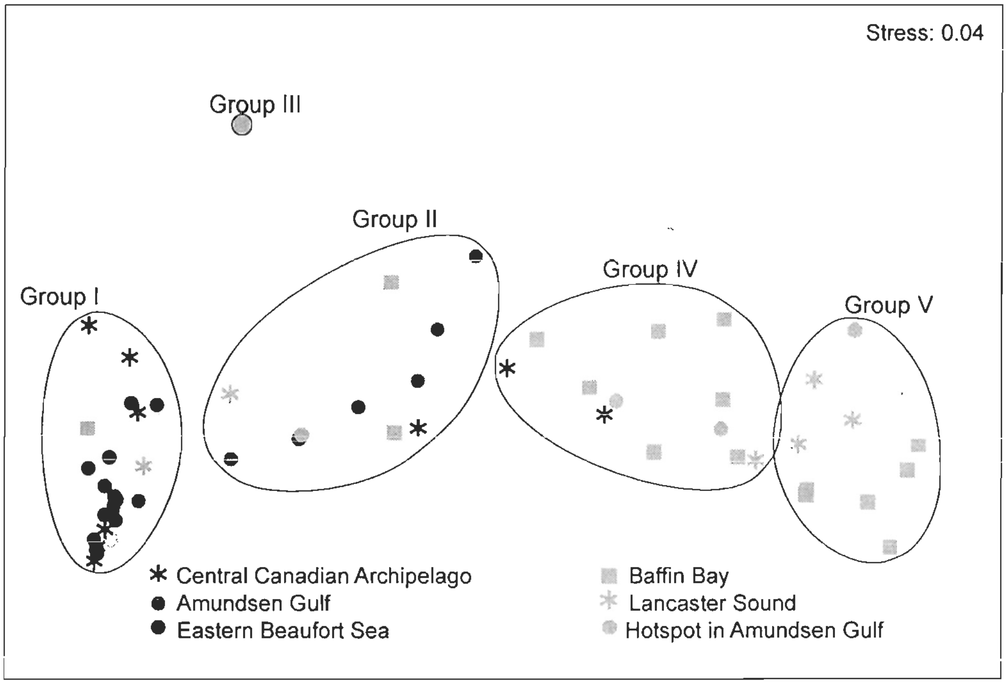

Fig. 6. Two-dimensional non-metric multidimensional scaling (MDS) of 58 stations across the Canadian High Arctic from 2005 to 2007. The five groups of stations with taxonomically similar protist composition, as determined with the group-average clustering (at a similarity level of 80%), are superimposed on the MDS.

Table 4. Breakdown of similarities (%) within groups of stations into contributions (%) from each taxonomic group of protists. The percent number of stations from each region that are present in each group is also presented as occurrence (%). Values ≥ 50% are in bold.

		Contribution (%)				
		Group I	Group II	Group III	Group IV	Group V
	Average similarity	88	84	100 (only one sample)	85	82
Taxonomic groups of protists	Centric diatoms		26	9	**58**	**76**
	Unidentified flagellates	**91**	**65**	**53**	35	17
	Prymnesiophytes			22		
	Chrysophytes			14		
		Occurrence (%)				
Sub-regions	Eastern Beaufort Sea	**89**	11			
	Amundsen Gulf (excluding hotspot stations)	**62**	39			
	Hotspot stations in Amundsen Gulf		25		**50**	25
	Central Canadian Archipelago	**67**	11		22	
	Lancaster Sound	17	17		17	**50**
	Baffin Bay	6	12	6	41	35

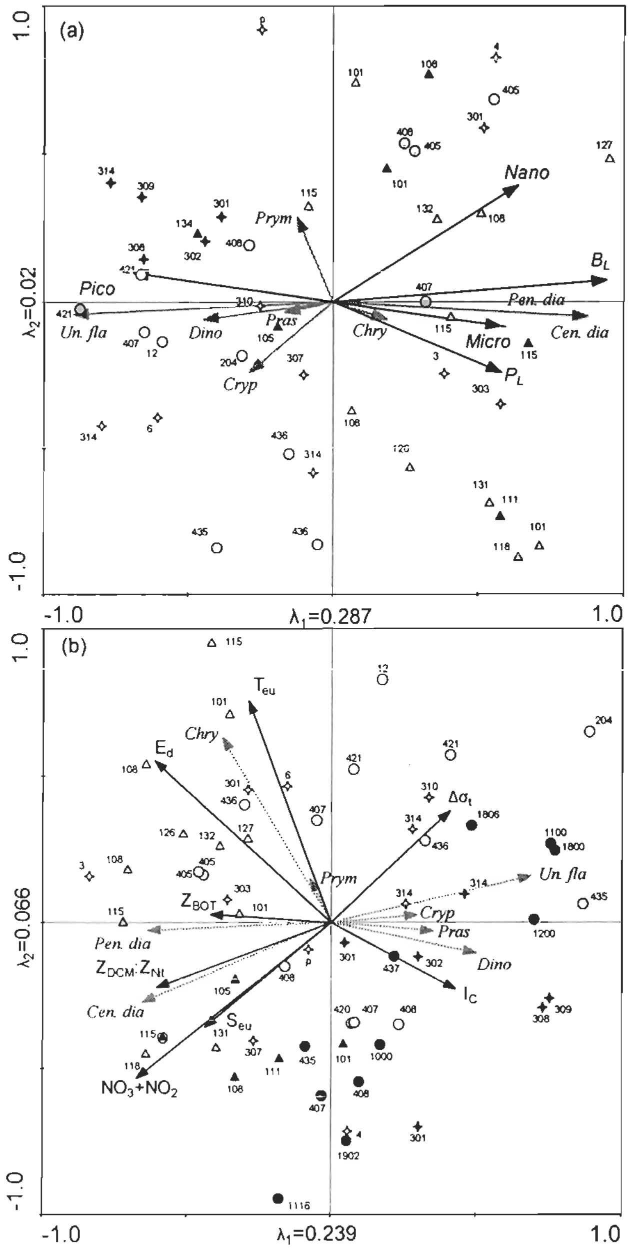

Fig. 7. Redundancy analysis (RDAs) ordination plots of axes I and II showing taxonomic groups of protists (grey arrows) in relation to (a) biological (black arrows) and (b) environmental (black arrows) variables for stations across the Canadian High Arctic, during late summer 2005 (white), early fall 2006 (grey) and fall 2007 (black). Symbols represent different regions: Beaufort Sea: circle; Canadian Arctic Archipelago: star; Baffin Bay: square. Full names of biological and environmental variables are listed in Table 5. Cen. dia: centric diatoms; Chry: chrysophytes; Cryp: cryptophytes; Dino: dinoflagellates; Pen. dia: pennate diatoms; Pras: prasinophytes; Prym: prymnesiophytes; Un. fla: unidentified flagellates.

Table 5. Forward selection of biological and environmental variables influencing the distribution of phytoplankton communities in the Canadian High Arctic during 2005, 2006 and 2007 (Monte Carlo with 9999 unrestricted permutations, $p \leq 0.05$).

Variable	Abbreviation	Eigenvalue	% explained	P value for unique explanation (n = 9999)
(1) Interaction of biological variables and phytoplankton groups				
Biomass of large phytoplankton	B_L	0.257	25.7	0.0001
Picophytoplankton	Pico	0.141	14.1	0.0001
Nanophytoplankton	Nano	0.125	12.5	0.0002
Microphytoplankton	Micro	0.106	10.6	0.002
Production of large phytoplankton	P_L	0.103	10.3	0.0012
Total			73.1	
(2) Interaction of environmental variables and phytoplankton groups				
Nitrate plus nitrite	NO_3+NO_2	0.135	13.5	0.0001
Daily irradiance	E_d	0.112	11.2	0.0003
$Z_{DCM}:Z_{Nit}$ ratio	$Z_{DCM}:Z_{Nit}$	0.092	9.2	0.0006
Salinity	S_{eu}	0.063	6.3	0.0084
Temperature	T_{eu}	0.06	6	0.013
Sea ice coverage	I_C	0.059	5.9	0.01
Bottom depth	Z_{BOT}	0.058	5.8	0.013
Stratification index	$\Delta\sigma_t$	0.058	5.8	0.011
Total			63.7	

Including covariances, % explained of (1) five biological variables = 33.7% and (2) eight variables = 37.1% (P = 0.0001, n = 9999).

The eigenvalue of the first RDA axis ($\lambda_1 = 0.287$) was significant ($p < 0.05$) and explained 81.6% of the total variance in taxonomic groups in relation to biological variables, including size structure. The biomass of large phytoplankton (B_L), relative abundances of pico- (Pico), nano- (Nano) and microphytoplankton (Micro) and production by large phytoplankton (P_L) were strongly correlated with the first RDA axis (r_p = 0.83, -0.55, 0.54, 0.46 and 0.26, respectively). The first axis is associated with the distribution of centric (Cen. dia) and pennate (Pen. dia) diatoms in opposition to flagellated cells represented by unidentified flagellates (Un. fla), dinoflagellates (Dino), cryptophytes (Cryp), prasinophytes (Pras) and prymnesiophytes (Prym). The percent abundance of diatoms was strongly correlated with B_L and P_L, corresponding to a high relative abundance of large sized-phytoplankton (Nano and Micro), mainly found in northern Baffin Bay, Lancaster Sound and the Amundsen Gulf hotspot. The percent abundance of flagellates, linked to the pico-sized fraction of the phytoplankton (Pico) was strongly correlated with B_L and P_L and observed mainly at stations in southeastern Beaufort Sea, Amundsen Gulf and the central part of the Canadian Arctic Archipelago. The eigenvalue of the second axis ($\lambda_2 = 0.02$) of the redundancy analysis was not significant ($p > 0.05$, Fig. 7a).

Constrained RDA with environmental variables resulted in eight significant variables accounting for 37.1% of the variation in taxonomic composition of protists (Fig. 7b, Table 5). The eigenvalue of the first two RDA axes ($\lambda_1 = 0.239$, $\lambda_2 = 0.066$) were both significant ($p < 0.05$) and explained 64.4% and 17.9% of the total variance in taxonomic groups of protists, including size structure, in relation to environmental variables, respectively. NO_3+NO_2 concentrations at Z_{DCM}, E_d, Z_{DCM}:Z_{Nit}, S_{eu}, I_C, $\Delta\sigma_t$ and

Z_{BOT} were strongly correlated with the first RDA axis (r_p values of -0.51, -0.46, -0.46, -0.33, 0.32 and 0.31, respectively). The first RDA axis (λ_1) explained the spatial variability in the Canadian High Arctic with distinct regional and intra-regional patterns associated with specific environmental variables. Highly productive regions, such as northern Baffin Bay, Lancaster Sound and the Amundsen Gulf hotspot were characterized by high values in E_d, S_{eu}, Z_{DCM}:Z_{Nit} and high NO_3+NO_2 concentrations at Z_{DCM}. Regions showing a predominance of picophytoplankton cells (i.e. southeastern Beaufort Sea, the Amundsen Gulf and the central part of the Canadian Arctic Archipelago) were controlled by the stratification of the water column. NO_3+NO_2 concentrations at Z_{DCM} were positively correlated with S_{eu} ($r_P = 0.39$, $p < 0.001$) and Z_{DCM}:Z_{Nit} ($r_P = 0.35$, $p < 0.001$), and S_{eu} was negatively correlated with $\Delta\sigma_t$ ($r_P = -0.59$, $p < 0.001$). T_{eu}, E_d, NO_3+NO_2 concentrations at Z_{DCM}, $\Delta\sigma_t$ and S_{eu} were highly correlated with the second RDA axis (r_p values of 0.53, 0.39, -0.38, 0.27 and 0.25, respectively). To a lesser extent, the second RDA axis (λ_2) explained the temporal variability in the Canadian High Arctic. The late summer period (white symbols in Fig. 7) was characterized by high values in E_d, T_{eu} and $\Delta\sigma_t$. In contrast, the fall period (black symbols in Fig. 7) was characterized by high S_{eu}, high NO_3+NO_2 concentrations at Z_{DCM} and the presence of sea ice. T_{eu} was positively correlated with E_d ($r_P = -0.38$, $p < 0.01$) and negatively correlated with I_C ($r_P = -0.435$, $p < 0.01$) and S_{eu} ($r_P = -0.299$, $p < 0.05$). The Z_{DCM}:Z_{Nit} ratio was positively correlated with E_d ($r_P = 0.305$, $p < 0.05$) and negatively correlated with I_C ($r_P = -0.30$, $p < 0.05$).

2.4 DISCUSSION

2.4.1 Distinct phytoplankton regimes in the Canadian High Arctic

Distinct phytoplankton regimes (Tables 2 & 3) were consistently observed during three successive sampling years along the 3500 km transect encompassing the Beaufort Sea, Canadian Arctic Archipelago and Baffin Bay (Fig. 1). The Beaufort Sea and the Canadian Arctic Archipelago showed large spatial variability in phytoplankton regimes compared to Baffin Bay.

The MDS analysis revealed that phytoplankton communities of the Canadian High Arctic were represented by two key groups: (1) unidentified flagellates in the eastern Beaufort Sea, Amundsen Gulf and the central part of the Canadian Arctic Archipelago, and (2) centric diatoms (namely *Chaetoceros* spp., data not shown) in the Amundsen Gulf hotspot, Lancaster Sound and Baffin Bay (Fig. 6, Table 4). These communities were also characterized by distinct phytoplankton size-structure, biomass and production (Fig. 7, Table 5). Flagellate-based systems were characterized by a high relative abundance of picophytoplankton and low biomass and production of large phytoplankton cells. In contrast, diatom-based systems were characterized by a high relative abundance of high nano- and microphytoplankton and high biomass and production of large phytoplankton cells.

Previous studies have shown the numerical dominance of flagellates in the western Arctic during the open water period (Hsiao et al. 1977, Schloss et al. 2008, Brugel et al. 2009), supported by regenerated nutrients (Simpson et al. 2008, Tremblay et al. 2008). In addition, flagellate-based systems have been reported in deep Arctic basins (Legendre et al. 1993, Booth & Horner 1997, Gosselin et al. 1997, Li et al. 2009). Diatom-based systems have been described for different shelf and deep areas of the Arctic Ocean (von Quillfeldt 1997, Mostajir et al. 2001, Booth et al. 2002, Lovejoy et al. 2002a, Hill et al. 2005), supported by new nitrogenous nutrients (Tremblay et al. 2002, Garneau et al. 2007).

Our results allowed to distinguish three sub-regions in the Beaufort Sea: the eastern Beaufort Sea, the central Amundsen Gulf hotspot, and the remainder of the Amundsen Gulf. The eastern Beaufort Sea, including the Mackenzie shelf, was characterized by low total chl *a* biomass (16.0 ± 3.2 mg m^{-2}) and phytoplankton production (73.4 ± 26.3 mg C m^{-2} d^{-1}) in the euphotic zone. Unlike the Amundsen Gulf hotspot, other sites of the Amundsen Gulf showed low total phytoplankton chl *a* biomass (19.4 ± 2.6 mg m^{-2}) and production (48.6 ± 26.6 mg C m^{-2} d^{-1}), comparable to values in the eastern Beaufort Sea. The Amundsen Gulf hotspot had the highest total phytoplankton chl *a* biomass (46.6 ± 3.2 mg m^{-2}) and production (158.8 ± 71.2 mg C m^{-2} d^{-1}) of the Beaufort Sea region. Phytoplankton biomass and production were generally dominated by small cells (< 5 µm) in the eastern Beaufort Sea and Amundsen Gulf, whereas phytoplankton biomass was dominated by large cells in the Amundsen Gulf hotspot. High abundances of zooplankton (G. Darnis, Univ. Laval., pers. comm.) and polar cod (Geoffroy et al. ms) have also been observed in the latter area. Observed values of phytoplankton biomass and production compare with values previously reported for the eastern Beaufort Sea (40 to 100 mg C m^{-2} d^{-1}, Carmack et al. 2004; 10.5 to 15.8 mg chl *a* m^{-2} and 15 to 119 mg C m^{-2} d^{-1}, Brugel et al. 2009) and the Amundsen Gulf (92 to 105 mg C m^{-2} d^{-1}, Brugel et al. 2009; 102 to 109 mg C m^{-2} d^{-1}, Juul-Pedersen et al. 2010).

The Canadian Arctic Archipelago can be divided into two distinct sub-regions consisting of the central part of the Archipelago and Lancaster Sound to the east. The central part of the Archipelago was mainly characterized by low total phytoplankton biomass (12.8 ± 2.2 mg chl *a* m^{-2}), production (78± 26 mg C m^{-2} d^{-1}), and a high relative abundance of small cells. In contrast, Lancaster Sound was characterized by high biomass (39.7 ± 10.0 mg chl *a* m^{-2}), production (251 ± 117 mg C m^{-2} d^{-1}) and a high relative abundance of large cells. This agrees with previous evidence that Lancaster Sound is a highly productive hotspot for several trophic levels (Michel et al. 2006), including phytoplankton and ice algae (Borstad & Gower 1984, Michel et al. 1996), zooplankton, polar cod (Welch et al. 1992, Crawford & Jorgenson 1996), birds and the benthos (Thomson 1982).

Over all the study area, Baffin Bay had the highest total phytoplankton biomass (64.1 ± 4.2 mg chl *a* m^{-2}) and production (361 ± 44 mg C m^{-2} d^{-1}), both dominated by large cells, and comparable to values previously reported for summer and early fall (41 to 68 mg chl *a* m^{-2} and 550 to 1719 mg C m^{-2} d^{-1}, Klein et al. 2002). This region is described as the most productive marine system north of the Arctic Circle (Tremblay et al. 2006) in terms of primary production (Klein et al. 2002, Tremblay et al. 2002), zooplankton abundance (Acuña et al. 2002), seabird (Karnovsky & Hunt 2002) and marine mammal (Stirling 1997) populations.

Based on the composition, size structure, biomass and production of the communities, two phytoplankton regimes (i.e. flagellate- and diatom-based systems) and six sub-regions (i.e. eastern Beaufort Sea, Amundsen Gulf, Amundsen Gulf hotspot, central Canadian Archipelago, Lancaster Sound and Baffin Bay) were distinguished across the Canadian High Arctic from late summer to fall. This novel information provides a framework to better understand the structure and function of marine phytoplankton communities in coastal Arctic seas and the fundamental processes influencing the transfer of carbon to higher trophic levels and to depth, as described below.

2.4.2 Influence of environmental factors on phytoplankton regimes

2.4.2.1 Spatial variability

Considering the three sampling years and all study regions, the main environmental factors explaining the variability in phytoplankton communities and regimes were nutrient concentrations (especially NO_3+NO_2) at the base of Z_{eu}, incident irradiance and the Z_{DCM}:Z_{Nit} ratio (Fig. 7b, Table 5).

Flagellate-based systems were associated with relatively fresh and stratified oligotrophic (NO_3+NO_2 depleted) waters (e.g. Beaufort Sea, central Canadian Archipelago), whereas diatom-based systems were associated with more saline and well-mixed eutrophic (NO_3+NO_2 repleted) waters (e.g. Baffin Bay, Lancaster Sound, Amundsen Gulf hot spot). Hence, transition from flagellate- to diatom-based systems was mainly controlled by the vertical stratification of the water column, which governed the supply of surface water nutrients. The (NO_3+NO_2):Si$(OH)_4$ and (NO_3+NO_2):PO_4 ratios were lower than Redfield values at most stations (Fig. 2d, Table 1), indicating that dissolved inorganic nitrogen was the macronutrient in shortest availability at Z_{DCM} throughout the sampling region. In Baffin Bay, however, (NO_3+NO_2):Si$(OH)_4$ ratios > 1 and low Si$(OH)_4$ concentrations (data not shown) indicate potential silicon limitation, as previously reported (Michel et al. 2002; Tremblay et al. 2002). Our results also agree with those of Carmack (2007) showing a longitudinal gradient in vertical stratification decreasing from the Beaufort Sea to Baffin Bay through the Canadian Archipelago (Fig. 7b). In the oligotrophic waters of the Beaufort Sea and Canada Basin (Carmack et al. 2004, Simpson et al. 2008, Tremblay et al. 2008), the numerical dominance of the small prasinophyte flagellate *Micromonas* was explained by strong surface density gradients (Li et al. 2009, Tremblay et al. 2009). Therefore, the structure and functioning of Arctic phytoplankton regimes appears to be determined by similar drivers, i.e. vertical stratification and nutrient availability, as tropical and temperate marine systems (Margalef 1978, Margalef et al. 1979, Cullen et al. 2002).

The vertical position of the maximum chl *a* fluorescence relative to the nitracline differed between the two distinct phytoplankton regimes (Fig. 7b), possibly reflecting differences in phytoplankton adaptive strategies. In stratified oligotrophic regions (i.e. eastern Beaufort Sea, Amundsen Gulf and the central part of the Canadian Arctic Archipelago), Z_{DCM} was above the nitracline (Z_{DCM}:$Z_{Nit} < 1$; Fig. 2e). This pattern was also observed in stratified temperate waters (Venrick 1988), where aggregated phytoplankton communities, generally dominated by flagellates, are called "layer-formers" by Cullen & MacIntyre (1998). Different adaptive mechanisms were proposed to explain this algal layer formation: (1) efficient nutrient consumption near water surface (Cullen & MacIntyre 1998), (2) physiological control of buoyancy, and (3) grazer avoidance (Turner & Tester 1997, Lass & Spaak 2003, van Donk et al. 2010). In well-mixed eutrophic regions (i.e. Baffin Bay, Lancaster Sound), the position of Z_{DCM} was located near or below the nitracline (Z_{DCM}:$Z_{Nit} \geq 1$). In this case, the algal layer was thicker and dominated by diatoms, a pattern described for "mixers" by Cullen &

MacIntyre (1998). These "mixers" are adapted to grow under variable light intensity (Legendre et al. 1987, Demers et al. 1991, Ibelings et al. 1994, Cullen & MacIntyre 1998). The Z_{DCM}:Z_{Nit} ratio is therefore a useful predictor of phytoplankton communities and regimes observed at the depth of maximum chl *a* fluorescence, which is a dominant feature of the Arctic Ocean (Hill et al. 2005, Martin et al. 2010, McLaughlin & Carmack 2010).

In addition to the large-scale phytoplankton regimes described above, highly productive hotspots (e.g. Amundsen Gulf, Lancaster Sound) reflect the influence of smaller scale processes on biological systems. In the Amundsen Gulf, hydrodynamic singularities and forcing events such as upwellings, eddies and storms are identified as key forcings (Carmack & Chapman 2003, Tremblay et al. 2008, Williams & Carmack 2008). This study reveals that productive hotspots occur throughout the coastal Canadian Arctic, yet their contribution to total primary production still remains to be determined. Such productive hotspots are expected to be widespread across the Arctic.

2.4.2.2 Temporal variability

One key aspect in early fall 2006 was the high chl *a* biomass of nano- and microphytoplankton as well as the high numerical contribution of centric diatoms (*Chaetoceros* spp.) to total cell counts across the transect (except at the two westernmost stations; Figs. 3-5). These findings confirm the widespread occurrence of fall blooms in the Canadian High Arctic, as previously reported for the Beaufort Sea (Arrigo & van Dijken 2004, Forest et al. 2008) and Baffin Bay (Booth et al. 2002, Caron et al. 2004). In addition, the relative abundance of dinoflagellates, mainly explained by the percent ice cover, was higher in fall (Fig. 7b, Table 3). Dinoflagellates were largely represented by heterotrophs *Gymnodinium/Gyrodinium*, indicating the potential significance of microzooplankton grazing at the end of the growing season. Recent studies have shown the importance of microzooplankton grazing towards the end of phytoplankton blooms in West Greenland (Levinsen & Nielsen 2002, Hansen et al. 2003). The relative abundance of chrysophyte and prymnesiophyte flagellates was positively correlated to daily irradiance and water temperature (Fig. 7b), thereby emphasizing the role of seasonal forcings on the composition of phytoplankton communities.

2.4.3 Ongoing responses of Arctic phytoplankton communities in a changing climate

Uncertainties and divergences remain with respect to the responses of Arctic phytoplankton dynamics to climate change (Behrenfeld et al. 2006, Arrigo et al. 2008, Vetrov & Romankevich 2009, Boyce et al. 2010). Boyce et al. (2010) underpinned the importance of understanding the role of environmental factors (especially the surface mixed layer depth and wind stress) in governing phytoplankton dynamics in the Arctic Ocean. The present study highlights the biogeographic complexity and the existence of distinct phytoplankton regimes in the Canadian High Arctic (flagellate- *versus* diatom-based systems). In this context, it is essential to take into account that biogeographic regions may respond differently to climate change in Arctic Ocean.

Based on the classification of phytoplankton regimes defined earlier, we investigated the relationship between phytoplankton biomass in eutrophic and oligotrophic waters and sea ice cover, using data from 2005 to 2010 (Fig. 8). Eutrophic regions considered are Lancaster Sound, Baffin Bay and the Amundsen Gulf hotspot.

Oligotrophic regions are the Beaufort Sea, Amundsen Gulf and the central Canadian Arctic Archipelago. This approach clearly shows that phytoplankton biomass decreases with increasing sea ice cover in eutrophic waters, whereas no such change is observed in oligotrophic waters (Fig. 8).

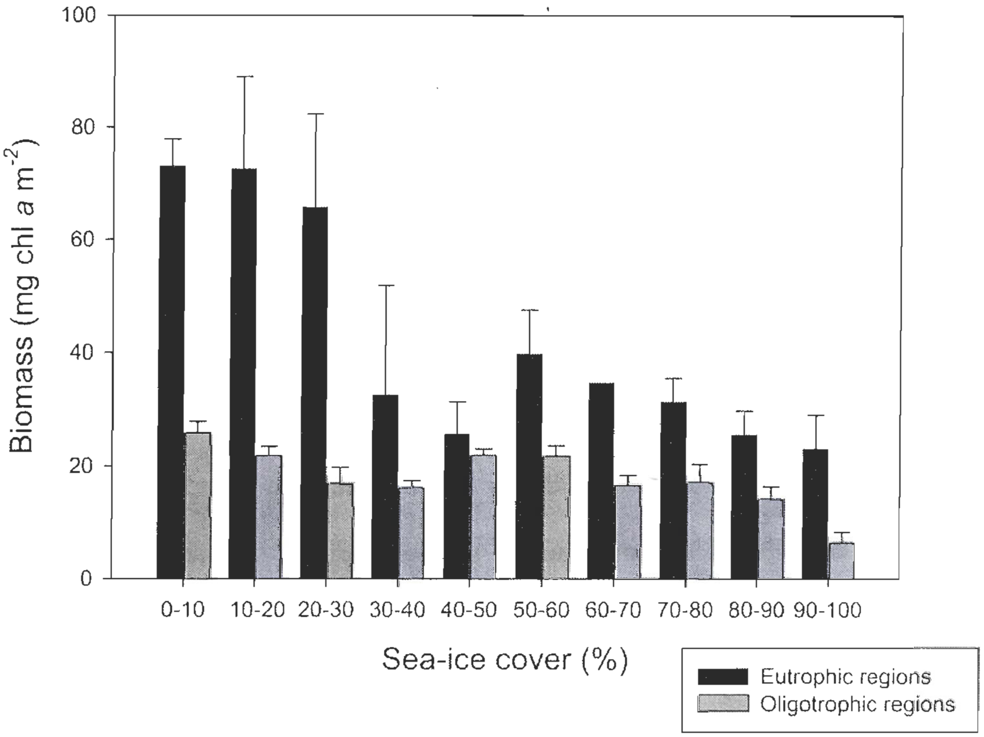

Fig. 8. Relationship between sea ice cover and phytoplankton chl *a* biomass integrated over the euphotic zone for eutrophic (i.e. the Lancaster Sound, Baffin Bay and the Amundsen Gulf hot spot) and oligotrophic regions (i.e. the Beaufort Sea, Amundsen Gulf and the central Canadian Archipelago) from 2005 to 2010. Bars and vertical lines represent average values and standard errors, respectively.

Different responses of oligotrophic *versus* eutrophic regions to the sea ice cover may provide interesting explanations to these divergent predictions (Arrigo et al. 2008, Li et al. 2009, Vetrov & Romankevich 2009, Boyce et al. 2010, Lavoie et al. 2010) for the future primary production in the Arctic Ocean. In accordance to Lavoie et al. (2010), a lengthening of the growing season would not induce a substantial increase in phytoplankton production and biomass in oligotrophic regions, due to persistent nutrient limitation. However, an increase in the frequency and intensity of storms (McCabe et al. 2001, Zhang et al. 2004) suggests that episodes of vertical mixing will be more frequent in the future. These changes in the stability of the water column could increase potential nutrient replenishment to surface waters, supporting episodes of enhanced primary production in oligotrophic regions. On the other hand, our results points to enhanced primary production as a result of the lengthening of the growing season in the eutrophic regions. In these productive regions, the annual primary production appears to be controlled by the photoperiod, as previously shown by Rysgaard et al. (1999). Altogether, the combined effect of a global increase in vertical stratification and lengthening of the growing season could alter the functioning and structure of eutrophic regions (i.e. diatom-based system), shifting to characteristics similar to oligotrophic regions (i.e. flagellate-based system). There is recent evidence that, picophytoplankton-based systems, favored by warmer temperature and stronger vertical stratification of the upper water column, are becoming more dominant in the Arctic Ocean (Li et al. 2009). Tremblay et al. (2009) also found a strong positive correlation between picophytoplankton abundance and water temperature in the circumpolar Arctic. Highly productive regions, crucial to carbon and energy transfers in Arctic marine ecosystems, are strikingly sensitive to potential changes in the stability of the water column. Changes in these regions could alter carbon flow to higher trophic levels and the capacity of the Arctic Ocean to act as a CO_2 pump, as suggested by Kirchman et al. (2009).

2.4.4 Conclusion

Repeated 3500 km transects were conducted across the Canadian High Arctic, from the Beaufort Sea to Baffin Bay through the Canadian Arctic Archipelago. Two distinct phytoplankton regimes were distinguished based on the production, biomass, abundance and size structure of phytoplankton communities: (1) a flagellate-based system extending over the eastern Beaufort Sea, Amundsen Gulf and the central part of the Canadian Arctic Archipelago, and (2) a diatom-based system centered in Baffin Bay, Lancaster Sound and the Amundsen Gulf hotspot. The oligotrophic regions were characterized by low production and biomass of large phytoplankton cells (> 5 µm) and high relative abundance of eukaryotic picophytoplankton (< 2 µm) and unidentified nanoflagellates (2 – 20 µm). The eutrophic regions were characterized by high production and biomass of large cells and high relative abundance of centric diatoms, mainly *Chaetoceros* species. As described by Carmack (2007), differences in the vertical stratification intensity in the Canadian High Arctic could explain various degrees of nutrient limitation (mainly NO_3), supporting these distinct phytoplankton communities and regimes. In this context, the present study reveals that the Z_{DCM}:Z_{Nit} ratio could be a useful predictor of phytoplankton communities and regimes of the maximum chl *a* fluorescence.

The occurrence of a fall bloom with high relative abundance of diatoms and nanophytoplankton was observed across the Canadian High Arctic. Furthermore, this study demonstrates that the timing and duration of the phytoplankton growing season are strongly constrained by sea ice melt and freezeup. Further research is warranted in order to better understand the spatio-temporal variability of the phytoplankton regimes in relation to environmental factors, particularly in the context of climate change.

Highly productive regions appear to be sensitive and to changes in the stability of the water column and sea ice dynamics, with possible alterations in the patterns of primary production and cascading effects to trophic structure and elemental cycling in the currently changing Arctic.

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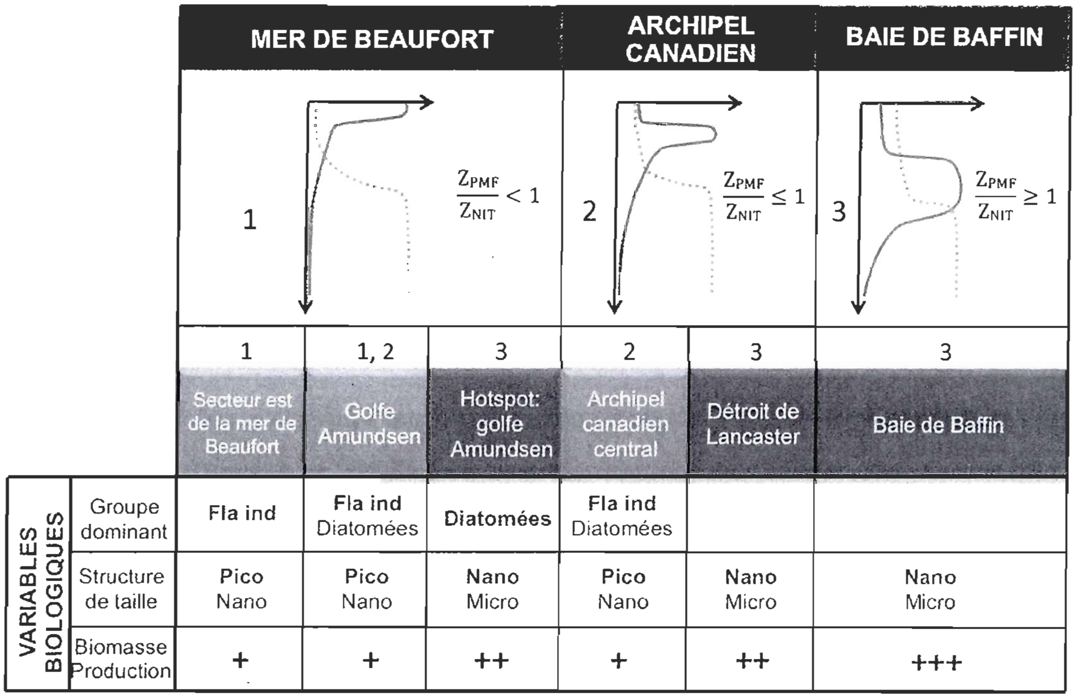
3. CONCLUSION GÉNÉRALE

Des perturbations environnementales associées aux changements climatiques ont présentement cours à l'échelle mondiale et ce, plus particulièrement, aux hautes latitudes (ACIA 2005, IPCC 2007). De plus, dans un contexte global de déclin de la biodiversité (Butchart et al. 2010), les écosystèmes marins et terrestres polaires requièrent des efforts d'inventaires (Poulin et al. 2010) et de monitorages (Grebmeier et al. 2006, Post et al. 2009). Des outils tels que la télédétection et la modélisation sont une aide précieuse permettant d'obtenir des suivis continus à grande échelle spatio-temporelle. Cependant, des études *in situ* sont indispensables afin de valider les algorithmes et modèles issus de ces nouvelles technologies. Cette étude s'intègre à cette problématique visant à documenter la variabilité du phytoplancton dans le Haut-Arctique canadien. Les objectifs spécifiques visaient à : (1) caractériser la variabilité spatio-temporelle de la production, de la biomasse et de la structure de taille des communautés phytoplanctoniques, (2) déterminer l'influence des variables abiotiques et biologiques sur les communautés phytoplanctoniques arctiques, et (3) discuter dans le contexte du changement climatique, de l'impact potentiel des changements environnementaux sur les communautés et régimes phytoplanctoniques arctiques.

Les résultats de ce mémoire ont d'abord permis d'établir un profil biogéographique de la structure et du fonctionnement des communautés phytoplanctoniques dans le Haut-Arctique canadien. Deux régimes phytoplanctoniques distincts, basés sur la production, la biomasse, l'abondance et la structure de taille ont ainsi pu être mis en évidence : (1) un système basé sur les flagellés, retrouvé dans le secteur oriental de la mer de Beaufort, le golfe Amundsen et la partie centrale de l'archipel canadien et (2) un système basé sur les diatomées caractérisant la baie de Baffin, le détroit de Lancaster et le centre du golfe Amundsen. Les systèmes basés sur les flagellés sont, d'une part, caractérisés par une faible production primaire et une faible biomasse de cellules phytoplanctoniques de grande taille et, d'autre part, par une abondance relative élevée de nanoflagellés indéterminés (2 – 20 µm). En revanche, les systèmes basés sur les diatomées sont caractérisés par une forte production primaire et une forte biomasse de cellules phytoplanctoniques de grande taille en majeure partie composées de diatomées centrales du genre *Chaetoceros*. Une complexité biogéographique évidente caractérise le phytoplancton du Haut-Arctique canadien avec des régions plus ou moins productives, ayant par conséquent, un rôle direct sur l'efficacité de la pompe biologique.

Par la suite, un effort a été porté sur la compréhension du rôle des facteurs environnementaux sur l'hétérogénéité spatiale des communautés et régimes phytoplanctoniques dans le Haut-Arctique canadien. Corroborant les récentes études réalisées dans l'océan Arctique (Carmack & Wassmann 2006, Carmack 2007, Tremblay & Gagnon 2009), l'intensité de la stratification verticale apparaît comme le principal facteur déterminant la répartition horizontale à grande échelle du phytoplancton, en régissant les apports en nutriments des eaux de surface. À une plus petite échelle, l'importance du couplage de la bathymétrie et de forçages physiques (tempêtes, courant de marée ou encore advection) jouerait un rôle clé dans la compréhension de la formation et de la récurrence de hotspot, tel que décrit dans le centre du golfe Amundsen.

La position verticale du maximum de fluorescence chlorophyllienne (Z_{DCM}) diffère distinctement entre les deux régimes phytoplanctoniques (systèmes basés sur les flagellés *versus* diatomées) (Fig. 1), suggérant des adaptations stratégiques du phytoplancton à la structure hydrographique.



		MER DE BEAUFORT			ARCHIPEL CANADIEN		BAIE DE BAFFIN
		1	1, 2	3	2	3	3
		Secteur est de la mer de Beaufort	Golfe Amundsen	Hotspot: golfe Amundsen	Archipel canadien central	Détroit de Lancaster	Baie de Baffin
VARIABLES BIOLOGIQUES	Groupe dominant	Fla ind	Fla ind Diatomées	Diatomées	Fla ind Diatomées		
	Structure de taille	Pico Nano	Pico Nano	Nano Micro	Pico Nano	Nano Micro	Nano Micro
	Biomasse Production	+	+	++	+	++	+++

Fig. 1: Modèle conceptuel des profils verticaux typiques des concentrations de la chlorophylle *a* et du nitrate présentés selon les différentes régions biogéographiques du Haut-Arctique canadien avec leurs caractéristiques biologiques respectives. Fla ind = flagellés indéterminés, Pico = picophytoplancton, Nano = nanophytoplancton, Micro = microphytoplancton; case gris foncée = région eutrophe, case gris claire = région oligotrophe, +++ > ++ > + = Intensité de la production et biomasse phytoplanctonique.

Dans les régions oligotrophes dominées par des flagellés, Z_{DCM} se situe nettement au-dessus de la nitracline, à l'inverse des régions eutrophes où Z_{DCM} semble proche, voir en dessous de la nitracline. De plus, l'épaisseur du maximum de chl *a* semble être plus grande dans les zones eutrophes qu'oligotrophes. Cela est probablement lié à un fort mélange de la colonne d'eau dans les zones eutrophes. Par conséquent, le rapport Z_{DCM}:Z_{Nit} est un bon indicateur pour prédire les communautés et régimes phytoplanctoniques dans les eaux ouvertes du Haut-Arctique canadien.

L'épisode de fortes concentrations de chlorophylle *a* et de grandes abondances de cellules phytoplanctoniques de grande taille a permis de mettre en évidence l'occurrence de floraisons automnales de façon ubiquiste à travers le Haut-Arctique canadien. La récurrence de ces floraisons automnales et leur importance biologique dans les écosystèmes arctiques demeurent présentement très peu documentées.

Cette maîtrise a permis en définitive de documenter la variabilité du phytoplancton dans le Haut-Arctique canadien, ainsi que l'influence des variables du milieu sur la structure et la dynamique des communautés phytoplanctoniques arctiques. La connaissance de ces processus clés au sein des écosystèmes polaires est un prérequis nécessaire à une meilleure compréhension de la pompe biologique, particulièrement dans le contexte du changement climatique. Dans l'océan Arctique, l'un des scénarios (ACIA 2005, IPCC 2007) du réchauffement climatique est une intensification de la stratification verticale de la colonne d'eau. Les régions hautement productives, importantes pour les écosystèmes marins arctiques, semblent intimement liées à la structure hydrographique de la colonne d'eau. Si les changements en cours perdurent dans l'océan Arctique, ces régions hautement productives pourraient être drastiquement affectées par de possibles changements dans les patrons de production primaire, influant directement sur la structure trophique et les cycles biogéochimiques.

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5. APPENDICE

Table 1. List of stations visited in three biogeographic regions of the Canadian High Arctic from 2005 to 2007. Environmental and biological variables were measured at each station, except primary production which was only measured at full stations.

Region	Period	Date	Basic station	Full station
Beaufort Sea	Late Summer 2005	2–13 Sept	204, 436, 12	10, 421, 408, 407,405
	Early fall 2006	29 Sept–17 Oct	434, 420, 408	421, 435, 408, 407, 436, 405
	Fall 2007	15 Oct–5 Nov	435, 434, 1606, 420, 1216, 1600, 1800, 1806, 408, 437, 1902, 1200, 1908, 1100, 407, 1116, 1110, 405, 1000	
Canadian Arctic Archipelago	Late Summer 2005	23–30 Aug	p	314, 6, 4, 3
	Early fall 2006	20–27 Sept	314, 301	310, 307, 303
	Fall 2007	7–12 Oct	314, 310, 308, 301	309, 302
Baffin Bay	Late Summer 2005	16–22 Aug	127	100, 101, 108, 115
	Early fall 2006	7–18 Sept	100, 108, 119, 122, 127	101, 115, 118, 126, 131, 132
	Fall 2007	29 Sept–4 Oct	134, 105, 111	101, 108, 115

Table 2. Abbreviations for biological and environmental variables and units. Avg: average value over the euphotic zone; Atm: atmospheric measurement; Z_{DCM}: depth of the maximum of chlorophyll *a* fluorescence; Int: integrated value over the euphotic zone; Prof: profile observation; Vis: visual observation.

	Measurement	**Abbreviation**	**Unit**
Environmental variable:			
Temperature	Avg	T_{eu}	°C
Salinity	Avg	S_{eu}	
Stratification index	Prof ($\sigma_{80m} - \sigma_{5m}$)	$\Delta\sigma_t$	
Euphotic zone	Prof	Z_{eu}	m
Surface mixed layer		Z_m	
Nitracline		Z_{Nit}	
Maximum chl *a* fluorescence		Z_{DCM}	
Nitrate + Nitrite	Z_{DCM}	NO_3+NO_2	µmol l^{-1}
Silicic acid		$Si(OH)_4$	
Phosphate		PO_4	
Sea ice cover	Vis	I_C	%
Daily incident irradiance	Atm	E_d	E m^{-2} d^{-1}
Bottom depth	Prof	Z_{BOT}	m
Biological variable:			
Biomass (≥ 0.7 µm) ; (0.7 – 5 µm) ; (≥ 5 µm)	Int	B_T ; B_S ; B_L	mg chl *a* m^{-2}
Production (≥ 0.7 µm) ; (0.7 – 5 µm) ; (≥ 5 µm)	Int	P_T ; P_S ; P_L	mg C m^{-2} d^{-1}
Community structure	Z_{DCM}		%
Picophytoplankton (< 2 µm)		Pico	
Nanophytoplankton (2 – 20 µm)		Nano	
Microphytoplankton (≥ 20 µm)		Micro	
Group structure	Z_{DCM}		%
Total diatoms		Diat	
Total flagellates		Flag	
Total dinoflagellates		Dino	
Total other protists		Others	
Composition	Z_{DCM}		10^6 cells l^{-1}
Centric diatoms		Cen. dia	
Chrysophytes		Chry	
Cryptophytes		Cryp	
Dinoflagellates		Dino	
Prasinophytes		Pras	
Pennate diatoms		Pen. dia	
Prymnesiophytes		Prym	
Unidentified flagellates		Un. fla	
Total abundance	Z_{DCM}	Total abund.	10^6 cells l^{-1}