TABLE DES MATIÈRES

Page

LISTE DES TABLEAUX

Page

II. PHYTOPLANKTON DISTRIBUTION ALONG A 3500 KM TRANSECT IN CANADIAN ARCTIC WATERS IN LATE SUMMER: STRONG DOMINANCE OF PICOEUKARYOTES

LISTE DES FIGURES

Page

I. INTRODUCTION GÉNÉRALE

II. PHYTOPLANKTON DISTRIBUTION ALONG A 3500 KM TRANSECT IN CANADIAN ARCTIC WATERS IN LATE SUMMER: STRONG DOMINANCE OF PICOEUKARYOTES

INTRODUCTION GÉNÉRALE

Le terme plancton a été défini scientifiquement pour la première fois par Hensen (1887) permettant de caractériser l'ensemble des organismes vivants, animaux et végétaux, qui flottent dans les eaux. Bien que certains organismes planctoniques puissent atteindre des tailles importantes, comme les méduses, la très grande majorité du plancton est tellement minuscule que l'utilisation d'un microscope devient essentielle pour en faire l'observation. Ces organismes planctoniques peuvent être caractérisés en se basant sur leur rôle fonctionnel dans l'écosystème, ou encore selon des critères génétiques, taxinomiques (Stockner et Antia 1986) ou de taille (Sieburth et al. 1978).

Dans sa conception la plus élémentaire, la classification des organismes planctoniques est constituée par le zooplancton (organismes animaux pluricellulaires), le phytoplancton (incluant les cellules végétales eucaryotes et procaryotes) et le bactérioplancton (cellules procaryotes hétérotrophes). Le critère de taille du plancton permet de distinguer des compartiments écologiques auxquels correspondent des classes de taille relativement bien définies. Dans ce mémoire nous nous intéresserons surtout au microphytoplancton (20–200 µm), au nanophytoplancton (2–20 µm) et au picophytoplancton (0,2–2 µm).

Réseaux trophiques pélagiques

Comme dans tous les écosystèmes terrestres et aquatiques, les végétaux chlorophylliens représentent le premier maillon de la chaîne trophique assurant la fixation du carbone. En se référant à la structure de taille des organismes phytoplanctoniques, notamment la partition entre les petites (<5 μm) et les grandes (>5 μm) cellules, quatre types d'écosystèmes pélagiques marins ont été décrits. Il est admis que lorsque les concentrations d'azote sont faibles, les petites cellules sont plus efficaces dans l'absorption de l'ammonium comparé aux grosses cellules. Seulement deux des quatre types d'écosystèmes pélagiques marins seront décrits dans le présent mémoire puisqu'ils représentent les situations extrêmes contrairement aux deux autres types intermédiaires.

La chaîne trophique classique dominée par le réseau herbivore représente le système le plus simple (Fig. 1). Il repose essentiellement sur l'assimilation des éléments nutritifs, principalement le nitrate, par de grandes cellules phytoplanctoniques lesquelles seront broutées par le zooplancton herbivore (e.g., les copépodes) qui sera à son tour consommé par les carnivores de premier ordre (Steele 1974). La forte concentration en nitrates dans le milieu va donc favoriser le développement des grosses cellules phytoplanctoniques au détriment des plus petites. Ce système est particulièrement efficace dans l'exportation du carbone en profondeur. Cette chaîne alimentaire simple est toutefois insuffisante pour comprendre l'ensemble des processus existant au sein du système planctonique.

Pomeroy (1974) et Azam et al. (1983) ont démontré que les cellules picophytoplanctoniques autotrophes et hétérotrophes constituent une importante source d'énergie au sein de ce que nous appelons maintenant la boucle microbienne (Fig. 1). Dans ce système, les apports en éléments azotés sont quasi nuls alors que la matière organique dissoute excrétée par le phytoplancton et générée par l'activité du zooplancton (e.g., bris de cellules, excrétion, pelotes fécales) est consommée efficacement par les bactéries hétérotrophes. Ces mêmes bactéries entrent alors en compétition directe avec le phytoplancton de petite taille pour l'ammonium. Le système repose sur l'excrétion d'ammonium et représente ainsi un circuit en boucle fermé. Ce type d'écosystème se caractérise par une relative inefficacité de l'exportation du carbone. La faible sédimentation et le recyclage rapide de la matière sédimentaire font en sorte que le transfert d'énergie vers le réseau trophique supérieur est faible.

L'instauration d'un réseau trophique pélagique dépend des conditions du milieu auxquelles est soumis le phytoplancton. Les algues phytoplanctoniques ont développé des adaptations morphologiques leur permettant de se maintenir dans la couche de surface où la photosynthèse est possible, résultant d'une adaptation acquise au fil du temps. Par contre, les organismes phytoplanctoniques subissent les variations de leur environnement et doivent donc s'y adapter de manière à pouvoir se développer. La lumière incidente et la turbulence constituent les principaux facteurs de contrôle de la production primaire dans les écosystèmes marins. De fait, Legendre et Rassoulzadegan (1995) ont démontré

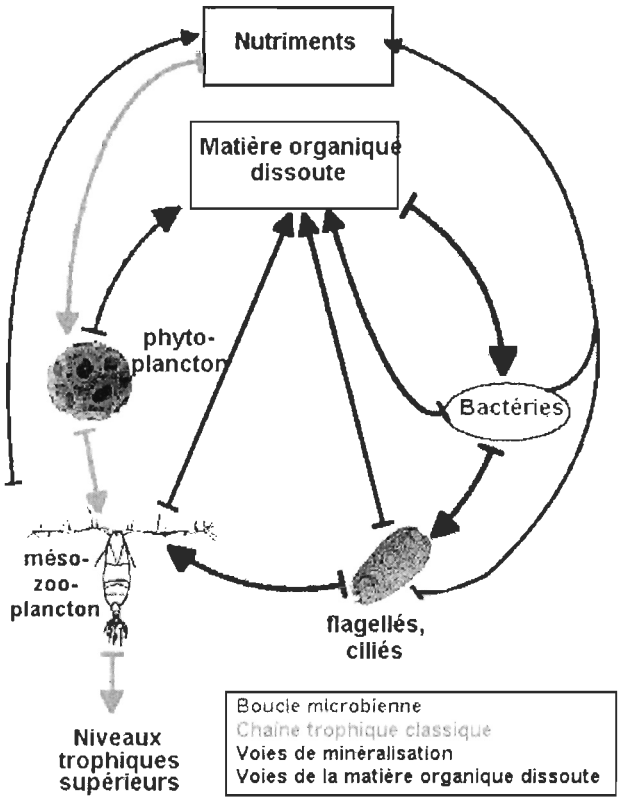

Figure 1 : Chaîne trophique classique (herbivore) *versus* la boucle microbienne (Tirée de Steele 1974).

que les caractéristiques hydrodynamiques de la colonne d'eau influençaient les apports en éléments nutritifs et la lumière incidente disponible, le type de production phytoplanctonique qu'elle soit nouvelle ou régénérée ainsi que le type de micro-organismes présents (Fig. 2). Dans un milieu bien mélangé, la lumière incidente devient la variable environnementale limitante et la production nouvelle est alors dominée par le nanophytoplancton et le microphytoplancton de telle sorte que s'installe un réseau trophique herbivore. Ce type de réseau trophique est principalement retrouvé dans les écosystèmes côtiers et eutrophes. En contrepartie dans un milieu stratifié, ce sont les éléments nutritifs qui deviennent limitants et la production régénérée est alors dominée par le picophytoplancton (cellules flagellées autotrophes, bactéries hétérotrophes et cyanobactéries) de telle sorte qu'un réseau trophique microbien prend place. Ce type de réseau est surtout observé dans les écosystèmes océaniques et oligotrophes, pauvres en éléments nutritifs.

Répartition du microphytoplancton et du nanophytoplancton

Le microphytoplancton (20–200 μm) et le nanophytoplancton (2–20 μm) se composent de diatomées, de dinoflagellés et de flagellés. Les diatomées (Bacillariophyta) ont longtemps été reconnues comme étant le principal groupe du phytoplancton marin. On estime annuellement la production primaire marine à 60 Gt de carbone, dont une contribution de quelque 25 Gt de carbone qui serait imputable aux diatomées (Nelson et al. 1995). Les diatomées sont divisées en deux groupes : les Centrales qui présentent une symétrie radiale et une forme généralement circulaire et les Pennales qui ont une symétrie

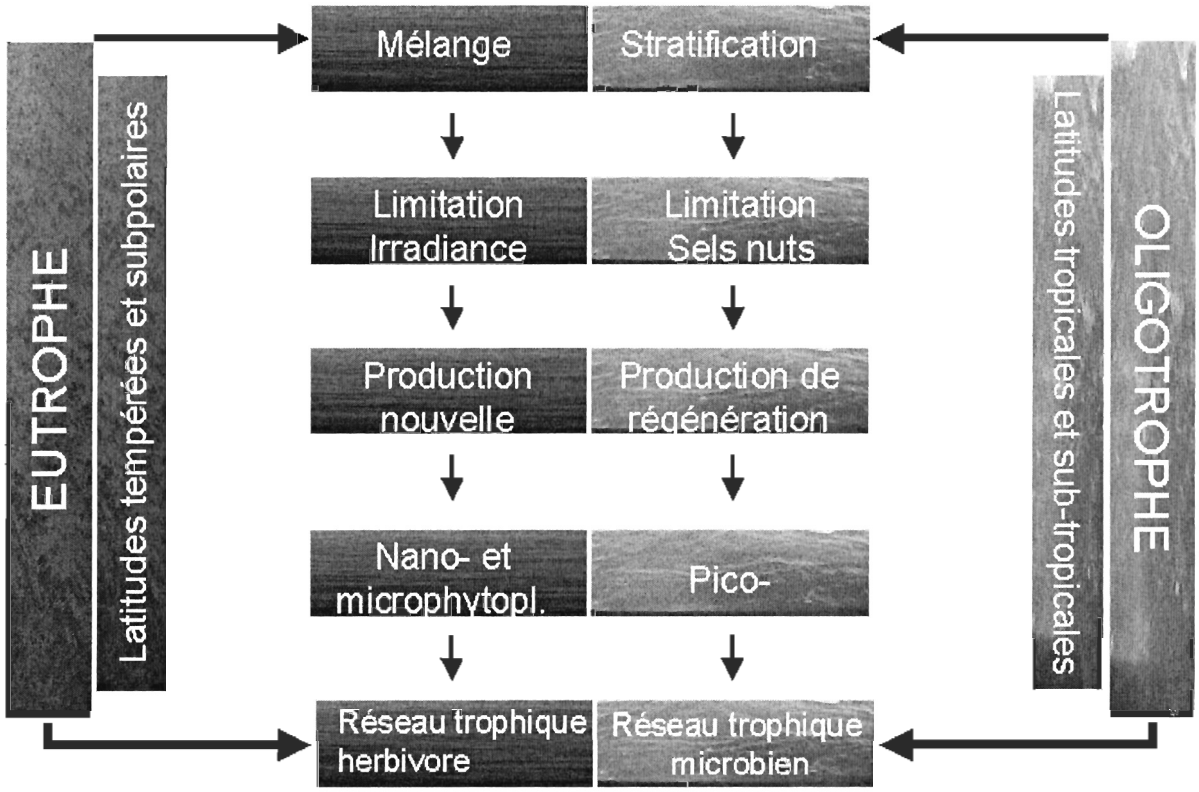

Figure 2 : Représentation schématique de l'installation des écosystèmes pélagiques (Adaptée de Legendre et Rassoulzadegan 1995).

bilatérale et une forme allongée linéaire-lancéolée. Il est à noter que l'usage de ces termes n'est aucunement valide sur le plan nomenclatural. Les diatomées centrales sont prépondérantes dans les écosystèmes marins côtiers et océaniques avec, par exemple, une abondance marquée du genre *Skeletonema* Greville lors des floraisons de fin d'hiver ou encore des genres *Chaetoceros* Ehrenberg et *Thalassiosira* Cleve rencontrés pendant les floraisons printanières. Quant aux dinoflagellés, ce sont des organismes autotrophes et hétérotrophes unicellulaires qui se retrouvent aussi bien parmi le microphytoplancton que le nanophytoplancton. Les dinoflagellés tirent avantage de leur capacité à se mouvoir puisqu'ils peuvent se déplacer dans la colonne d'eau lorsque, par exemple, la turbulence des eaux est faible.

La première étude sur la composition du phytoplancton des mers arctiques remonte à Cleve (1896) qui a analysé une cinquantaine d'échantillons de la baie de Baffin et du détroit de Davis. Quelques années plus tard, Gran (1904) a recensé les mêmes espèces retrouvées par Cleve (1896), en y ajoutant deux nouvelles espèces en provenance de la mer du Groenland. Il a de plus distingué les espèces issues des glaces de mer telles que *Nitzschia frigida* Grunow et *Melosira hyperborea* Grunow (=*Melosira arctica* Dickie) de celles de la colonne d'eau (*Chaetoceros* spp. et *Thalassiosira* spp.). Selon Heimdal (1989), aucune recherche sur la dynamique du phytoplancton en relation avec son environnement arctique n'a été faite avant les années 1930. Grøntved et Seidenfaden (1938) ont été les premiers à présenter les données sur la répartition spatiale du phytoplancton dans la région de la polynie des Eaux du Nord (NOW), à l'ouest du Groenland. C'est pour ainsi dire la

première étude exhaustive démontrant que la polynie NOW est parmi les régions maritimes les plus productives au nord du cercle arctique. D'autres études ont suivi fournissant des comptes-rendus sur la répartition du phytoplancton dans d'autres régions de l'Arctique telles que la côte ouest de Svalbard (Ramsfjell 1954), la baie d'Hudson (Bursa 1961), Pond Inlet (Cross 1982), et en bordure de la banquise en mer du Groenland (Spies 1987). Des études plus récentes ont permis la reconnaissance d'espèces dominantes en régions arctiques (Booth et Horner 1997, Booth et Smith 1997, Jensen et Hansen 2000, von Quillfeldt 2000, Booth et al. 2002, Lovejoy et al. 2002, Rat'kova et Wassmann 2002), contribuant ainsi à améliorer nos connaissances sur la répartition du phytoplancton dans l'Arctique et, plus particulièrement, celle des cellules de taille plus grande que 2 μm.

Le microphytoplancton et le nanophytoplancton sont généralement associés aux latitudes nord et sud des eaux tempérées ainsi que dans les régions de résurgence équatoriale (Tarran et al. 2006). En régions polaires, la présence du microphytoplancton et du nanophytoplancton dépend surtout de la fonte des glaces de mer annuelles et elle est restreinte essentiellement à certaines périodes de l'année (Gosselin et al. 1997, Lovejoy et al. 2002, Wassmann et al. 2006). L'étendue et la couverture des glaces de mer de première année contrôlent la disponibilité de la lumière incidente, limitent la formation d'une stratification de la colonne d'eau et empêchent un mélange vertical normalement induit par l'action du vent (e.g. Mei et al. 2003). La compilation de résultats échelonnés sur une dizaine d'années dans le détroit de Barrow et le Passage du nord-ouest a permis à Michel et al. (2006) d'établir que la floraison phytoplanctonique survenait au cours du mois de juillet

au moment même de la fonte des glaces de mer annuelles. Pour sa part, Hsiao (1996) a établi pour la mer de Beaufort que les diatomées et les flagellés représentaient les organismes phytoplanctoniques contribuant le plus à la production primaire pendant la saison estivale libre de glace, c'est-à-dire en juillet et en août. Par contre, dans les polynies des Eaux du Nord (NOW) et du Nord-Est (NEW), de part et d'autre du Groenland, les diatomées ont fait leur apparition aussi hâtivement qu'en mars, permettant ainsi de rallonger la période de production (Mei et al. 2002, Tremblay et al. 2006).

Répartition du picophytoplancton

Le microphytoplancton et le nanophytoplancton peuvent être facilement filtrés sur différents types de membranes pour ensuite y être identifiés et dénombrés par la microscopie optique. Par contre, les cellules picophytoplanctoniques, étant de plus petites tailles, deviennent pratiquement impossibles à y être observées par la microscopie conventionnelle. Les avancés technologiques récentes ont toutefois permis non seulement de reconnaître mais aussi d'identifier des cellules de plus en plus petites (Stockner et Antia 1986). Les études en cytométrie de flux ont ainsi permis de démontrer que le picophytoplancton autotrophe est composé de deux principaux genres de cyanobactéries, *Prochlorococcus* Chisholm, Frankel, Goericke, Olson, Palenik, Waterbury, West-Johnsrud et Zettler (Johnson et Sieburth 1979) et *Synechococcus* Nägeli (Waterbury et al. 1979), ainsi que de très petites cellules eucaryotes (Campbell et al. 1994). La principale distinction entre ces deux genres de cyanobactéries repose essentiellement sur la forte fluorescence orange émise par le pigment de la phycoérythrine présente chez les *Synechococcus*.

L'utilisation de la biologie moléculaire a aussi permis d'améliorer nos connaissances des caractéristiques physiologiques et des mécanismes d'adaptation des cyanobactéries. Par contre, nous commençons à peine à mettre en lumière le picophytoplancton eucaryote et d'en identifier les principaux groupes (Worden 2006).

Depuis la découverte des cyanobactéries *Prochlorococcus* et *Synechococcus*, de nombreuses études ont porté sur le rôle exercé par le picophytoplancton dans le fonctionnement des écosystèmes côtiers pélagiques (e.g., Li 1994, Worden et al. 2004, Maixandeau et al. 2005). Le picophytoplancton se retrouve habituellement dans les régions océaniques oligotrophes avec des abondances relativement constantes et élevées variant entre 10^7 et 10^9 cellules l^{-1} (Stockner et Antia 1986). Le picophytoplancton est dominant non seulement en terme de production primaire en dehors des périodes de floraisons habituelles de diatomées ou de dinoflagellés (Bell et Kalff 2001, Durand et al. 2001), mais il représente aussi une contribution importante à la biomasse phytoplanctonique (Partensky et al. 1999, Sherr et al. 2003). Cette prépondérance du picophytoplancton s'explique, entre autres, par la très petite taille des cellules associée à une faible vitesse de chute (loi de Stokes), leur assurant ainsi un avantage certain sur l'absorption d'éléments nutritifs en faible concentration ambiante (Raven 1998).

Le genre *Prochlorococcus* fait partie des cyanobactéries marines photosynthétiques dont la taille des cellules est d'environ 0,6 µm. Ce genre est surtout numériquement dominant sur toute la profondeur de la zone euphotique des océans entre les latitudes 40°N

et 40°S, quoique Buck et al. (1996) ont observé la présence de *Prochlorococcus* jusqu'à la latitude 61°N. Selon Partensky et al. (1999), il serait l'organisme photosynthétique le plus abondant en terme de nombre d'individus dans les océans. Dans les eaux oligotrophes de l'Atlantique et du Pacifique, les cellules de *Prochlorococcus* sont présentes jusqu'à des profondeurs largement supérieures à celles de la zone euphotique (Partensky et al. 1999). Dans l'océan Atlantique, *Prochlorococcus* est particulièrement abondant dans les gyres tropicales où les éléments nutritifs sont presque absents alors que la température de l'eau se situe autour de 24°C, se rapprochant ainsi des conditions optimales pour leur croissance (Partensky et al. 1999). Agustí (2004) a d'ailleurs démontré que la croissance des cellules de *Prochlorococcus* était négativement corrélée avec la concentration en nitrate des eaux de surface (Pearson $r = -0,77$, $p < 0,05$). De plus, Vaulot et al. (1995) et DuRand et al. (2001) ont calculé que les cellules de *Prochlorococcus* contribueraient entre 21% et 43% de la biomasse phytoplanctonique et entre 13% et 48% de la production primaire dans les océans oligotrophes.

Pour sa part, le genre *Synechococcus* dont la taille des cellules varie entre 0,8 et 1,5 µm regroupe des cyanobactéries planctoniques photosynthétiques abondantes en milieu marin, et plus particulièrement en milieu côtier (Stockner 1988, Partensky et al. 1999). Plusieurs espèces dulcicoles de *Synechococcus* ont aussi été décrites récemment, certaines occupant même des habitats extrêmes tels que des sources géothermales, des eaux riches en soufre ou encore pauvres en oxygène, et même des milieux appauvris en éléments nutritifs (Stockner et al. 2000). *Synechococcus* est principalement retrouvé dans la plupart des

océans et des mers oligotrophes-mésotrophes des Tropiques jusqu'aux régions polaires (Shapiro et Haugen 1988). D'ailleurs Gradinger et Lenz (1989) et Not et al. (2005) ont démontré la présence de *Synechococcus* dans les eaux arctiques, plus particulièrement dans les masses d'eau influencées par les courants en provenance de l'Atlantique. Tout récemment, Waleron et al. (2007) ont mis en évidence l'importance des apports allochtones de *Synechococcus* dans l'Arctique de l'ouest par l'intermédiaire des rivières Mackenzie en mer de Beaufort et Horton en baie de Franklin. L'importance des cellules de *Synechococcus* sur le transfert d'énergie vers les niveaux trophiques supérieurs dans les eaux arctiques n'a pas autant d'impact que dans le cas des cellules picoeucaryotes (Gradinger et Lenz 1995), ces dernières étant plus importantes à la fois en terme de biomasse et d'abondance dans les eaux arctiques (Smith et al. 1985).

Quant aux cellules picoeucaryotes, elles présentent une très grande diversité et elles dominent numériquement la communauté picophytoplanctonique dans les gyres oligotrophes de l'Atlantique et du Pacifique (Tarran et al. 2006). Certaines études ont même démontré que les cellules picoeucaryotes, incluant les chlorophytes et les prasinophytes dont principalement *Micromonas pusilla* (Butcher) Manton et Parke, peuvent aussi être prépondérantes en milieu côtier (Not et al. 2004, Romari et Vaulot 2004, Worden 2006). En milieu océanique, les cellules picoeucaryotes sont surtout observées en profondeur à la base de la zone euphotique correspondant au 0,5% de la lumière incidente de surface (Glover et al. 1986). L'abondance du picophytoplancton suit également un cycle saisonnier semblable à celui des cellules phytoplanctoniques de plus grande taille, avec un

maximum généralement observé en été (Stockner et Antia 1986). Les cellules picoeucaryotes sont responsables d'une grande fraction de la biomasse de carbone en comparaison des cyanobactéries (Li 1994, Tarran et al. 2006). Par exemple, dans le Pacifique nord et le sud de la mer de Béring, Liu et al. (2002) ont démontré qu'à la fin de la saison estivale, les cellules eucaryotes étaient beaucoup plus importantes en terme de biomasse pour le compartiment pico-autotrophe.

Les études sur la répartition géographique du phytoplancton dans les régions arctiques ont longtemps mis l'emphase sur les cellules microphytoplanctoniques et nanophytoplanctoniques (Murphy et Haugen 1985, von Quillfeldt 1997), favorisant ainsi la conception d'un réseau trophique classique ou herbivore. Au cours de la dernière décennie, plusieurs travaux ont démontré que les régions arctiques favorisaient la prépondérance de cellules picoeucaryotes (Booth et Smith 1997, Booth et Horner 1997, Not et al. 2005, Lovejoy et al. 2006). En mer de Barents, Not et al. (2005) ont mesuré des abondances de cellules picoeucaryotes dans les eaux d'origine Arctique variant entre 2600 et 10 200 cellules ml^{-1}. Les cellules picoeucaryotes, plus particulièrement la classe des Prasinophyceae, sont aussi très présentes dans les régions arctiques représentant entre 40% et 80% de la biomasse chlorophylienne annuelle, à l'exception toutefois du mois de juillet (Lovejoy et al. 2007). Selon les études de Not et al. (2005) et de Lovejoy et al. (2007), *Micromonas pusilla* est l'organisme eucaryote dominant dans les eaux arctiques. Cette prasinophyte représente un écotype distinct pour les régions arctiques avec une étroite niche thermale (Lovejoy et al. 2007). Ces dernières découvertes mettent ainsi en évidence

l'importance du réseau pélagique microbien dans l'Arctique (Lovejoy et al. 2007). Il en ressort que l'observation des spectres de taille dans l'environnement peut donner une très bonne indication de la structure trophique du domaine pélagique d'une région aussi vaste que celle représentée, par exemple, par l'Arctique.

Région sous étude

La région étudiée se situe en plein cœur du Haut Arctique canadien, s'étalant depuis la baie de Baffin jusqu'en mer de Beaufort en passant par le Passage du nord-ouest, c'est-à-dire représentant une distance d'à peu près 3500 km. Cette vaste région est sous l'influence d'entrée d'eaux du Pacifique à l'ouest et de l'Atlantique à l'est. Par conséquent, ces deux types de masses d'eau ont des propriétés physico-chimiques différentes; l'eau provenant du Pacifique est moins salée et riche en éléments nutritifs et l'eau originant de l'Atlantique est plus salée et moins riche en éléments nutritifs (Jones et al. 1998, Tremblay et al. 2002). Les changements apportés par le réchauffement planétaire (ACIA 2005) entraînent déjà (1) une réduction de la couverture des glaces annuelles influençant la pénétration de la lumière et la stratification des eaux ouvertes (Smetacek et Nicol 2005) et (2) des changements dans la circulation océanique (Kliem et Greenberg 2003) qui résultent en une augmentation de la température de l'eau atlantique entrant dans l'océan Arctique (Polyakov et al. 2004). Il est très certainement envisageable de prévoir de nouvelles perturbations du milieu qui influenceront alors la répartition du micro-, du nano- et du picophytoplancton dans le Haut Arctique canadien, modifiant ainsi le réseau trophique pélagique arctique et les flux verticaux de carbone. Une meilleure connaissance de la dominance et de la répartition

spatiale actuelle des différents groupes phytoplanctoniques nous permettra de mieux prévoir la réponse du phytoplancton arctique à une réduction de la couverture de glace, à un accroissement de la stratification de la colonne d'eau et à une augmentation de la température des eaux de surface.

Objectifs de la recherche

La présente étude vise à évaluer la répartition spatiale et l'abondance du pico-, du nano- et du microphytoplancton du Haut Arctique canadien depuis la baie de Baffin jusqu'en mer de Beaufort en passant par le Passage du nord-ouest à la fin de la période estivale. Les deux objectifs spécifiques à cette étude sont: 1) décrire la répartition spatiale du micro-, du nano- et du picophytoplancton dans les trois régions océanographiques du Haut Arctique canadien et 2) évaluer les variables environnementales gouvernant la répartition du phytoplancton.

II. PHYTOPLANKTON DISTRIBUTION ALONG A 3500 KM TRANSECT IN CANADIAN ARCTIC WATERS IN LATE SUMMER: STRONG DOMINANCE OF PICOEUKARYOTES

ABSTRACT

A number of recent studies showed that photosynthetic picoeukaryotes are an active and often dominant component of the Arctic algal assemblage. In order to extend these observations, samples from the euphotic zone were collected at 18 stations along a transect from the northern Baffin Bay to the Beaufort Sea through the Northwest Passage in late summer 2005. Picophytoplankton (<2 μm) and nanophytoplankton cells (2–20 μm) were enumerated using flow cytometry and phytoplankton cells >2 μm were identified and counted by light microscopy. In addition, algal pigment composition was assessed by reverse-phase high-performance liquid chromatography to determine to which algal groups belong the smallest cells. The spatial phytoplankton distribution was heterogeneous along the transect. Maximum picophytoplankton abundance was observed in the Beaufort Sea/Northwest Passage region, whereas nanophytoplankton abundance tended to increase toward the eastern Canadian Arctic. Picophytoplankton abundance and total chlorophyll *a* biomass reached values as high as 18,400 cells ml^{-1} and 6 μg l^{-1}. Picophytoplankton abundance and chlorophyll *a* <5 μm made up >70 % of total phytoplankton abundance and biomass in 70 % of the collected samples. Throughout the transect, picophytoplankton cells were largely dominated by eukaryotes (presumably the Prasinophyceae *Micromonas*). Maximum abundances of picocyanobacteria (120 cells ml^{-1}) were observed in brackish waters of the Beaufort Sea. These results confirm that picophytoplankton can dominate not only in warm oligotrophic waters, but also in a perennially cold ocean in late summer.

INTRODUCTION

The size distribution of phytoplankton assemblages is a major biological factor that governs the functioning of the pelagic food web and, consequently, affects the rate of carbon export from the open ocean surface waters to the deep layers (Legendre & LeFèvre 1991). Large, rapidly sinking phytoplankton cells such as diatoms, are believed to control the carbon flux from the upper ocean layers (Michaels & Silver 1988), and to efficiently transfer energy to the upper trophic levels (Cushing 1989). Large diatoms are at the base of herbivorous food webs, supporting renewable marine resources such as herbivorous zooplankton and fish (Cushing 1989). In contrast, small phototrophic picoplankton (cells from 0.2 to 2 μm; Sieburth et al. 1978) are believed to be recycled within the microbial loop (Azam et al. 1983) contributing less efficiently to the transfer of energy and matter to the upper trophic levels. Picophytoplankton cells are also considered to contribute less to the sinking material because of their low sinking fluxes (Michaels & Silver 1988). However, Richardson & Jackson (2007) have shown that the relative contribution of picophytoplankton to carbon export can be proportional to their total net primary production because of their incorporation into aggregates that can settle or be grazed by mesozooplankton. Considering the finding of Richardson & Jackson (2007), the conventional view that picophytoplankton contribute little to carbon export should be revisited.

Large phytoplankton cells, including diatoms, prymnesiophytes and dinoflagellates, produce seasonal blooms under specific hydrographic conditions (Mei et al. 2002). For instance, the production of large phytoplankton is governed by variations in the vertical stability of the water column, through the effects on nutrient replenishment and the residence time of algal cells in the euphotic zone (Tremblay et al. 1997). In addition, the duration of the production period is sensitive to the seasonal melt dynamics of sea ice (Fortier et al. 2002). In northern Baffin Bay, intense diatom bloom characterized by cells >5 μm, begins as early as the end of April when the North Water polynya opens up (Mei et al. 2003). In the Canadian Archipelago, particularly in Barrow Strait, the phytoplankton bloom typically develops in July and August, corresponding to the timing of the ice break-up for this region (Michel et al. 2006). In the Chukchi and Beaufort seas, high chlorophyll concentrations are observed in regions along the ice edge, and are associated with an overwhelming predominance of diatoms and haptophytes (Hill et al. 2005). In the Barents Sea, large-celled phytoplankton dominate during blooms occurring in the marginal ice zone (Wassmann et al. 2006) and are of particular importance to the production of organic matter and vertical export of carbon (Sakshaug & Skjoldal 1989).

Several studies have shown that small phytoplankton cells (<5 μm) can also have an important role in carbon fixation in the Arctic Ocean and adjacent seas (Legendre et al. 1993, Pesant et al. 1996, Gosselin et al. 1997). Picophytoplankton contribute for most of the production and biomass in warm and nutrient-poor waters (Agawin et al. 2000). Recent studies have shown that picophytoplankton are often well-represented in terms of abundances in cold Arctic seawaters. Indeed, eukaryotic cells <2 μm often dominate the

phytoplankton assemblage reaching abundances in the order of 1000–10,000 cells ml^{-1} in the central Arctic Ocean (Booth & Horner 1997) in summer, of 2600–10,200 cells ml^{-1} in Arctic waters of the Barents Sea (Not et al. 2005) in late summer, and up to 28,000 cells ml^{-1} during the initial spring bloom and between 1000 to 10,000 cells ml^{-1} during the rest of the growth season in the central Arctic Ocean (Sherr et al. 2003). Within these small eukaryotic cells, Not et al. (2005) showed that the prasinophyte *Micromonas pusilla* (Butcher) Manton et Parke made up 32 % of total picoeukaryotic cells at stations located in truly Arctic waters, but only 9 % at stations influenced predominantly by Atlantic waters. In addition, Lovejoy et al. (2007) recently demonstrated that picoprasinophytes are spatially and temporally prevalent throughout the Arctic region where *M. pusilla* is the most abundant picoeukaryote representing a single high-latitude ecotype.

In contrast to photosynthetic picoeukaryotes, picocyanobacteria are generally poorly represented in the Arctic seas (Murphy & Haugen 1985, Booth & Horner 1997, Mostajir et al. 2001, Sherr et al. 2003), in strong contrast with their high abundance in Arctic lakes and rivers (Vincent 2000). In the Southern Ocean, picocyanobacteria abundance decreases with increasing latitude, i.e. with decreasing temperature (Marchant et al. 1987). In the Arctic Ocean and adjacent seas, the two main sources of picocyanobacteria are Atlantic waters and freshwater river input. Not et al. (2005) have shown high abundances of the picocyanobacteria *Synechococcus* Nägeli in the Atlantic influenced-waters of the Barents Sea, which are characterized by high surface water temperature. This corroborates earlier studies, which identified cyanobacteria as bioindicators for the advection of Atlantic

influenced-waters into the Arctic seas (Murphy & Haugen 1985, Gradinger & Lenz 1989). In the Laptev Sea, Moreira-Turcq & Martin (1998) observed maximum picocyanobacteria concentration in brackish water near the Lena River delta, but their absence at salinity >20. More recently, Waleron et al. (2007) suggested from 16S rRNA gene clone libraries that picocyanobacteria present in the Canadian Beaufort Sea originated from the Mackenzie River and other nearby inflows.

The cell size of phytoplankton taxa present in the ocean is, in part, determined by environmental and physiological factors, as demonstrated by Parsons & Takahashi (1973). Given the transition towards a new, warmer state (Polyakov et al. 2005), it is expected that the relative abundance of pico- *versus* larger phytoplankton will change in Arctic regions. The objectives of the present study were to (1) determine the distribution of pico-, nano- and microphytoplankton in three contrasted oceanographic provinces of the Canadian High Arctic in late summer and (2) assess the influence of environmental factors on the phytoplankton abundance and biomass of each size fraction. It was hypothesized that picocyanobacteria would be present in Atlantic influenced-waters and nearby river inflows. The photosynthetic picoeukaryote abundance was expected to be higher in warm stratified waters than in cold deeply mixed waters. Finally, in agreement with comprehensive reviews of the available literature (Agawin et al. 2000, Bell & Kalff 2001), the large phytoplankton (>2 μm) was expected be more abundant in nutrient-rich than in nutrient-poor waters.

MATERIALS AND METHODS

Study sites and sampling

This study was conducted in the Canadian High Arctic from 16 August to 13 September 2005, hereafter referred to as late summer, over a 3500 km longitudinal transect, as part of the ArcticNet research program on board the CCGS *Amundsen*. A total of 18 stations were visited consisting of five stations in northern Baffin Bay (northern BB: Stns BA01 to BA04 and 2), five stations in the Northwest Passage (NWP: Stns 3, 4, p, 6 and 7) and eight stations in the Beaufort Sea (Stns 10 to 12, 204, CA04, CA05, CA08 and CA18) (Fig. 1). Water samples were collected at three depths (50, 15 % of surface irradiance and at the maximum chlorophyll *a* (Chl *a*) fluorescence depth) with a rosette sampler equipped with 12 l Niskin-type bottles (OceanTest Equipment), an *in situ* fluorometer (SeaPoint) and a high precision CTD (conductivity-temperature-depth instrument) probe (Sea-Bird 911 +). Since the depth of the maximum Chl *a* fluorescence was generally located between 0.2 and 5 % surface irradiance, the three sampling depths are hereafter referred to as surface, intermediary and bottom layers of the euphotic zone, respectively.

Physical and chemical measurements

Incident photosynthetically available radiation (E_d(PAR); 400–700 nm) was measured continuously during the expedition with a LICOR sensor (LI-190SA). Downwelling PAR underwater profiles were measured using a light sensor (Biospherical QCP-2300) mounted on the CTD rosette, except at Stns 3, 7, 11 where a PNF-300

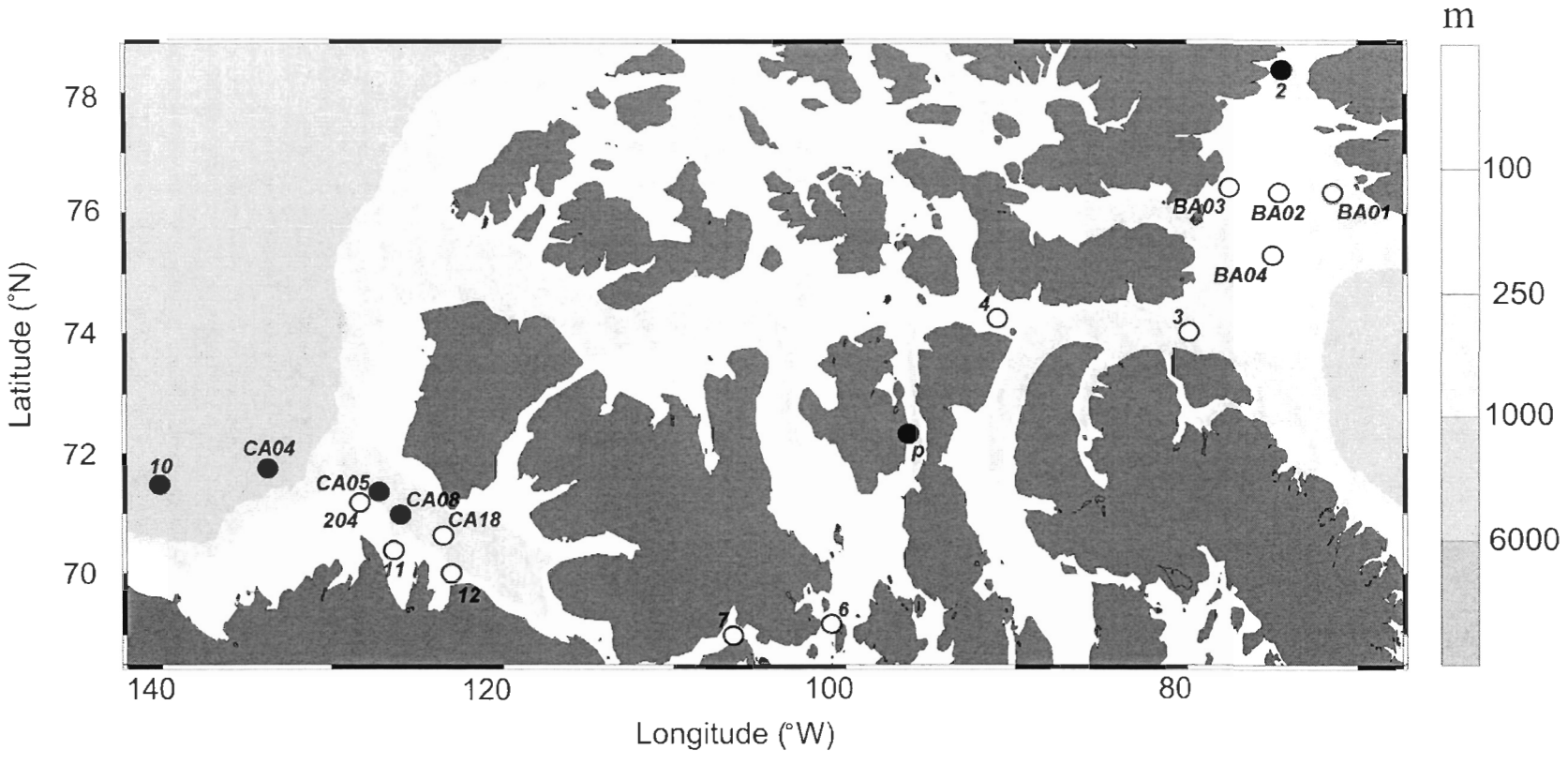

Fig. 1. Location of the sampling stations in the Canadian High Arctic visited from 16 August to 13 September 2005. Open (O) and solid (•) dots indicate open water and ice-covered conditions, respectively. Three oceanographic provinces were identificd: the Beaufort Sea (Stns 10, 11, 12, 204, CA04, CA05, CA08 and CA18), the Northwest Passage (Stns 3, 4, p, 6 and 7) and the northern Baffin Bay (Stns BA01, BA02, BA03, BA04 and 2)

radiometer (Biospherical Instruments) was used. The vertical attenuation coefficient for downward PAR (K_d(PAR)) in the euphotic zone was determined by linear regression of the natural logarithm of E_d(PAR) *versus* depth. The euphotic depth (Z_{eu}) was defined as the depth receiving 1 % of the surface irradiance. The surface mixed layer depth (Z_m) was determined using a split-and-merge method (Thomson & Fine 2003). Z_m was also determined from the density (sigma-*t*) differences of 0.03 kg m^{-3}. There was a strong linear relationship between the surface mixed layer depths determined from the 0.03 kg m^{-3} criterion (y) and the Thomson & Fine method (x) ($y = 0.98x - 0.10$; 95 % CI from 0.66 to 1.20, $r^2 = 0.91$, $p < 0.0001$). An index of the vertical stratification of the water column was estimated as the difference in the sigma-*t* between 80 and 5 m. The presence of ice was estimated visually at each station. Samples for nitrate (NO_3), nitrite (NO_2), silicic acid ($Si(OH)_4$) and phosphate (PO_4) determination were processed immediately after sampling on board the ship using a Bran-Luebbe III autoanalyzer (Grasshoff et al. 1999).

Biological measurements

Flow cytometry (FCM) analysis. Duplicate water samples (5 ml) for the determination of pico- and nanophytoplankton abundance were fixed with 0.1 % final concentration glutaraldehyde (Marie et al. 2005), stored in liquid nitrogen on board the ship and kept frozen at –80°C for a week before analysis. Samples were analyzed using an Epics Altra flow cytometer (Beckman-Coulter) equipped with a 488 nm laser (15 mW output). Forward angle light scatter (FALS), right angle light scatter (RALS), orange fluorescence from phycoerythrin (575 ± 20 nm) and red fluorescence from chlorophyll (675 ± 10 nm) were measured. Prior to analysis, samples were pre-screened on a 40 µm Nylon cell strainer.

One μm microspheres (Fluoresbrite plain YG, Polysciences) were added to each sample as an internal Standard. Pico- (<2 μm) and nanophytoplankton (2–20 μm) were discriminated based on forward scatter calibration with polystyrene microspheres of known size. The average coefficients of variation on the duplicate samples were 5.7 % and 12.5 % for pico- and nanophytoplankton abundances, respectively. The average of the two duplicates is presented thereafter.

Light microscopy (LM) analysis. Samples for the identification and enumeration of eukaryotic cells >2 μm were collected at two depths (the surface and at the bottom layers of the euphotic zone). They were preserved in acidic Lugol's solution (Parsons et al. 1984) and stored in the dark at 4°C until analysis. Samples were identified to the lowest possible taxonomic rank using an inverted microscope (WILD Heerburgg) according to Utermöhl (1931) and Lund et al. (1958). For each sample, at least 300 cells were counted. The main taxonomic references used to identify the phytoplankton were Tomas (1997) and Bérard-Therriault et al. (1999). For comparison with the flow cytometric counts, autotrophic cells enumerated by microscopy were subdivided into the <20 μm (nanophytoplankton) and >20 μm (microphytoplankton) size classes. In the case of chain-forming diatoms, the size of the individual cells was considered as the criterion.

Pigment analysis. Water samples (2.5–3.5 l) for the identification of the phytoplankton pigment signature, collected in the surface layer, were filtered onto Whatman GF/F filters that were immediately frozen in liquid nitrogen on board the ship and stored at –80°C prior

to analysis. Algal pigments were extracted in 95 % methanol (MeOH), sonicated for a few seconds and centrifuged 5 min at 7100 rpm. Pigment extracts were then filtered onto 0.2 μm polytetrafluoroethylene (PTFE) Gellman Acrodisc filters into amber glass vials, stored under argon gas at 4°C in darkness until measurement by reverse-phase high-performance liquid chromatography (HPLC) within 24 h of extraction. The pigment extract was analyzed following Zapata et al. (2000) using eluant solution A (MeOH:acetonitrile: aqueous pyridine, 50:25:25, v/v), solution B (MeOH:acetonitrile:acetone, 20:60:20, v/v), and solution C (acetonitrile) at a flow rate of 3 ml min^{-1}. The HPLC system consisted of a Thermo Separation Products (TSP) P4000 pump, an AS-3000 autoanalyzer, a Waters Symmetry C_8 column (4.6 x 150 mm, 3.5 μm particle size), and two detectors in series: a TSP-UV 6000 LP absorbance detector (400–700 nm), and a TSP-FL3000 fluorescence detector. Absorbance chromatograms were obtained at 440 nm (for chlorophylls) and 450 nm (for carotenoids). Calibration was done with external Standards obtained commercially from DHI Water and Environment (Denmark) and extinction coefficients were taken from Jeffrey et al. (1997). Marker pigments were identified through comparison with the retention and spectral properties of Standards. Phytoplankton taxonomic groups with their identifying pigments are listed in Table 1.

Phytoplankton biomass. Subsamples for the determination of Chl *a* were filtered onto Whatman GF/F glass-fiber filters (nominal pore size of 0.7 μm) and onto 5 μm Nuclepore polycarbonate membranes. Following a 18 h extraction in 90 % acetone at 4°C in the dark without grinding, Chl *a* concentrations were determined on a 10-005R Turner

Designs fluorometer (Parsons et al. 1984). Chl *a* biomass of small phytoplankton (0.7–5 μm) was obtained by subtracting the biomass concentration of large phytoplankton by the total biomass concentration. The contribution of cells <2 μm to total Chl *a* was estimated by multiplying the picophytoplankton abundance by a value of 0.02 pg Chl *a* per cell. This Chl *a* cellular quota is a median value (range: 0.01–0.03 pg Chl *a* per cell) representative of the picoeukaryote *Micromonas pusilla* (Montagnes et al. 1994, DuRand et al. 2002), a common species in the Arctic (Lovejoy et al. 2007).

Statistical analyses

Before undertaking the different parametric tests, the normality of distribution and the homogeneity of variance of each variable were tested with the Lilliefors and the Levine tests, respectively. When required, data were log-transformed. For each variable, 1-way analysis of variance (ANOVA) was performed to seek any significant differences between the three oceanographic provinces (i.e. northern BB, NWP and Beaufort Sea). The ANOVA was completed by a multiple comparison test of means (Tukey's honestly significant difference [HSD] test for unequal sample sizes (Sokal & Rohlf 1995). When assumptions were not met, the Kruskal-Wallis test was used instead of the ANOVA. Simple linear (model I) and reduced major axis regressions (model II) were used to determine the relationship between two variables; the latter takes into account measurement errors for both dependent and independent variables (Sokal & Rohlf 1995). When the relationship between two variables was monotonic, Spearman's rank correlations (r_s) was computed (Sokal & Rohlf 1995). Statistical analyses were carried out using SYSTAT version 10.2.

Table 1. Distribution of major taxonomically significant pigments in algal classes using SCOR abbreviations (Jeffrey & Vesk 1997)

Pigment	Abbreviation	Specificity
Chlorophylls		
Chlorophyll *b*	Chl *b*	Chlorophytes, Prasinophytes, Euglenophytes
Chlorophyll c_3	Chl c_3	Prymnesiophytes, several diatoms and Dinoflagellates
Chlorophyll $c_2 + c_1$	Chl $c_{2+}c_1$	Most diatoms, Dinoflagellates, Cryptophytes, Prymnesiophytes, Chrysophytes
Mg 3,8 DVP	MgDVP	Some Prasinophytes
Carotenoids		
Alloxanthin	Allo	Cryptophytes
19'-Butanolyoxyfucozanthin	But-fuco	Prymnesiophytes, Chrysophytes
β,β-carotene	β,β-carot	All algae except Cryptophytes and Rhodophytes
Diadinoxanthin	Diadino	Diatoms, Dinoflagellates, Prymnesiophytes, Chrysophytes
Diatoxanthin	Diato	Diatoms, Dinoflagellates, Prymnesiophytes, Chrysophytes
Fucoxathin	Fuco	Diatoms, Prymnesiophytes, Chrysophytes, Raphidophytes, some Dinoflagellates
19'-Hexanolyoxyfucozanthin	Hex-fuco	Prymnesiophytes
Lutein	Lut	Chlorophytes, Prasinophytes
Micromonal	Mmnal	Chlorophytes, Prasinophytes
9'-*cis* Neoxanthin	Neo	Chlorophytes, Prasinophytes, Euglenophytes
Peridinin	Per	Dinoflagellates
Prasinoxanthin	Pras	Prasinophytes
Uriolide	Uriolide	Chlorophytes, Prasinophytes
Violaxanthin	Viola	Chlorophytes, Prasinophytes, Eustigmatophytes
Zeaxanthin	Zea	Cyanophytes, Prochlorophytes, Chlorophytes
Chlorophyll degradation products		
Chlorophyllide *a*	Chlde *a*	Senescent diatoms; extraction artifact
Pheophorbide *a*	Phe	Protozoan fecal pellets
Pyropheophorbide *a*	Pyro-Pheo	Copepod grazing; fecal pellets

RESULTS

Physical and chemical environment

The stations sampled along the 3500 km transect across the Canadian Arctic in late summer encompassed three distinct oceanographic provinces: the northern BB, the NWP and the Beaufort Sea. Physical and chemical variables measured in these provinces showed a large spatial variability. During the expedition, incident irradiance ranged from 8.2 to 24.7 mol photons m^{-2} d^{-1} with an average of 16.2 mol photons m^{-2} d^{-1}. Along the transect, water depth varied between 64 and 2478 m with 83 % of stations located at depth >200 m (Fig. 2A). Sea-ice coverage ranged from 0 to 70 % with the highest values at both end of the transect (Fig. 2B). Water depth, incident irradiance and sea-ice coverage were not significantly different between the three provinces (Kruskal-Wallis tests, $p > 0.05$). The Z_m was shallow throughout the three regions, with depths varying between 4 and 21 m (Fig. 2C). The depth of Z_{eu} varied between 22 and 79 m with significantly higher values in the Beaufort Sea than in the NWP and northern BB (ANOVA, $p < 0.0001$) (Fig. 2C). The nitracline was always located below the Z_m and above the Z_{eu} (data not shown), except at Stns BA01, BA03 and 2 in northern BB, where the nitracline was ~ 5 m below the euphotic zone (data not shown). The water column stratification index was significantly higher in the Beaufort Sea and NWP than in the northern BB (Kruskal-Wallis test, $p < 0.0001$) (Fig. 2D).

Surface water temperature ranged from –0.98 to 5.05°C, with the colder temperatures recorded at stations with sea-ice coverage (<0°C, Figs. 2B & 3A). Water

temperature in intermediate and bottom layers ranged from –1.21 to 3.92°C and from –1.66 to 2.86°C, respectively. Salinity ranged from 23.8 to 32.5, 24.6 to 33.3 and 25.4 to 33.4 in surface, intermediate and bottom layers, respectively (Fig. 3B). At the base of the euphotic zone (the bottom layer), salinity was >31 at all stations, except at the shallow Stn 12 in the Beaufort Sea and Stns 6 and 7 in the NWP. In the northern BB, salinity showed the least vertical and horizontal variability (Fig. 3B). The euphotic zone was significantly less saline in the Beaufort Sea and NWP than in northern BB (ANOVA, $p < 0.01$).

Generally, NO_3 represented the largest fraction (64.3 ± 20.3 %) (mean ± SD) of the dissolved inorganic nitrogen (DIN, the sum of $NO_3 + NO_2 + NH_4$) available in Z_{eu}. DIN concentrations were <0.8 μmol l^{-1} in surface and intermediate layers, except at Stn p (Fig. 3C). In the bottom layer, DIN concentrations ranged from 0.1 to 11.5 μmol l^{-1}. $Si(OH)_4$ concentrations ranged from 0.6 to 22.1 μmol l^{-1} (Fig. 3D). $Si(OH)_4$ concentrations were sometimes higher in the bottom layer than in the shallower layers. $Si(OH)_4$ concentrations were significantly higher in the NWP than in the northern BB (ANOVA, $p < 0.05$). PO_4 concentrations ranged from 0.42 to 1.44 μmol l^{-1} throughout the transect (data not shown). The molar ratios of DIN to $Si(OH)_4$ and of DIN to PO_4 were 0.14 ± 0.20 and 1.06 ± 1.99, respectively. These values were significantly lower than the Redfield's ratios of 1.1 and 16, respectively (Redfield et al. 1963).

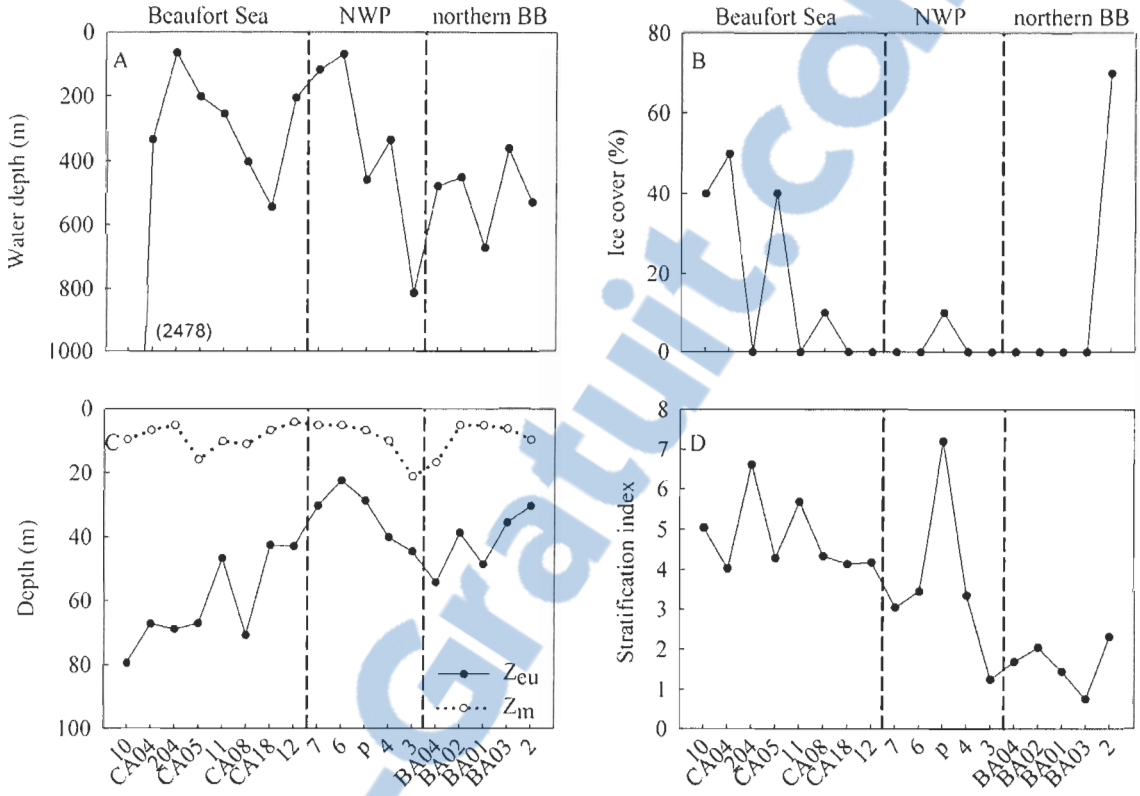

Fig. 2. Variations of the (A) water depth, (B) sea-ice coverage, (C) depths of the euphotic zone (Z_{eu}) and the surface mixed layer (Z_m), and (D) vertical stratification index (the difference in sigma-*t* between 80 and 5 m) along a transect across the Canadian High Arctic. All stations are plotted against longitude, except for stations in northern Baffin Bay, which are plotted against latitude. In (C), Z_{eu} at Stns p and 204 were estimated from the values measured at the two nearest stations

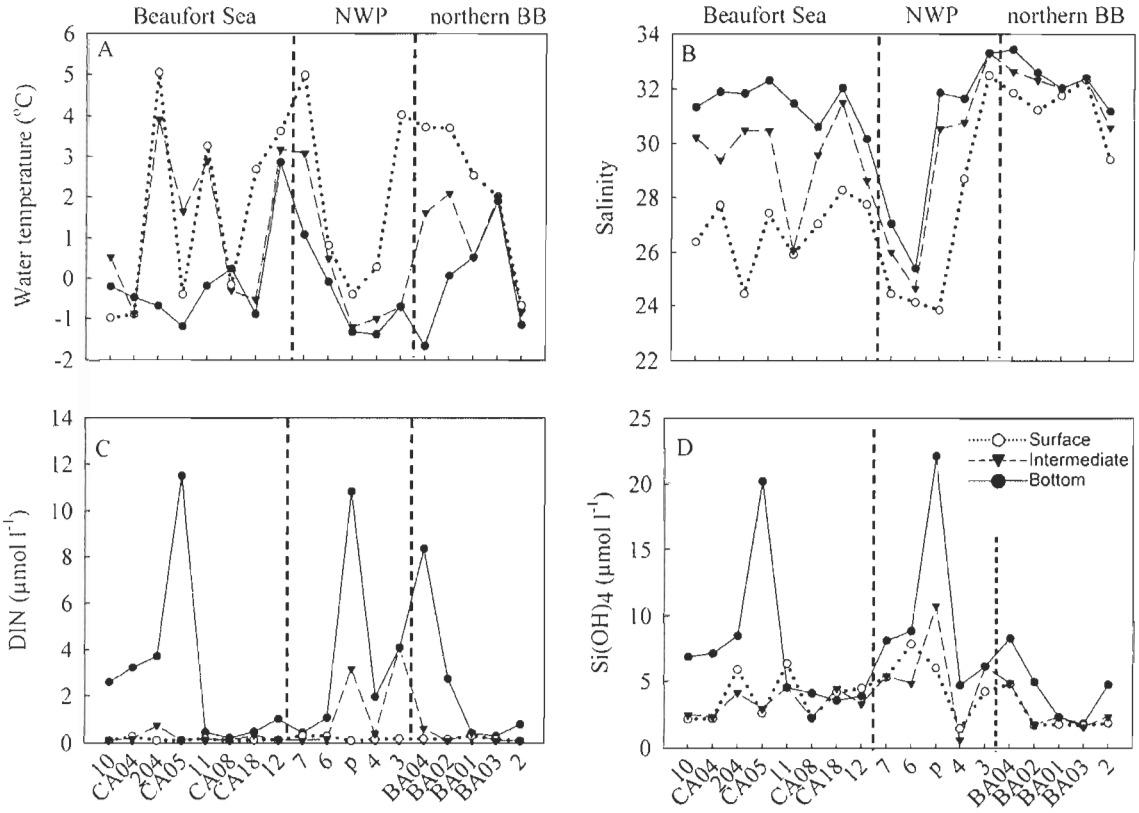

Fig. 3. Variations of (A) water temperature, (B) salinity, (C) dissolved inorganic nitrogen (DIN = $NO_3 + NO_2 + NH_4$) concentration, and (D) silicic acid ($Si(OH)_4$) concentration at three sampled depths in the euphotic zone along a transect across the Canadian High Arctic

Phytoplankton biomass and abundance

Chl *a* concentrations were highly variable but generally low (i.e. <0.5 μg l^{-1} in 73 % of samples; Fig. 4A). However, relatively high Chl *a* concentrations (>2 μg l^{-1}) were observed at the bottom layer in the Beaufort Sea (Stn CA18), NWP (Stns 4 and 3) and northern BB (Stns BA03 and 2). At half of the 18 stations, more than 70 % of the total Chl *a* biomass was represented by cells <5 μm (Fig. 4B).

Small phototrophic eukaryotes were abundant at most of the stations (Fig. 4C). Picoeukaryote abundance varied between 150 and 18,400 cells ml^{-1}, with the highest abundances observed in the surface waters at Stns 204 in the Beaufort Sea and 3 in the NWP. The lowest picoeukaryote abundances (<1000 cells ml^{-1}) were measured at Stn CA05 in the Beaufort Sea in the bottom layer, at Stn 4 in the NWP in the intermediate layer and at the northernmost Stn 2 in the northern BB at all sampling depths. Picocyanobacteria always represented a small percentage (< 2 %) of the picophytoplankton cells with abundances never exceeding 120 cells ml^{-1}. The highest values were recorded at Stns 11 and 12 in the Beaufort Sea (Fig. 4D). The picophytoplankton abundance was positively correlated with water temperature ($r_s = 0.55$, $p < 0.001$) (Fig. 5A), $Si(OH)_4$ concentration ($r_s = 0.37$, $p < 0.01$) and Chl *a* <5 μm ($r_s = 0.35$, $p < 0.05$), and negatively correlated with the sea-ice coverage ($r_s = 0.44$, $p < 0.01$) (Table 2). There was no significant correlation with the other variables.

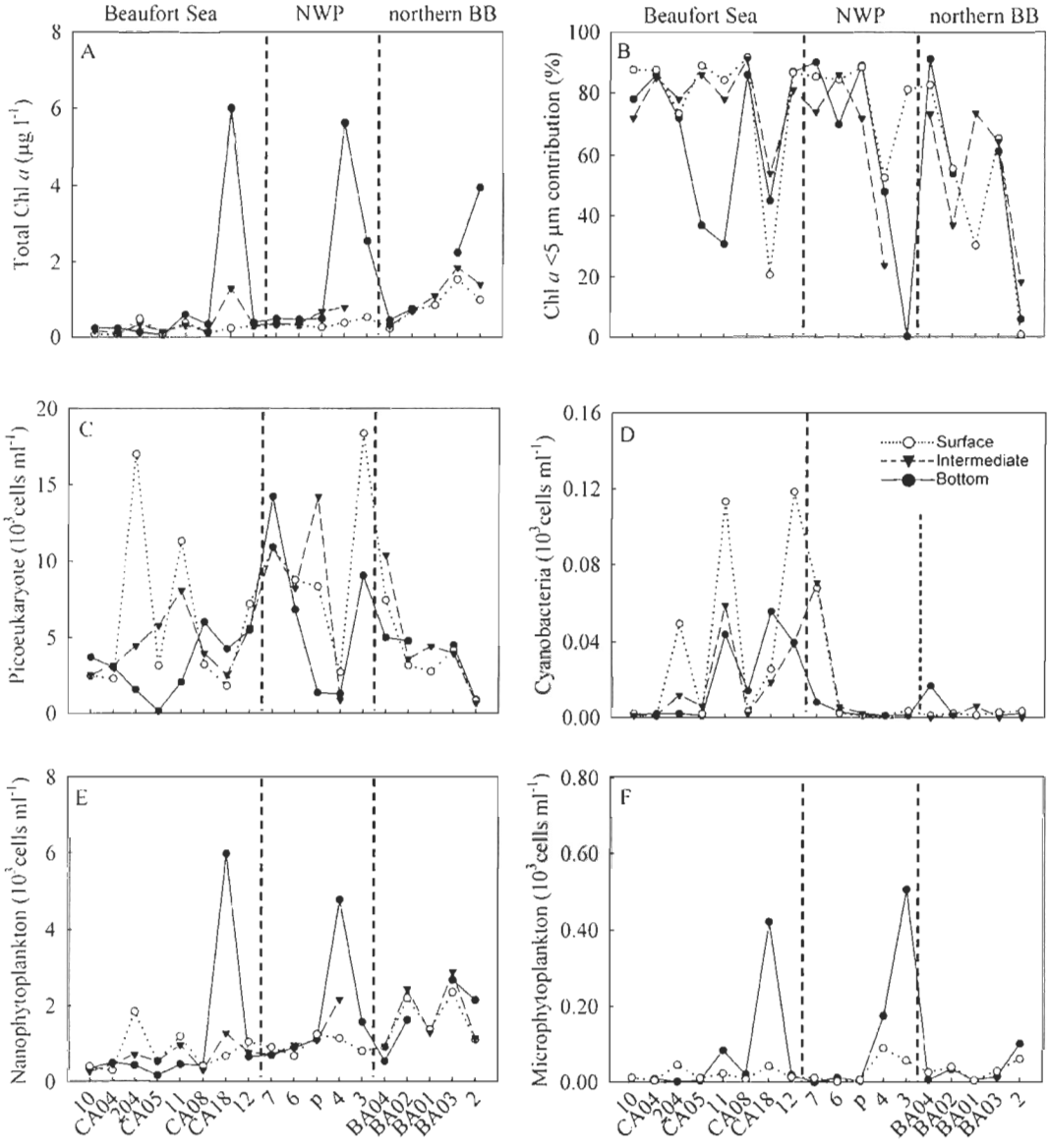

Fig. 4. Variations of (A) total chlorophyll *a* (Chl *a*) biomass, (B) percent contribution of small algae (<5 μm) to total Chl *a* biomass, (C) picoeukaryote abundance, (D) cyanobacteria abundance, (E) nanophytoplankton abundance, and (F) microphytoplankton abundance at three sampled depths in the euphotic zone. In (F), the intermediate depth was not sampled

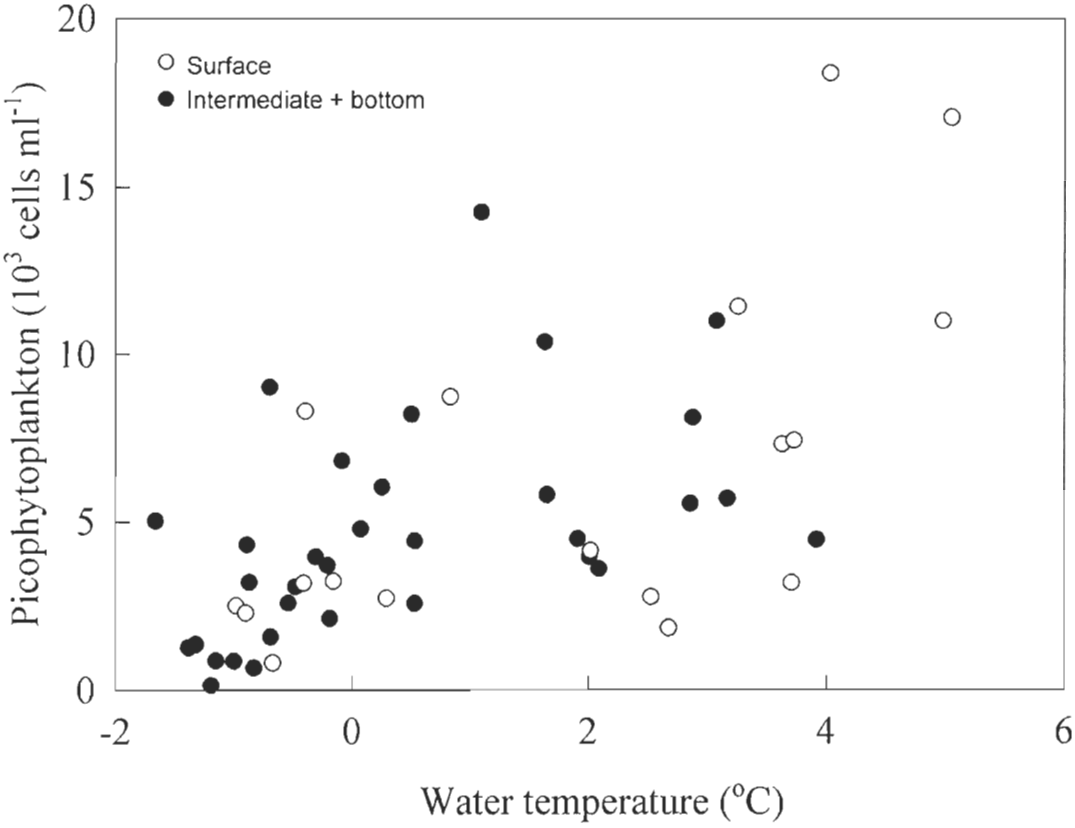

Fig. 5. Relationship between picophytoplankton abundance and water temperature ($x_2 = 2.2x_1 + 3.4$, $r^2 = 0.35$). Black dots represent samples collected in the intermediate and bottom layers of the euphotic zone whereas the open dots represent samples collected in the surface layer

Table 2. Spearman correlation coefficients between phytoplankton abundance and environmental and biological factors at all stations and depths. Because of their low abundance, excluding picocyanobacteria and microphytoplankton from these correlations do not affect the significance of the correlation coefficients. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns: not significant

	<2 µm phytoplankton	>2 µm phytoplankton
Temperature	0.55 ***	ns
Salinity	ns	0.29 *
Stratification index	ns	-0.46 ***
Sea-ice coverage	-0.44 **	-0.46 ***
Z_m	ns	ns
Z_{eu}	ns	-0.58 ***
DIN	ns	ns
$SI(OH)_4$	0.37 **	ns
PO_4	ns	-0.36 **
Total Chl *a*	ns	0.84 ***
Chl *a* > 5 µm	ns	0.80 ***
Chl *a* < 5 µm	0.35 *	0.57 ***

Nanophytoplankton (2–20 μm) abundance was an order of magnitude lower than picophytoplankton cells, ranging from 160 to 6000 cells ml^{-1} with abundances generally increasing toward the eastern part of the transect (Fig. 4E). The highest nanophytoplankton abundances were observed at Stn CA18 in the Beaufort Sea and Stn 4 in the NWP in the bottom layer with 6000 and 4800 cells ml^{-1}, respectively, paralleling the highest Chl *a* concentrations that were also recorded at these stations and depths (Fig. 4A). Nanophytoplankton abundance was significantly lower in the Beaufort Sea than in the northern BB (ANOVA, $p < 0.05$). Microphytoplankton abundance determined by LM was generally less than 100 cells ml^{-1}, except in the bottom layer at Stns CA18, 4 and 3, with values of 420, 175 and 500 cells ml^{-1}, respectively (Fig. 4F). The large phytoplankton (>2 μm) abundance was positively correlated with the total Chl *a* ($r_s = 0.84$, $p < 0.001$), Chl *a* >5 μm ($r_s = 0.80$, $p < 0.001$), Chl *a* <5 μm ($r_s = 0.57$, $p < 0.001$) and the salinity ($r_s = 0.29$, $p < 0.05$), and negatively correlated with the Z_{eu} ($r_s = -0.58$, $p < 0.001$), the vertical stratification index ($r_s = -0.46$, $p < 0.001$), the sea-ice coverage ($r_s = -0.46$, $p < 0.001$), and the phosphate concentration ($r_s = -0.36$, $p < 0.01$) (Table 2). Overall, the contribution of pico-, nano- and microphytoplankton to total phytoplankton abundance was 76.2 ± 20.1 %, 23.2 ± 19.6 %, and 0.6 ± 1.1 %, respectively.

Taxonomic composition and accessory pigments

There was a strong linear relationship between nanophytoplankton FCM and LM counts, with a slope of 0.7 and 95 % CI ranging from 0.6 to 0.8 ($r^2 = 0.91$, $p < 0.0001$, Fig. 6). Counts were very similar for abundances of <1500 cells ml^{-1}, but for higher

abundances, LM counts gave higher estimates of the number of nanophytoplankton cells. This discrepancy may be explained by the strong coloration of the acidic Lugol's solution making difficult to distinguish autotrophic from heterotrophic cells using LM (Sherr & Sherr 1993). Hence, FCM may give a more realistic abundances estimate of nanophytoplankton compared to LM counts.

In the surface layer, flagellates represented >75 % of the total nanophytoplankton abundance (i.e. flagellates + dinoflagellates + diatoms), except at Stns 4 in the NWP and 2 in the northern BB where diatoms were abundant (Fig. 7A). In the bottom layer, diatoms were predominant (>50 %) at Stns CA18 in the Beaufort Sea, 3 and 4 in the NWP and 2 in the northern BB, but flagellates were the most abundant nanophytoplankton at the other stations (Fig. 7B). The taxonomic composition of the surface and bottom layer nanophytoplankton assemblages was mainly composed of unidentified flagellate cells, centric diatoms of the genus *Chaetoceros* Ehrenberg, mostly *C. socialis* Lauder, flagellates belonging to the prymnesiophytes *Chrysochromulina* Lackey, the prasinophytes *Pyramimonas* Schmarda, and the chrysophyte *Dinobryon balticum* (Schütt) Lemmermann, The low cell abundance of microphytoplankton prevented a detailed description of the taxonomic composition of that size class; in many samples one or a few cells were observed. Nevertheless, within the >20 µm size fraction, the pennate diatoms *Pseudo-nitzschia* spp. and *Cylindrotheca closterium* (Ehrenberg) Reimann et Lewin were the dominant group present throughout the Canadian Arctic, followed by a few ciliates (*Strombidium* spp.). Some genera belonged, in term of size, to both nano- and

microphytoplankton as the dinoflagellate *Gyrodinium/Gymnodinium* spp. that was present throughout the transect and the centric diatom *Thalassiosira* spp. that was present at stns 2, CA18, 4, 3, and BA01.

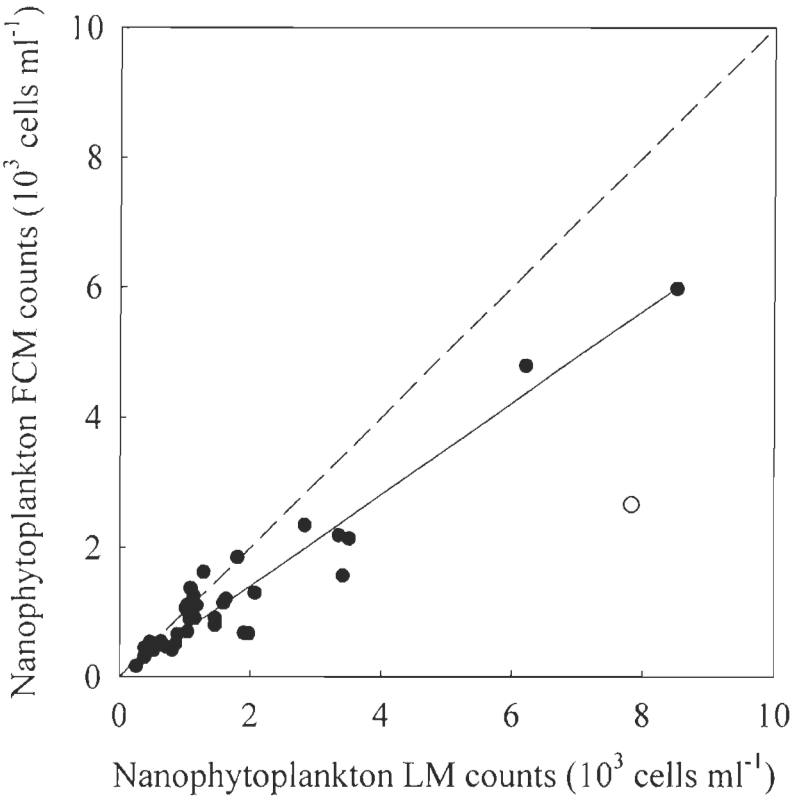

Fig. 6. Relationship between nanophytoplankton abundance estimated by flow cytometry (FCM) and light microscopy (LM) ($y = 0.7x + 85.8$, $r^2 = 0.91$, $p < 0.0001$). The outlier identified by an open circle was excluded from the regression. The dashed line represents a slope of 1

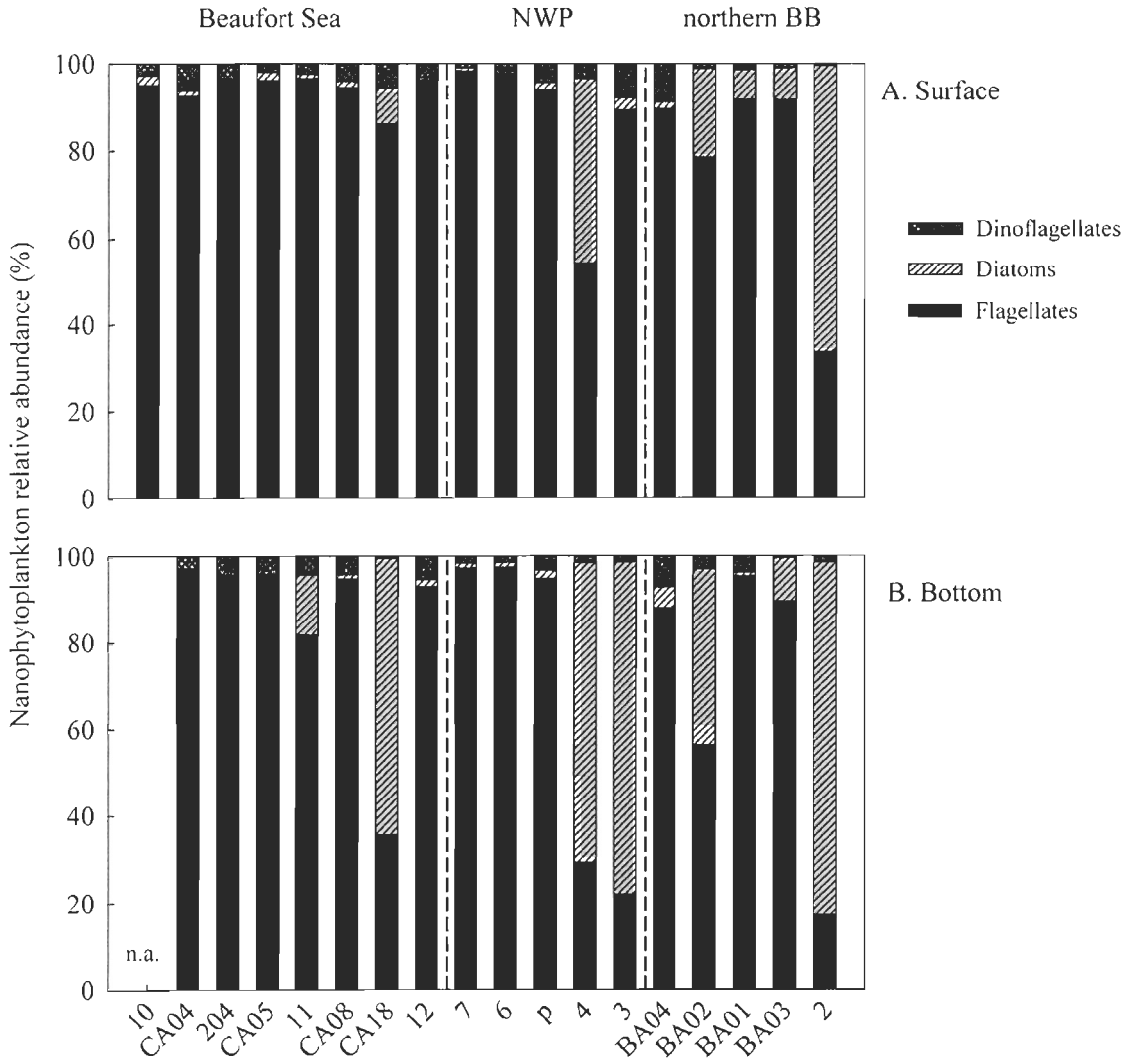

Fig. 7. Variations of the relative abundance of three different plankton groups (diatoms, dinoflagellates, flagellates) in (A) the surface layer, and (B) at the bottom layer of the euphotic zone along a transect across the Canadian High Arctic

The HPLC analysis of chlorophylls and carotenoids from the surface layer along the transect provided additional information for the identification of the algal community (Fig. 8). The pigment distribution showed similarities with the abundance of pico- and nanophytoplankton measured by FCM and the dominant groups identified by LM. The pigments known to be part of the picophytoplankton-size fraction, characterizing prasinophytes and chlorophytes (Chl *b*, MgDVP in addition to Mmnal, Neo, Lut, Viola, Pras, Uriolide and Zea; Table 1) (Jeffrey & Wright 1997) contributed to 48.1 ± 21.6 % of the total pigments identified in the Beaufort Sea and NWP, but only 7.9 ± 6.3 % in the northern BB. Maximum contributions (>70 %) were observed at Stns CA04, CA08 and 6. When detected, mostly in the Beaufort Sea and NWP, zeaxanthin, which is a major accessory pigment of cyanobacteria and a minor pigment in prasinophytes and chlorophytes, accounted for low concentrations (average 0.003 μg l^{-1}, maximum = 0.01 μg l^{-1} at Stn 11) (data not shown).

The pigments known to be found mostly in the nanophytoplankton-size fraction (Fuco, Chl $c_{2+}c_1$, Chl c_3, Hex-fuco, But-fuco, Allo, Diato and Diadino) were the major pigments detected in the northern BB (BA01 to BA03, and 2), and at Stns 10, 204, 11 in the Beaufort Sea and 4 in the NWP (Fig. 8). Even though Fuco is often associated with the microphytoplankton, we included it in the nanophytoplankton-size fraction since microphytoplankton represented only 1 % of the total LM count. Furthermore, most diatoms enumerated and identified were in the <20 μm fraction. Stations showing >15 % of degraded products (pheophorbide *a*, chlorophyllide *a* and pyropheophorbide *a*, Jeffrey &

Vesk 1997) had the highest Chl *a* biomass concentration (Stns CA18, 4, BA01, and 2; Figs. 4A & 8).

In this study, β,β-carot and Per were included in the group labeled other (Fig. 8). They contributed only 4.4 ± 2.8 % of the pigments identified. β,β-carot is known to represent various algal groups, which can be included in the pico-, nano- and microphytoplankton-size fraction, and Per is a biomarker for dinoflagellates. In the samples examined by LM, dinoflagellates were present in the nano- and microphytoplankton-size fraction. Hence, it is difficult to use these two pigments as biomarkers of algal group composition. As the algal community in the Arctic, at least in late summer, is well represented by pico- and nanophytoplankton, we did not use the method of Uitz et al. (2006) to derive community composition. These authors include the pigment Fuco as a tracer of diatoms, which in their study belong to microphytoplankton size-class. In this study, most of the diatoms belong to the nanophytoplankton size-class.

Dominance of small phytoplankton cells

The relationship between the percent contribution of picophytoplankton to total phytoplankton abundance (pico- + nano- + microphytoplankton) and their estimated contribution to total Chl *a* biomass is presented in Fig. 9. Along the transect, the picophytoplankton were responsible for 1 to 65 % of the total Chl *a*. In the Beaufort Sea and NWP, the estimated Chl *a* biomass of cells <2 μm represented between 40 and 50 % of the total Chl *a* with the exception of Stns CA18 and 4, and showed a maximum of 62 % at

Stn 7 in the NWP. In the northern BB, this proportion was considerably lower with on average an estimated Chl *a* biomass of cells <2 µm representing 16 %, except for Stations BA04 in the southernmost region of the northern BB.

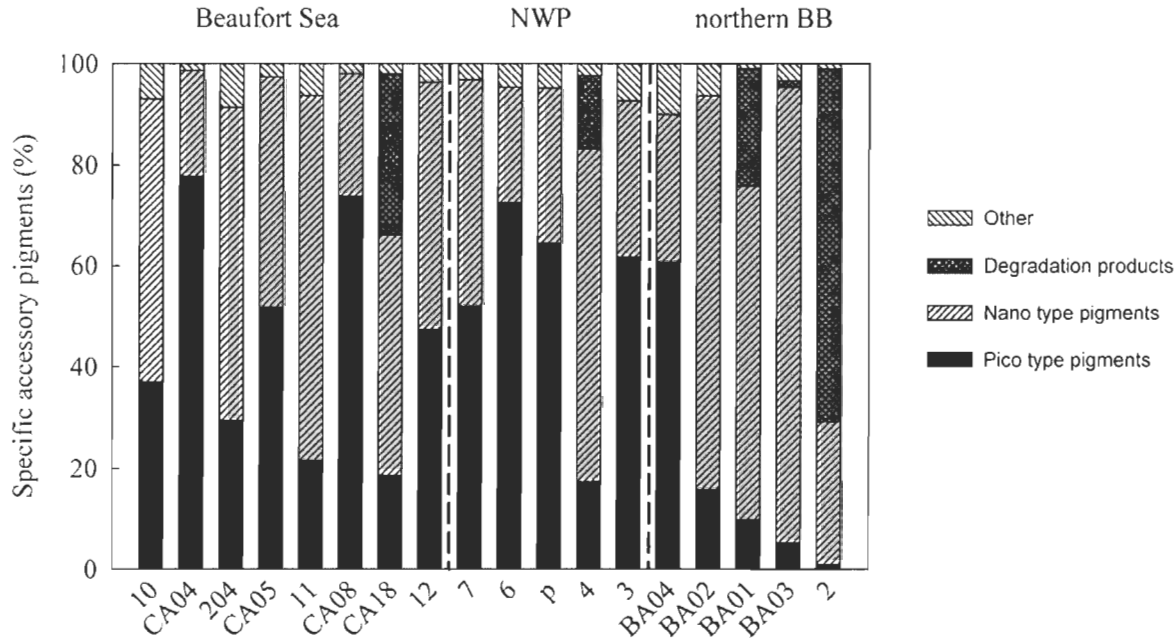

Fig. 8. Percent contribution of specific accessory pigments (SAP) to total pigments for four groups of biomarkers collected in the surface waters. SAP for the pico type group are: Chl *b*, MgDVP, Mmnal, Neo, Lut, Viola, Pras, Uriolide and Zea. SAP for the nano type group are: Fuco, Chl $_{C2+C1}$, Chl $_{C3}$, Hex-fuco, But-fuco, Allo, Diato and Diadino. SAP for the degradation products group are: Chlde *a*, Phe and Pyro-Pheo. SAP for the other group are: Per and β,β-carot. See Table 1 for pigment abbreviations

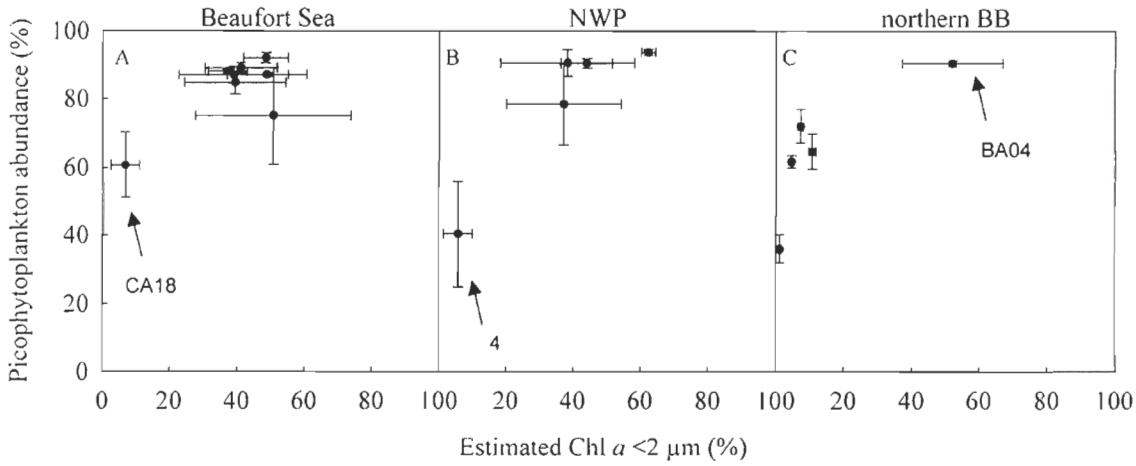

Fig. 9. Relationships between percent contribution of picophytoplankton to total phytoplankton abundance (pico- + nano- + microphytoplankton) and percent contribution of picophytoplankton to total Chl *a* biomass for (A) Beaufort Sea, (B) Northwest Passage (NWP), and (C) northern Baffin Bay (BB). The error bars represent the standard error for the three sampled depths in the euphotic zone (i.e. surface, intermediate and bottom)

DISCUSSION

Dominance of photosynthetic picoeukaryotes throughout the Arctic Ocean

The distribution of pico-, nano- and microphytoplankton was studied along a 3500 km transect from northern BB to Beaufort Sea passing through the NWP in late summer of 2005. Picophytoplankton were consistently the most abundant algal cells in the euphotic zone, with maximum values reaching 17,000, 18,400, and 10,400 cells ml^{-1} in the Beaufort Sea, NWP and northern BB, respectively (Fig. 4C, D, Table 3). In addition, the vertical distribution of picophytoplankton within the euphotic zone was, in general, more homogeneous in the northern BB. In the latter provinces, the upper water column was more stratified (Fig. 2D). The picophytoplankton assemblage was overwhelmingly dominated by photosynthetic eukaryotes, with picocyanobacteria representing at most 2 % of total picophytoplankton cells. This contrast from studies conducted in mid- and low latitude marine systems where picocyanobacteria can be numerically dominant (Buck et al. 1996, Zubkov et al. 2000) as discussed below.

Recent observations also provided evidence of a high abundance of picoeukaryotes and a scarcity of cyanobacteria in the Arctic Ocean and adjacent seas (Table 3). Not et al. (2005) studied the picophytoplankton distribution at the boundary between the Norwegian, Greenland, and Barents seas in late summer. They found picoeukaryote abundances reaching 10,200 cells ml^{-1} in Arctic waters and no occurrence of picocyanobacteria. However, they recorded up to 30,000 cells ml^{-1} of the picocyanobacteria *Synechococcus* in

Table 3. Abundance of photosynthetic picoeukaryotes and the picocyanobacteria *Synechococcus* sp. in the Arctic Ocean and adjacent seas. Sea surface temperature and salinity are shown. [a]: picoeukaryote <5 μm; [b]: early fall (September-October); [c]: summer (July-September); [d]: late summer (August-September); [e]: spring (April- May);[f]:earlysummer(June-July)

Location	Method	Picoeukaryote (cells ml^{-1})	*Synechococcus* (cells ml^{-1})	Temperature (°C)	Salinity	Reference
Chukchi Sea to Makarov Basin	Epifluorescence Microscopy	1000–10,000	not observed	–1.8 to –1.5	29–34	Booth & Horner 1997[c]
Beaufort Shelf and Amundsen Gulf	Epifluorescence Microscopy	215-2110	470-2425	–1.3 to 0.1	20.3–26.9	Waleron et al.2007[b]
Northern Baffin Bay	Flow cytometry	18–4067	not observed	–1 to 0.7	29.4 -33.3	Mostajir et al. 2001[b]
Resolute Passage	Epifluorescence Microscopy	0–5860[a]	0–6330	–1.79 to –1.73	32.7–33.5	Robineau et al. 1999[e]
Northeast Water Polynya	Epifluorescence Microscopy	20–7430[a]	0–330	–1.73 to 4.23	25.1–33.9	Robineau et al. 1999[f]
Northern Baffin Bay	Flow cytometry	661–10,365	0–17	–1.66 to 3.73	29.4–33.4	This study
Northwest Passage	Flow cytometry	864–18,357	1–71	–1.38 to 4.98	23.8–33.3	This study
Beaufort Sea/ Amundsen Gulf	Flow cytometry	146–16,992	1–118	–1.19 to 5.05	24.4–32.3	This study
Greenland, Norwegian and Barents Sea (Arctic waters)	Flow cytometry FISH cells count	2600–10,200	not observed	4.5	34.5	Not et al. 2005[d]
Greenland, Norwegian and Barents Sea (Atlantic waters)	Flow cytometry FISH cells counts	< 3000–17,000	0–30,000	7	> 34.5	Not et al. 2005[d]

the more saline and warmer Atlantic waters. During the Arctic Ocean Section, Booth & Horner (1997) recorded in summer similar picoeukaryote abundances and did not observe *Synechococcus*. In the northern BB, Mostajir et al. (2001) found lower picoeukaryote abundances (Table 3), but still without any occurrence of picocyanobacteria in early fall.

The analysis of the pigment composition by HPLC allowed us to determine the main classes among the picoeukaryote cells. The ubiquity of Chl *b* + MgDVP chlorophylls in the Beaufort Sea, NWP and at Stn BA04 in the northern BB, is an indication of the occurrence of prasinophytes and chlorophytes in the euphotic zone (Jeffrey & Vesk 1997). In addition, the carotenoids typical of the prasinophytes (i.e. Neo, Pras, Mmnal, Lut, Uriolide and Zea; Table 1) were recorded in this study. We presume that a fraction of these pigments belong to the species, *Micromonas pusilla*, which is now thought to be the major component of the photosynthetic picoeukaryote community in Arctic waters (Lovejoy et al. 2007). This prasinophyte was observed in many regions of the Arctic, such as in the central Arctic Ocean (Booth & Horner 1997), the Chukchi Plateau and the Canada Basin (Sherr et al. 2003), the Norwegian and Barents seas (Not et al. 2005), and the northern Baffin Bay (Lovejoy et al. 2007). This species was formerly identified through TSA-FISH and18S rDNA analyses by Not et al. (2005) and Lovejoy et al. (2007), respectively. In this study, zeaxanthin, the major tracer of cyanophytes, was in very low concentration, confirming the low abundance of picocyanobacteria compared to picoeukaryotes along the transect. The strong predominance of *M. pusilla* over other picophytoplankton species in Arctic waters is similar to the cyanobacteria dominance observed in tropical and temperate open gyres,

where the genera *Prochlorococcus* Chisholm, Frankel, Goericke, Olson, Palenik, Waterbury, West-Johnsrud et Zettler and *Synechococcus* are dominant (Partensky et al. 1999).

In the Canadian Arctic, picocyanobacteria were slightly more abundant in the Beaufort Sea and NWP, especially at brackish shallow stations without sea-ice coverage (Stns 204, 11, CA18, 12 and 7, Fig. 4D). Such low abundance (i.e. 10–120 cells ml^{-1}) is not indicative of an ecologically important role played by these cells. However, their presence is in agreement with other studies showing a higher abundance of cyanobacteria in the plume of rivers and deltas. Along a salinity gradient from the Lena River delta (salinity <1.26) to the open Laptev Sea (salinity = 14.04–32.43), Moreira-Turcq & Martin (1998) showed a decrease in the number of *Synechococcus* cells (from >20,000 to 0 cells ml^{-1}). More recently, Waleron et al. (2007) described a similar decrease of picocyanobacteria abundance from the Mackenzie River (up to 6713 cells ml^{-1}) to offshore sites near the Arctic pack ice (225–560 cells ml^{-1}). From Stn p toward the eastern Canadian Arctic, picocyanobacteria were quasi-absent except at the bottom of the euphotic zone of Stn BA04 (Fig. 4D), where they reached 20 cells ml^{-1}. The occurrence of these cells at the southernmost station of northern BB, can be explained by the northward transport of the West Greenland Current Atlantic water into Baffin Bay (Ingram et al. 2002). These data agree with observations of Gradinger & Lenz (1995) and Not et al. (2005) showing the quasi-absence of cyanobacteria in surface Arctic-influenced waters and higher abundance in Atlantic-influenced waters. Hence, these results support the hypothesis that Atlantic-

influenced waters and river inflows favor the growth (or transport) of picocyanobacteria in Arctic marine systems.

Picophytoplankton abundance showed the strongest correlation with water temperature (Fig. 5, Table 2). It can be hypothesized that temperature allowed the accumulation of picophytoplankton within the euphotic zone through its direct effect on algal growth rate. These results agree with the experimental data of Lovejoy et al. (2007) showing a maximum specific growth rate of *Micromonas pusilla* (collected in northern BB) of 0.55 d^{-1} achieved at 6–8°C and lower, but significant specific growth rate of 0.20 d^{-1} at 0°C and 12°C, and the absence of growth at 15°C. In these culture experiments, the same growth was achieved at irradiance of 50 and 100 µmol photons m^{-2} s^{-1} (Lovejoy et al. 2007). During this study, the average irradiance within the euphotic zone ranged from 20 to 61 µmol photons m^{-2} s^{-1}. These in situ light and temperature conditions are nearly optimal for the growth of the cold-adapted ecotype of *M. pusilla* found throughout the Arctic Basin (Lovejoy et al. 2007).

Distribution of picophytoplankton vs larger phytoplankton

Picoeukaryote were the most abundant cells throughout the transect, but they did not dominate the phytoplankton biomass at most stations (Fig. 9). They represented, on average, 82, 77 and 64 % of the total phytoplankton abundance but 39, 37 and 16 % of the total phytoplankton Chl *a* biomass in the Beaufort Sea, NWP, and northern BB, respectively. Contributions to total Chl *a* biomass, similar to that observed in the western

part of the transect, were reported in the Barents and Greenland seas in August-September (mean: 45 %, Not et al. 2005) and in near surface waters in Franklin Bay from November to August (mean: 40–80%, Lovejoy et al. 2007). The contribution of picophytoplankton to total phytoplankton carbon biomass was, on average, 36 % in the Canada and Makarov basins in July-August (Booth & Horner 1997). Hence, picophytoplankton contribution to total phytoplankton biomass in Arctic waters is similar to the average contribution found at lower latitudes (i.e. 40–50 % of the total Chl *a* biomass, Agawin et al. 2000). It should be noted, however, that due to their fast turnover (Raven 1998, Agawin et al. 2000), picophytoplankton cells might have a larger contribution to the community primary production than suggested by their biomass.

In late summer, nanophytoplankton biomass dominated over microphytoplankton in northern BB. Similarly, Sherr et al. (2003) reported that nanophytoplankton dominated the carbon biomass over microphytoplankton in winter (November-May, 57.5 %) and summer (June-September, 83.8 %) in the Canada Basin/Chukchi Plateau and the Chukchi Plateau/Mendeleyev Basin, respectively. In contrast, Lovejoy et al. (2002) reported that microphytoplankton dominated the total phytoplankton carbon biomass (72–98%) in the North Water polynya (northern BB) from spring to early summer (April-July). Hence, persistent bloom (Lovejoy et al. 2002), or more occasional blooms, as observed in this study (Fig. 4A, E, F), can be dominated by nano- and microphytoplankton biomass in Arctic waters.

Throughout the transect, flagellates (<10 μm) dominated numerically the surface nanophytoplankton community, except at the northernmost Stn 2 of northern BB where the centric diatom *Chaetoceros* spp. (diameter = 12–16 μm) and *C. socialis* (16 μm), which formed blooms in cold waters (Rat'kova & Wassmann 2002), dominated the assemblage (Fig. 7A). In the bottom layer of the euphotic zone, *Chaetoceros* spp. (12–16 μm), *Cylindrotheca closterium* (>20 μm), *Pseudo-nitzschia* spp. (2 x 40 μm) and *Thalassiosira* spp. (often >20 μm) were associated with peaks in Chl *a* concentration and cell abundance observed along the transect (Figs. 4A, E, F & 7A, B). At most of these stations (Stns CA18, 4, BA01, and 2), post-bloom conditions were encountered as indicated by the high concentrations of chlorophyll degradation products (i.e. pyro-pheo, phe, and chlde *a*) (Fig. 8, Table 1). The pigment signatures suggest that the decline of the bloom was associated, in part, with microzooplankton grazing at Stn CA18, to diatom senescence at Stn 4, and mesozooplankton grazing at Stns BA01 and 2. Stn 2 was also characterized by the highest abundance of empty frustules of *Chaetoceros*, especially *C. socialis*. This confirms that late summer bloom of *C. socialis* occurred in northern BB, as shown by Booth et al. (2002).

Nanophytoplankton were more abundant in the less stratified waters of the northern BB than in the two other provinces (Figs. 2D, 3C & 4E). Since the polar mixed layer (PML), which extends from the surface to between 25 and 50 m, is relatively depleted in nitrate throughout the Arctic Ocean (Codispoti et al. 2005, Wang et al. 2006, this study), our results support the hypothesis that vertical mixing, through its effect on upward nutrient

flux to the euphotic zone, governs the horizontal distribution of large phytoplankton (>2 μm, mainly diatoms) across the Canadian High Arctic in late summer. The enhancement of the nutrient supply by vertical mixing could have given a competitive advantage to the nanophytoplankton cells over the smaller cells in the northern BB.

Ecological implications in a changing climate

A primary incentive for undertaking this study was to describe the phytoplankton distribution in the Canadian High Arctic in late summer when sea-ice coverage and surface water temperature are at their minimum and maximum yearly values, respectively. High latitude marine ecosystems are particularly sensitive to climate change (ACIA 2005) because small temperature difference can have large effects on the extent and thickness of sea ice (Smetacek & Nicol 2005). Indeed, the Canadian Arctic is already experiencing a thinning of the sea-ice thickness and a decrease of the sea-ice extent (Rothrock et al. 1999, Holland et al. 2006, Comiso et al. 2008). Rising air temperature and the resulting reduced mutli-year ice cover will increase the width of the seasonal ice zone (i.e. zone lying between maximum (winter) and minimum (summer) ice cover that freezes and melts annually) reaching farther north into the Arctic Ocean in late summer (Carmack & Wassmann 2006, Serreze et al. 2007). Predicting the effects of these sea-ice cover change on stratification and the resulting impacts on light availability and nutrients supply for phytoplankton is not straightforward. The upper water column stratification can be enhanced by increased freshwater inputs from melting of sea ice and glaciers, excess net precipitation and increased river discharge (Peterson et al. 2002) or solar heating. These

processes would expose the phytoplankton to higher irradiance, although light availability might also decrease because of suspended sediment and colored dissolved organic matter inputs from river runoff (Dittmar & Kattner 2003). The increased stratification can also decrease the nutrient supply from deeper waters. However, with a reduced sea-ice cover extent, increased winds may also deepen the surface mixed layer (Carmack & Wassmann 2006), enhancing the nutrient supply but also decreasing light availability for phytoplankton (Behrenfeld et al. 2006, Carmack & Wassmann 2006, Doney 2006).

Water temperature was the environmental parameter the most strongly correlated to picophytoplankton abundance along the transect, the abundance of picophytoplankton increasing with water temperature within the euphotic zone (Fig. 5). This positive correlation is also found in a compilation of the published picophytoplankton abundance data from the Arctic Ocean (Fig. 10). This would suggest that factors responsible for warmer water temperatures in the Arctic Ocean are also favoring high abundances of picophytoplankton. It is not possible to identify causal relationships from correlations, but the conditions favoring warmer water temperature are likely to be affected by ongoing and predicted climate change. These environmental changes will have cascading effects throughout the ecosystem, from altering the patterns of primary production to changing the trophic structure and the elemental cycling pathways (Grebmeier et al. 2006). Our present findings may be of particular relevance for further analyses and investigations on the consequences of climate change on the pelagic food web.

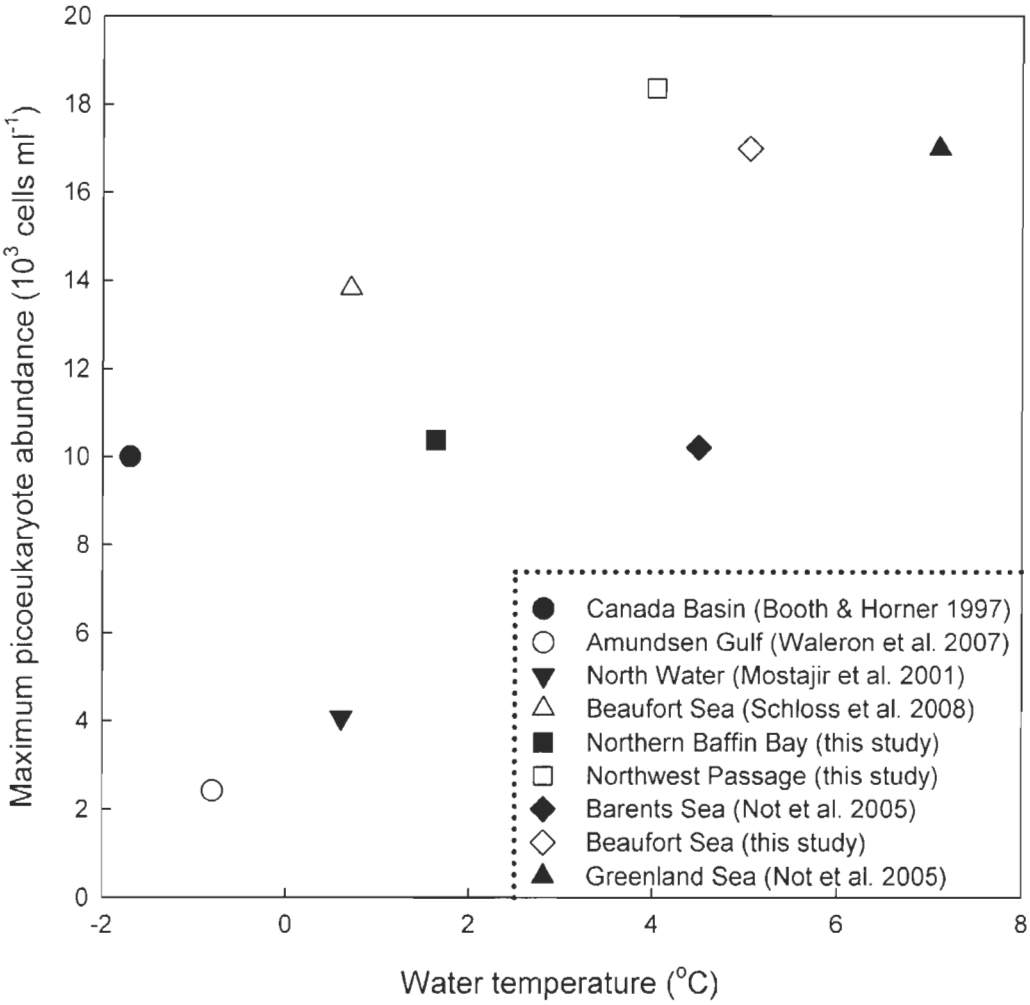

Fig. 10. Relationship between maximum eukaryote picophytoplankton abundance and surface water temperature from six studies conducted in circumarctic regions in summer-autumn ($x_2 = 1.9x_1 + 6.9$, $r^2 = 0.43$)

CONCLUSION

This study was conducted across the Canadian High Arctic during a single, late summer field season. It presents the distribution within the euphotic zone, arguably the most biogeochemically active layer, of all phytoplankton size classes at 18 stations in the seasonal ice zone, the region where most of the Arctic Ocean production take place (Carmack & Wassmann 2006). Flow cytometry, light microscopy and HPLC pigment analyses showed that the small eukaryote cells <2 μm were the numerically dominant phytoplankton size class and often represented nearly 50 % of total Chl *a* biomass in late summer in the Beaufort Sea and NWP. The hypothesis that picocyanobacteria would be more abundant in Atlantic influenced-waters and the vicinity of freshwater rivers input was validated. In the northern BB, nanophytoplankton were significantly more abundant than in the other two oceanographic provinces. It is likely that vertical mixing was a key factor regulating the large-scale distribution of phytoplankton, through its effect on light availability and nutrient supply from deeper waters. Finally, our results confirm that the picophytoplankton can dominate numerically not only in warm oligotrophic gyres, but also in the cool, nutrient-depleted waters of the Arctic Ocean in late growth season.

III. CONCLUSION GÉNÉRALE

Le réchauffement planétaire qui sévit actuellement dans l'Arctique entraîne déjà une réduction du couvert de glace ce qui a pour conséquence d'influencer la pénétration de la lumière et la stratification des eaux ouvertes ainsi que la circulation océanique. Ces modifications peuvent à leur tour influencer la production, la biomasse et la composition spécifique du phytoplancton de l'océan Arctique. Au cours de cette étude, notre attention s'est portée plus particulièrement sur la répartition des classes de taille du phytoplancton dans le Haut Arctique canadien. Il est important d'étudier ces microorganismes puisqu'ils sont les premiers maillons de la chaîne trophique, responsables de la photosynthèse. Les objectifs de ce travail visaient à 1) décrire la répartition spatiale du micro-, du nano- et du picophytoplancton dans les trois régions océanographiques du Haut Arctique canadien, à savoir la mer de Beaufort, le Passage du nord-ouest et la baie de Baffin, et 2) d'évaluer les variables environnementales responsables de la répartition spatiale du phytoplancton.

Les études sur la répartition du phytoplancton dans les régions arctiques ont longtemps mis l'emphase sur les cellules micro- et nanophytoplanctoniques (Murphy et Haugen 1985, von Quillfeldt 1997). Au cours de la dernière décennie, plusieurs travaux ont démontré que les cellules picoeucaryotes étaient prépondérantes dans les régions arctiques (Booth et Smith 1997, Booth et Horner 1997, Not et al. 2005, Lovejoy et al. 2006). La microscopie optique, la fluorométrie, la cytométrie en flux et les analyses pigmentaires nous ont permis d'obtenir des données sur l'abondance, la biomasse et la composition du

phytoplancton dans le Haut Arctique canadien. Les résultats démontrent tout d'abord que la communauté phytoplanctonique dans le Haut Arctique canadien en fin de saison estivale est numériquement dominée par des cellules de petite taille (<2 μm). Cette fraction du phytoplancton représente à elle seule la quasi-totalité des cellules phytoplanctoniques (pico- + nano- + micro-) présentes avec une moyenne de 76,2% ± 20,1 (n = 52). La corrélation positive entre l'abondance du picophytoplancton et la température des eaux de surface et la faible concentration en éléments nutritifs (DIN <0,5 μM) explique en partie l'efficacité des petites cellules à subsister dans la colonne d'eau par rapport aux plus grosses cellules. Les résultats obtenus démontrent aussi que ces petites cellules ne sont pas seulement abondantes dans les gyres oligotrophes de l'Atlantique et du Pacifique (Tarran et al. 2006) ou encore en milieu côtier (Not et al. 2004, Romari et Vaulot 2004, Worden 2006), mais qu'elles le sont aussi dans les eaux froides de l'Arctique.

Le nanophytoplancton et le microphytoplancton sont moins abondants que le picophytoplancton dans le Haut Arctique canadien en saison estivale. Le nanophytoplancton, significativement plus abondant dans la baie de Baffin que dans la mer de Beaufort, semble être avantagé par le mélange vertical dû à la faible intensité de la stratification. Quant au microphytoplancton, il ne représente qu'une minime fraction, en terme d'abondance, de la communauté phytoplanctonique du Haut Arctique canadien (0,6% ± 1,1, n = 52).

Cette étude nous a permis aussi de démontrer que le picophytoplancton est principalement constitué de cellules eucaryotes. En milieu Arctique, la prépondérance des cellules eucaryotes sur les cyanobactéries concorde avec plusieurs études qui ont démontré que la présence des cyanobactéries diminuait avec la latitude (Shapiro et Haugen 1988). Par contre, Gradinger et Lenz (1989) et Not et al. (2005) ont démontré la présence de *Synechococcus* dans les eaux arctiques, plus particulièrement dans les masses d'eau influencées par les courants en provenance de l'Atlantique. De plus, Waleron et al. (2007) ont mis en évidence l'importance des apports allochtones de *Synechococcus* dans l'Arctique de l'ouest par l'intermédiaire des rivières Mackenzie en mer de Beaufort et Horton en baie de Franklin. La présence et la dominance des picoeucaryotes dans le Haut Arctique canadien ont mis en évidence l'importance du réseau pélagique microbien dans l'Arctique, tout comme l'a récemment démontré Lovejoy et al. (2007).

Finalement, les analyses pigmentaires ont permis d'identifier les principaux pigments présents chez le picophytoplancton. Les pigments classiques aux prasinophytes et aux chlorophytes contribuent à 48,1% ± 21,6 de tous les pigments identifiés dans la mer de Beaufort et le Passage du nord-ouest. Il s'avère même fort probable qu'une fraction de ces pigments pourrait correspondre à la prasinophyte, *Micromonas pusilla*, qui est l'organisme eucaryote dominant dans les eaux arctiques (Not et al. 2005, Lovejoy et al. 2007). Cette prasinophyte représente un écotype distinct pour les régions arctiques avec une étroite niche thermale (Lovejoy et al. 2007). Les pigments typiques des prasinophytes, des chlorophytes et de *M. pussila* contribuent à ≥70% aux stations CA04, CA08 et 6 et à seulement 7,9% ±

6,3 dans la partie nord de la baie de Baffin. De plus, la zeaxanthine, qui est un pigment majeur pour les cyanobactéries, n'est retrouvée qu'en très faible concentration (moyenne de 0.003 $\mu g\ l^{-1}$). D'après les analyses en microscopie optique, la composition spécifique du nanophytoplancton consiste principalement de flagellés non identifiés, de diatomées centrales du genre *Chaetoceros*, de prymnesiophytes, de prasinophytes et de chrysophytes. La très faible abondance du microphytoplancton par rapport aux deux autres classes de taille ne nous a pas permis d'effectuer une description détaillée de ces espèces. Malgré tout, parmi les cellules >20 µm, les dinoflagellés sont la classe dominante suivie par les diatomées.

Cette étude a permis d'analyser en détail les classes de taille des populations phytoplanctoniques depuis la baie de Baffin jusqu'en mer de Beaufort en passant par le Passage du nord-ouest. D'autres études seront nécessaires afin d'élucider l'implication écologique de la dominance des picoeucaryotes dans le système pélagique arctique. Les efforts de recherche dans ce domaine seront d'autant plus importants puisqu'une étude récente (Richardson et Jackson 2007) a indiqué que les connaissances conventionnelles, sur le fait que le picophytoplancton contribue faiblement à l'exportation du carbone vers les océans profonds, devrait être révisées.

IV. RÉFÉRENCES

ACIA (2005) Scientific Report: Arctic Climate Impact Assessment. Cambridge University Press, Cambridge, UK

Agawin NSR, Duarte CM, Agustí S (2000) Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production. Limnol Oceanogr 45:591–600

Agustí S (2004) Viability and niche segregation of *Prochlorococcus* and *Synechococcus* cells across the Central Atlantic Ocean. Aquat Microb Ecol 36:53–59

Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. Mar Ecol Prog Ser 10:257-263

Behrenfeld MJ, O'Malley RT, Siegel DA, McClain CR, Sarmiento JL, Feldman GC, Milligan AJ, Falkowski PG, Letelier RM, Boss ES (2006) Climate-driven trends in contemporary ocean productivity. Nature 444:752–755

Bell J, Kalff J (2001) The contribution of picophytoplankton in marine and freshwater systems of different trophic status and depth. Limnol Oceanogr 46:1243–1248

Bérard-Therriault L, Poulin M, Bossé L (1999) Guide d'identification du phytoplancton marin de l'estuaire et du golfe du Saint-Laurent incluant également certains protozoaires. Publ spéc can sci halieut aquat 128:1–387

Booth BC, Horner RA (1997) Microalgae on the Arctic Ocean Section, 1994: species abundance and biomass. Deep-Sea Res II 44:1607–1622

Booth BC, Smith WO Jr (1997) Autotrophic flagellates and diatoms in the Northeast Water polynya, Greenland: summer 1993. J Mar Syst 10:241–261

Booth BC, Larouche P, Bélanger S, Klein B, Amiel D, Mei Z-P (2002) Dynamics of *Chaetoceros socialis* blooms in the North Water. Deep-Sea Res II 49:5003–5025

Buck KR, Chavez FP, Campbell L (1996) Basin-wide distributions of living carbon components and the inverted trophic pyramid of the central gyre of the north Atlantic Ocean, summer 1993. Aquat Microb Ecol 10:283–298

Bursa AS (1961) Phytoplankton of the Calanus expedition in Hudson Bay, 1953 and 1954. J Fish Res Bd Can 18:51–83

Carmack E, Wassmann P (2006) Food webs and physical biological coupling on pan-Arctic shelves: comprehensive perspectives, unifying concepts and future research. Prog Oceanogr 71:449–480

Campbell L, Nolla HA, Vaulot D (1994) The importance of *Prochlorococcus* to community structure in the Central North Pacific Ocean. Limnol Oceanogr 39:954–961

Cleve PT (1896) Diatoms from Baffin Bay and Davis Strait collected by M.E. Nilsson. K Svenska Vetensk-Akad Handl 22:1–22

Codispoti LA, Flagg C, Kelly V, Swift JH (2005) Hydrographic conditions during the 2002 SBI process experiments. Deep-Sea Res II 52:3199–3226

Comiso JC, Parkinson CL, Gersten R, Stock L (2008) Accelerated decline in the Arctic sea ice cover. Geophys Res Lett 35, L01703, doi:1029/2007GL031972

Cross WE (1982) Under-ice biota at the Pond Inlet ice edge and adjoining fast ice areas during spring. Arctic 35:13–27

Cushing DH (1989) A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. J Plankton Res 11:1–13

Dittmar T, Kattner G (2003) The biogeochemistry of the river and shelf ecosystem of the Arctic Ocean: a review. Mar Chem 83:103–120

Doney SC (2006) Plankton in a warming world. Nature 444:695–696

DuRand MD, Olson RJ, Chisholm SW (2001) Phytoplankton population dynamics at the Bermuda Atlantic Time-series station in the Sargasso Sea. Deep-Sea Res II 48:1983–2003

DuRand MD, Green RE, Sosik HM, Olson RJ (2002) Diel variations in optical properties of *Micromonas pusilla* (Prasinophyceae). J Phycol 38:1132–1142

Fortier M, Fortier L, Michel C, Legendre L (2002) Climatic and biological forcing of the vertical flux of biogenic particles under seasonal Arctic sea ice. Mar Ecol Prog Ser 225:1–16

Glover HE, Keller MD, Guillard RRL (1986) Light quality and oceanic ultraphytoplankton. Nature 319:142–143

Gosselin M, Levasseur M, Wheeler PA, Horner RA, Booth BC (1997) New measurements of phytoplankton and ice algal production in the Arctic Ocean. Deep-Sea Res II 44:1623–1644

Gradinger R, Lenz J (1989) Picocyanobacteria in the high Arctic. Mar Ecol Prog Ser 52:99–101

Gradinger R, Lenz J (1995) Seasonal occurrence of picocyanobacteria in the Greenland Sea and central Arctic Ocean. Polar Biol 15:447–452

Gran HH (1904) Diatomaceae from the ice-floes and plankton of the Arctic Ocean. Sci Res Norw North Polar Exped 4:3–74

Grasshoff K, Kremling K, Ehrhardt M (1999) Methods of seawater analysis, 3rd edn, Wiley-VCH, New York

Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt SL (2006) A major ecosystem shift in the northern Bering Sea. Science 311:1461–1464

Grøntved J, Seidenfaden G (1938) The Godthaab Expedition 1928. The phytoplankton of the waters west of Greenland. Medd Grønl 82:1–380

Heimdal BR (1989) Arctic ocean phytoplankton. In: Herman Y (ed) The Arctic seas. Climatology, oceanography, geology, and biology. Van Nostrand Reinhold Company, New York, p 193–222

Hensen V (1887) Über die Bestimmung des Planktons oder des im Meer treibenden Materiales an Pflanzen und Tieren. Ber Komm Wiss Unters Dt Meere 5:1–109

Hill V, Cota G, Stockwell D (2005) Spring and summer phytoplankton communities in the Chukchi and Eastern Beaufort Seas. Deep-Sea Res II 52:3369–3385

Holland MM, Bitz CM, Tremblay B (2006) Future abrupt reductions in the summer Arctic sea ice. Geophys Res Lett 33,L23503, doi:1029/2006GL028024

Hsiao SIC (1996) Biological productivity of the southern Beaufort Sea: phytoplankton and seaweed studies. Beaufort Sea Technical Report no 12c, Department of the Environment, Victoria BC

Ingram RG, Bâcle J, Barner DG, Gratton Y, Melling H (2002) An overview of physical processes in the North Water. Deep-Sea Res II 49:4893–4906

Jeffrey SW, Vesk M (1997) Introduction to marine phytoplankton and their pigment signatures. In: Jeffrey SW, Mantoura RFC, Wright SW (eds) Phytoplankton pigments in oceanography. UNESCO, Paris, p 37–84.

Jeffrey SW, Wright SW (1997) Qualitative and quantitative HPLC analysis of SCOR reference algal cultures. In: Jeffrey SW, Mantoura RFC, Wright SW (eds) Phytoplankton pigments in oceanography. UNESCO, Paris, p 343–360.

Jeffrey SW, Mantoura RFC, Wright SW (1997) Phytoplankton pigments in oceanography. UNESCO, Paris

Jensen F, Hansen BW (2000) Ciliates and heterotrophic dinoflagellates in the marginal ice zone of the central Barents Sea during spring. J Mar Biol Ass UK 80:45–54

Johnson PW, Sieburth J (1979) Chroococcoid cyanobacteria in the sea: a ubiquitous and diverse phototrophic biomass. Limnol Oceanogr 24:928–935

Jones EP, Anderson LG, Swift JH (1998) Distribution of Atlantic and Pacific waters in the upper Arctic Ocean: implications for circulation. Geophys Res Lett 25:765–768

Kliem N, Greenberg DA (2003) Diagnostic simulations of the summer circulation in the Canadian Arctic Archipelago. Atmos Ocean 41:273–289

Legendre L, LeFèvre J (1991) From individual plankton cells to pelagic marine ecosystems and to global biogeochemical cycles. In: Demers S (ed) Particle analysis in oceanography. Springer-Verlag, Berlin, p. 261–300

Legendre L, Gosselin M, Hirche H-J, Kattner G, Rosenberg G (1993) Environmental control and potential fate of size-fractionated phytoplankton production in the Greenland Sea (75°N). Mar Ecol Prog Ser 98:297–313

Legendre L, Rassoulzadegan F (1995) Plankton and nutrient dynamics in marine waters. Ophelia 41:153–172

Li WKW (1994) Primary production of *Prochlorococcus*, cyanobacteria, and eukaryotic ultraphytoplankton: measurements from flow cytometric sorting. Limnol Oceanogr 39:169–175

Liu H, Suzuki K, Minami C, Saino T, Watanabe M (2002) Picoplankton community structure in the subarctic Pacific Ocean and the Bering Sea during summer 1999. Mar Ecol Prog Ser 237:1–14

Lovejoy C, Massana R, Pedrós-Alió C (2006) Diversity and distribution of marine eukaryotes in the Arctic Ocean and adjacent seas. Appl Environ Microbiol 72:3085–3095

Lovejoy C, Legendre L, Martineau M-J, Bâcle J, von Quillfeldt CH (2002) Distribution of phytoplankton and other protists in the North Water. Deep-Sea Res II 49:5027–5047

Lovejoy C, Vincent WF, Bonilla S, Roy S, Martineau M-J, Terrado R, Potvin M, Massana R, Pedrós-Alió C (2007) Distribution, phylogeny and growth of cold-adapted picoprasinophytes in Arctic seas. J Phycol 43:78–89

Lund JWG, Kipling C, Le Cren ED (1958) The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11:143–170

Maixandeau A, Lefèvre D, Karayanni H, Christaki U, Van Wambeke F, Thyssen M, Denis M, Fernandez CI, Uitz J, Leblanc K, Quéguiner B (2005) Microbial community production, respiration, and structure of the microbial food web of an ecosystem in the northeastern Atlantic Ocean. J Geophys Res 110, C07S17, doi:10.1029/2004JC002694

Marchant HJ, Davidson AT, Wright SW (1987) The distribution and abundance of chroococcoid cyanobacteria in the Southern Ocean. Proc Nat Inst Polar Res (NIPR) Symp Polar Biol 1:1–9

Marie D, Simon N, Vaulot D (2005) Phytoplankton cell counting by flow cytometry. In: Andersen RA (ed) Algal Culturing Techniques, vol 17. Academic Press, London, p 253–267

Mei Z-P, Legendre L, Gratton Y, Tremblay J-É, LeBlanc B, Klein B, Gosselin M (2003) Phytoplankton production in the North Water Polynya: size-fractions and carbon fluxes, April to July 1998. Mar Ecol Prog Ser 256:13–27

Mei Z-P, Legendre L, Gratton Y, Tremblay J-É, LeBlanc B, Mundy CJ, Klein B, Gosselin M, Larouche P, Papakyriakou TN, Lovejoy C, von Quillfeldt CH (2002) Physical control of spring-summer phytoplankton dynamics in the North Water, April-July 1998. Deep-Sea Res II 49:4959–4982

Michaels AF, Silver MW (1988) Primary production, sinking fluxes and the microbial food web. Deep-Sea Res 35:473–490

Michel C, Ingram RG, Harris LR (2006) Variability in oceanographic and ecological processes in the Canadian Arctic Archipelago. Prog Oceanogr 71:379–401

Montagnes DJS, Berges JA, Harrison PJ, Taylor FJR (1994) Estimating carbon, nitrogen, protein, and chlorophyll *a* from volume in marine phytoplankton. Limnol Oceanogr 39:1044–1060

Moreira-Turcq PF, Martin JM (1998) Characterisation of fine particles by flow cytometry in estuarine and coaStnl Arctic waters. J Sea Res 39:217–226

Mostajir B, Gosselin M, Gratton Y, Booth B, Vasseur C, Garneau M-È, Fouilland E, Vidussi F, Demers S (2001) Surface water distribution of pico- and nanophytoplankton in relation to two distinctive water masses in the North Water, northern Baffin Bay, during fall. Aquat Microb Ecol 23:205–212

Murphy LS, Haugen EM (1985) The distribution and abundance of phototrophic ultra-plankton in the North Atlantic. Limnol Oceanogr 30:47–58

Nelson DM, Tréguer P, Brzezinski MA, Leynaert A, Quéguiner B (1995) Production and dissolution of biogenic silica in the ocean: revised global estimates, comparison with regional data and relationship to biogenic sedimentation. Global Biogeochem Cycles 9:359–732

Not F, Latasa M, Marie D, Cariou T, Vaulot D, Simon N (2004) A single species, *Micromonas pusilla* (Prasinophyceae), dominates the eukaryotic picoplankton in the Western English Channel. Appl Environ Microbial 70:4064–4072

Not F, Massana R, Latasa M, Marie D, Colson C, Eikrem W, Pedrós-Alió C, Vaulot D, Simon N (2005) Late summer community composition and abundance of photosynthetic picoeukaryotes in Norwegian and Barents Seas. Limnol Oceanogr 50:1677–1686

Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, Toronto

Parsons TR, Takahashi M (1973) Environmental control of phytoplankton cell size. Limnol Oceanogr 18:511–515

Partensky F, Hess WR, Vaulot D (1999) *Prochlorococcus*, a marine photosynthetic prokaryote of global significance. Microbiol Mol Biol Rev 63:106–127

Pesant S, Legendre L, Gosselin M, Smith REH, Kattner G, Ramseier RO (1996) Size-differential regimes of phytoplankton production in the Northeast Water Polynya (77°-81°N) Mar Ecol Prog Ser 142:75–86

Peterson BJ, Holmes RM, McClelland JW, Vorosmarty CJ, Lammers RB, Shiklomanov AI, Shiklomanov IA, Rahmstorf S (2002) Increasing river discharge to the Arctic Ocean. Science 298:2171-2173

Polyakov I, Alekseev GV, Timokhov LA, Bhatt US, Colony RL, Simmons HL, Walsh D, Walsh JE, Zakharov VF (2004) Variability of the intermediate Atlantic water of the Arctic Ocean over the last 100 years. J Clim 17:4485–4497

Polyakov IV, Beszczynska A, Carmack EC, Dmitrenko IA, Fahrbach E, Frolov IE, Gerdes R, Hansen E, Holfort J, Ivanov VV, Johnson MA, Karcher M, Kauker F, Morison J, Orvik KA, Schauer U, Simmons HL, Skagseth Ø, Sokolov VT, Steele M, Timokhov LA, Walsh D, Walsh JE (2005) One more step toward a warmer Arctic. Geophys Res Lett 32, L17605, doi:10.1029/2005GL023740

Pomeroy LR (1974) The ocean's food webs: a changing paradigm. BioScience 24:409–504

Ramsfjell R (1954) Fytoplanktonet i den nordlige delen av Norskehavet i begynnelsen av juni 1952 og 1953. Master of Science Thesis, University of Olso, 158 pp.

Rat'kova TN, Wassmann P (2002) Seasonal variation and spatial distribution of phyto- and protozooplankton in the central Barents Sea. J Mar Syst 38:47–75

Raven JA (1998) The twelfth Tansley Lecture. Small is beautiful: The picophytoplankton.

Redfield AC, Ketchum BH, Richards FA (1963) The influence of organisms on the composition of seawater. In: Hill MN (edn). The sea, volume II, John Wiley, New York, p 26–77

Richardson TL, Jackson GA (2007) Small phytoplankton and carbon export from the surface ocean. Science 315:838–840

Robineau B, Legendre L, Michel C, Budéus G, Kattner G, Schneider W, Pesant S (1999) Ultraphytoplankton abundances and chlorophyll *a* concentrations in ice-covered waters of northern seas. J Plankton Res 21:735–755

Romari K, Vaulot D (2004) Composition and temporal variability of picoeukaryote communities at a coastal site of the English Channel from 18S rDNA sequences. Limnol Oceanogr 49:784–798

Sakshaug E, Skjoldal HR (1989) Life at the ice edge. Ambio 18:60–67

Schloss IR, Nozais C, Mas S, van Hardenberg B, Carmack E, Tremblay J-É, Brugel S, Demers S (2008) Picophytoplankton and nanophytoplankton abundance and distribution in the southeastern Beaufort Sea (Mackenzie Shelf and Amundsen Gulf) during fall 2002. J Mar Syst, doi:10.1016/j.jmarsys.2008.01.004

Serreze MC, Holland MM, Stroeve J (2007) Perspectives on the Arctic's shrinking sea-ice cover. Science 315:1533–1536

Shapiro LP, Haugen EM (1988) Seasonal distribution and temperature tolerance of *Synechococcus* in Boothbay Harbor, Maine. Estuar Coast Shelf Sci 26:517–525

Sherr EB, Sherr BF (1993) Preservation and storage of samples for enumeration of heterotrophic protists. In: Kemp P, Sherr B, Sherr E, Cole J (eds) Current methods in aquatic microbial ecology. Lewis Publications, New York, p 207–212

Sherr EB, Sherr BF, Fessenden L (1997) Heterotrophic protists in the Central Arctic Ocean. Deep-Sea Res II 44:1665–1682

Sherr EB, Sherr BF, Wheeler PA, Thompson K (2003). Temporal and spatial variation in stocks of autotrophic and heterotrophic microbes in the upper water column of the central Arctic Ocean. Deep-Sea Res I 50:557–571

Sieburth JM, Smetacek V, Lenz J (1978) Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. Limnol Oceanogr 23:1256–1263

Smetacek V, Nicol S (2005) Polar ocean ecosystems in a changing world. Nature 437:362–368

Smith JC, Platt T, Li WKW, Horne EPW, Subba Rao DV, Irwin BD (1985) Arctic marine photoautotrophic picoplankton. Mar Ecol Prog Ser 20:207–220

Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research, 3rd edn, WH Freeman, New York

Spies A (1987) Phytoplankton in the marginal ice zone of the Greenland Sea. Polar Biol 7:195–205

Steele JH (1974) The structure of marine ecosystems. Harvard University Press, Cambridge, MA

Stockner JG (1988) Phototrophic picoplankton: an overview from marine and freshwater ecosystems. Limnol Oceanogr 33:765–775

Stockner JG, Antia NJ (1986) Algal picoplankton from marine and freshwater ecosystems: a multidisciplinary perspective. Can J Fish Aquat Sci 43:2472–2503

Stockner JG, Callieri C, Cronberg G (2000) Picoplankton and other non-bloom forming cyanobacteria in lakes. In: Whitton B, Potts M (eds) Ecology of cyanobacteria: their diversity in time and space. Kluwer Academic Publishers, Dordrecht, p 195–231

Tarran G, Heywood JL, Zubkov MV (2006) Latitudinal changes in the standing stocks of nano- and picoeukaryotic phytoplankton in the Atlantic Ocean. Deep-Sea Res II 53:1516–1529

Thomson RE, Fine IV (2003) Estimating mixed layer depth from oceanic profile data. J Atmos Oceanic Tech 20:319–329

Tomas CR (1997) Identifying marine phytoplankton. Academic Press, San Diego

Tremblay J-É, Legendre L, Therriault J-C (1997) Size-differential effects of vertical stability on the biomass and production of phytoplankton in a large estuarine system. Est Coast Shelf Sci 45:415–431

Tremblay J-É, Gratton Y, Fauchot J, Price NM (2002) Climatic and oceanic forcing of new, net and diatom production in the North Water Polynya. Deep-Sea Res II 49:4927–4946

Tremblay J-É, Michel C, Hobson KA, Gosselin M, Price NM (2006) Bloom dynamics in early opening waters of the Arctic Ocean. Limnol Oceanogr 51:900–912

Uitz J, Claustre H, Morel A, Hooker SB (2006) Vertical distribution of phytoplankton communities in open ocean: An assessment based on surface chlorophyll. J Geophys Res 111, C08005, doi: 10.1029/2005JC003207

Utermöhl von H (1931) Neue Wege in der quantitativen Erfassung des Planktons (Mit besondere Beriicksichtigung des Ultraplanktons). Verh Int Verein Theor Angew Limnol 5:567–595

Vaulot D, Marie D, Olson RJ, Chisholm SW (1995) Growth of *Prochlorococcus*, a photosynthetic prokaryotes, in the equatorial Pacific Ocean. Science 268:1480–1482

Vincent WF (2000) Cyanobacterial dominance in the polar regions. In: Whitton BA, Potts M (eds) Ecology of the Cyanobacterial: their diversity in space and time. Kluwer Academic Publishers, Dordrecht, the Netherlands, p 321–340

von Quillfeldt CH (1997) Distribution of diatoms in the Northeast Water Polynya, Greenland. J Mar Syst 10:211–240

von Quillfeldt CH (2000) Common diatom species in Arctic spring blooms: their distribution and abundance. Bot Mar 43:499–516

Waleron M, Waleron K, Vincent WF, Wilmotte A (2007) Allochthonous inputs of riverine picocyanobacteria to coastal waters in the Arctic Ocean. FEMS Microbiol Ecol 59:356–365

Wang D, Henrichs SM, Guo LD (2006) Distributions of nutrients, dissolved organic carbon and carbohydrates in the western Arctic Ocean. Cont Shelf Res 26:1654–1667

Wassmann P, Reigstad M, Haug T, Rudels B, Carroll ML, Hop H, Gabrielsen GW, Falk-Petersen S, Denisenko SG, Arashkevich E, Slagstad D, Pavlova O (2006) Food webs and carbon flux in the Barents Sea. Prog Oceanogr 71:232–287

Waterbury JB, Watson SW, Guillard RR, Brand LE (1979). Wide-spread occurrence of a unicellular, marine planktonic, cyanobacterium. Nature 277:293–294.

Worden AZ (2006) Picoeukaryote diversity in coastal waters of the Pacific Ocean. Aquat Microb Ecol 43:165–175

Worden AZ, Nolan JK, Palenik B (2004) Assessing the dynamics and ecology of marine picophytoplankton: the importance of the eukaryotic component. Limnol Oceanogr 49:168–179

Zapata M, Rodríguez F, Garrido JL (2000) Separation of chlorophylls and carotenoids from marine phytoplankton: a new HPLC method using a reversed phase C_8 column and pyridine-containing mobile phases. Mar Ecol Prog Ser 195:29–45