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INFLUENCE DES FACTEURS DU MILIEU SUR LA COMPOSITION TAXONOMIQUE ET LE DÉVELOPPEMENT DES ALGUES ET AUTRES PROTISTES DE LA GLACE DE MER DANS LE SECTEUR CANADIEN DE LA MER DE BEAUFORT

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INFLUENCE OF THE ENVIRONMENTAL FACTORS ON THE TAXONOMIC COMPOSITION AND THE DEVELOPMENT OF SEA-ICE ALGAE AND OTHER PROTISTS IN THE CANADIAN BEAUFORT SEA

THESIS

PRESENTED TO

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BY

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AVANT-PROPOS

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This thesis is composed of a general introduction and conclusion with three main chapters, each representing an individual research topic. The first chapter of this thesis is published in *Journal of Marine Systems* as a special volume dedicated to CASES, while the second chapter is accepted in *Marine Ecology Progress Series* and the third chapter will be submitted to a peer-reviewed journal.

RÉSUMÉ

L'évolution saisonnière des algues et autres protistes du niveau inférieur de la glace de première année a été suivie dans le Haut-Arctique occidental canadien dès leur piégeage en automne 2003 jusqu'à leur prolifération printanière et leur déclin à la fin de juin 2004. Cette étude s'est principalement intéressée aux changements temporels de composition taxonomique entre différents types de glace de mer nouvellement formée et l'eau de surface sous-jacente, à l'incorporation sélective des cellules dans la glace et à leurs stratégies de survie. Les variations de la biomasse chlorophyllienne, de l'abondance et de la composition des protistes du niveau inférieur de la glace côtière ont aussi été étudiées de la fin de l'hiver à la fin du printemps à deux sites représentatifs d'un couvert de neige mince et épais. Enfin, la répartition horizontale à petite échelle (< 25 m) de la communauté de protistes du niveau inférieur de la glace de mer et des facteurs du milieu influençant leur biomasse, leur abondance et leur composition taxonomique a été évaluée à diverses périodes au cours de la saison de croissance printanière.

Cette étude montre que les protistes s'établissent dans la glace de mer dès sa formation à l'automne. La composition taxonomique des protistes dans la glace nouvellement formée et les eaux de surface change au cours de l'automne. La composition des protistes dans la glace nouvelle est similaire à celle de l'eau de surface mais elle diffère dans les glaces plus âgées. Les petites algues (< 4 µm) sont les cellules pigmentées les plus abondantes dans la glace de mer nouvellement formée et l'eau de surface sous-jacente. Toutefois, elles sont moins abondantes dans la glace de mer que dans l'eau de surface. En revanche, les grosses cellules (≥ 4 µm) sont plus abondantes dans la glace de mer que dans l'eau de surface. Ces résultats montrent clairement une incorporation sélective de grosses cellules (≥ 4 µm) dans la glace de mer nouvellement formée. Enfin, cette étude suggère que la formation de spores et de kystes est une stratégie de survie mineure chez les protistes des glaces des mers arctiques.

Dans la baie Franklin, l'accumulation de protistes dans le niveau inférieur de la glace de la banquise côtière commence dès la fin février. Avant la période de floraison, les protistes photosynthétiques (surtout des diatomées) dominent sous couvert de neige mince tandis que des flagellés vraisemblablement hétérotrophes dominent sous couvert de neige épais. Pendant la floraison printanière, que la banquise soit faiblement couverte de neige ou non, la communauté de protistes du niveau inférieur de la glace est dominée par des diatomées coloniales (*Nitzschia frigida*, *N. promare*, *Navicula* sp. 6, *N. pelagica* et *Fragilariopsis cylindrus*), la diatomée *N. frigida* étant la plus abondante. Après la floraison,

l'abondance des diatomées diminue plus rapidement que celle des flagellés. Ceci suggère que les flagellés sont moins sensibles à la fonte de la glace que les diatomées. Enfin, les résultats montrent que, pour le niveau inférieur de la glace, la biomasse algale maximum atteinte pendant la saison de croissance printanière dépend des apports en nitrates provenant de la couche supérieure de la colonne d'eau. Ainsi, la quantité d'éléments nutritifs présente à la surface de l'eau à la fin de l'hiver est un facteur important qui détermine l'ampleur de la floraison algale au printemps.

La biomasse de chlorophylle *a* (chl *a*) et l'abondance des protistes du niveau inférieur de la glace ont montré une répartition horizontale hétérogène à trois reprises entre la fin avril et la fin mai 2004. La répartition horizontale de la biomasse chlorophyllienne était différente de celle de l'abondance des protistes de glace. Cette divergence peut être liée à des différences dans la teneur intracellulaire en chl *a* chez les divers taxons photosynthétiques et à l'absence de pigments chez les protistes hétérotrophes. Les flagellés étaient abondants par rapport à l'abondance totale des protistes sous couvert de neige épais alors que celle des diatomées était très élevée sous couvert de neige mince. La composition taxonomique des protistes a changé au cours de la période d'échantillonnage, en raison de la diminution du couvert de neige et de l'augmentation de l'irradiance incidente transmise à la base de la glace. La répartition horizontale des taxons de diatomées et de flagellés peut s'expliquer, entre autres, par les variations de l'épaisseur du couvert de neige à la fin avril et par les variations de la salinité de la glace et de l'épaisseur du couvert de neige à la fin mai. L'ensemble des résultats de cette thèse suggère que les flagellés tolèrent davantage les changements du milieu que les diatomées.

ABSTRACT

The seasonal development of bottom ice algae and other protists was studied in the western Canadian High Arctic from the period of their entrapment in autumn 2003 through the spring bloom until the decline in late June 2004. This investigation describes the temporal changes in the taxonomic composition of these ice protists between different types of newly formed sea ice and the underlying surface water, the selective incorporation of cells in sea ice and their survival strategies. The algal biomass, protist abundance and taxonomic composition were also examined under two contrasting snow covers during the winter–spring season. Finally, small-scale patchiness (< 25 m) of bottom ice protist community and the environmental factors controlling their biomass, abundance and taxonomic composition was assessed at different periods during the vernal growth season.

This study demonstrated that the protist community is established in the sea ice during the first stages of its formation in autumn. The taxonomic composition of protists in the newly formed sea ice and the underlying surface water changed through the autumn. The composition was similar in both new ice and underlying surface water, but was markedly different in older ice types. Small photosynthetic algae (< 4 μm) were the most abundant cells in the newly formed sea ice and underlying surface water, but they were less abundant in sea ice than in surface water, while larger cells (≥ 4 μm) were more abundant in sea ice. These results clearly showed a selective incorporation of large cells (≥ 4 μm) in newly formed sea ice. Finally, this study suggested that the spore and cyst formation is a minor survival strategy for Arctic sea-ice protists.

In Franklin Bay, the accumulation of protists in the bottom ice horizon started as early as the end of February. During the pre-bloom period, autotrophic protists (mainly diatoms) dominated under low snow cover whereas flagellates, which were presumably heterotrophic, dominated under high snow cover. During the bloom period, the bottom ice protist community under both snow conditions was dominated by colonial diatoms (*Nitzschia frigida*, *N. promare*, *Navicula* sp. 6, *N. pelagica* and *Fragilariopsis cylindrus*), with *N. frigida* being the most abundant. During the post-bloom period, diatom abundance declined more rapidly than flagellates. This suggests that flagellates are less sensitive than diatoms to melting sea-ice conditions. Finally, the results showed that the maximum bottom ice algal biomass attained during the vernal growth season depends on nitrate supply from the upper water column. Thus, the amount of nutrients available in the surface water at the end of the winter is a critical factor determining the magnitude of the ice algal spring bloom.

At three different periods of the vernal growth season, bottom ice chlorophyll *a* (chl *a*) biomass and protist abundance showed a patchy horizontal distribution which seemed to be mainly governed by the snow cover. The horizontal distribution of bottom ice chl *a* biomass was different from that of protist abundance. This discrepancy may be related to differences in intracellular chl *a* content among the autotrophic taxa and absence of pigments in the heterotrophic protists. Flagellates showed a high contribution to total protist abundance under high snow cover, while diatoms were highly abundant under low snow cover. The protist taxonomic composition changed during the three sampling days due to the seasonal decrease of the snow depth and increase of the transmitted incident irradiance in the bottom ice horizon. The horizontal distribution of diatom and flagellated taxa was mainly explained, among other things, by variations in snow depth at the end of April and in bottom ice salinity and snow depth at the end of May. Overall, the results of this thesis suggest that bottom ice flagellates are more tolerant to changing environmental conditions than diatoms.

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INTRODUCTION GÉNÉRALE

The Changing Arctic Environment

Growing evidence has shown that the Earth's and, more particularly, the Arctic's climates are changing more rapidly and persistently than at any time since the beginning of civilization (ACIA 2005). The entire planet is currently part of a warming trend, with atmospheric temperatures increasing most significantly in the Arctic (ACIA 2005, IPCC 2007). During the past 40 years, the average land–surface temperature in the Arctic has increased nearly twice as much as the global average (ca. 0.4°C per decade), with some regions even experiencing higher increases (ACIA 2005). Warmer atmospheric conditions (IPCC 2007) increased the tendency toward higher winter precipitation (Serreze et al. 2000, ACIA 2005) and earlier snowmelt across much of the western Arctic (Anderson & Drobot 2001). Declines in sea-ice extent (Serreze et al. 2007, Comiso et al. 2008) and thickness (Rothrock et al. 1999, Rothrock & Zhang 2004) are widely acknowledged. Part of these changes reflect natural variability; there is, however, growing evidence that human activities that emit *green house gases*, mainly carbon dioxide and methane, are responsible for most of the warming processes of our planet (ACIA 2005, Holland et al. 2006, IPCC 2007, Serreze et al. 2007).

Since 1978, the extent of Arctic multi-year ice cover has diminished by approximately 9–10% per decade (Comiso 2002, Stroeve et al. 2007, Comiso et al. 2008). This great loss was recognized in the central Arctic Ocean since 1960, with a reduction in

the sea-ice thickness of ca. 0.5 m north of the Canadian Archipelago and up to 2 m in East Siberian seas (Rothrock & Zhang 2004). In addition, the reduction of sea-ice cover triggers a positive feedback mechanism, accelerating the temperature increase in the Arctic due to the reduction in surface albedo associated with a shift from sea-ice to open-water conditions (Johannessen et al. 2004, Serreze et al. 2007).

The consistent trend toward warmer temperatures and less ice is leading to a replacement over the Arctic Ocean of the multi-year ice by annually forming sea ice (Melling 2003, Comiso et al. 2008). Similarly, seasonal first-year ice cover is predicted to show earlier ice breakup in spring and delayed formation in autumn (Serreze et al. 2007, Comiso et al. 2008). The successive unusually low September sea-ice minima observed from 2002 to 2007 (NSIDC 2006, Comiso et al. 2008) suggest that the shrinking of the sea-ice cover is accelerating; an ice-free Arctic summer is expected within the next few decades (Holland et al. 2006, Serreze et al. 2007, Comiso et al. 2008).

Reduction in the volume of Arctic sea ice may have a striking impact on the global scale, changing the Earth's surface heat balance or slowing down global thermohaline circulation (Dickson et al. 2002, ACIA 2005). On the regional scale, reduced sea-ice cover will affect the Arctic marine ecosystem and its associated biogeochemical fluxes (Grebmeier et al. 2006). Because sea ice supports a significant part of the total primary production of polar oceans (Wheeler et al. 1996, Arrigo 2003, Gosselin et al. 2008), we now have to pay more attention to the role of organisms associated with sea ice in Arctic and Antarctic marine ecosystems.

Importance of Sea Ice

Sea ice covers approximately 7% of the Earth's surface at its maximum extent in winter (Dieckmann & Hellmer 2003), and is one of the largest biomes on the planet (Comiso 2003). It is an important feature of the physical environment in polar regions and strongly affects all organisms living in these areas (Horner 1985a). Sea ice effectively reduces heat and gas exchange between the atmosphere and the upper layers of the ocean. It also reduces vertical mixing and the amount of incident irradiance reaching the ice–water interface and the water column, which in turn affect the photosynthesis of ice algae and under-ice phytoplankton (Horner 1985a, Melnikov et al. 2001). At the same time, the ice's upper surface provides a unique habitat for a number of bird and mammal species (Horner 1985a, Stirling 2002), while an important network of brine pockets, channels and capillaries in the lower ice horizon offers a dynamic substrate for a high diversity of heterotrophic organisms ranging from viruses (Maranger et al. 1994, Wells & Deming 2006), bacteria (Junge et al. 2004, Riedel et al. 2006, 2007a) and micro- and meiofauna (Carey 1985, Grainger et al. 1985, Nozais et al. 2001) to highly productive communities of ice algae (Horner 1985a, Arrigo 2003, Ban et al. 2006). Thus, this immense sheet of frozen water usually covered with snow is the determinant factor for structuring the polar community. It plays a significant role in regulating the global climate of our planet by increasing the albedo and affecting the energy balance between the atmosphere and the upper layers of the ocean (Comiso 2003, Mundy et al. 2005).

Ecological Role and Importance of Ice Algae in Polar Ecosystems

Ice algae contribute up to ca. 57% of the total annual primary production in the central Arctic Ocean (Gosselin et al. 1997), and between 3 and 25% in Arctic shelf regions (Legendre et al. 1992). Blooms of ice algae generally occur before the phytoplankton bloom (Cota et al. 1991, Arrigo 2003). In early spring, planktonic grazers depend heavily on ice algae as the only available food source, ensuring their growth and reproductive success, while benthic communities benefit from the sinking flux of algal cells and organic aggregates released to the water column during ice-melt events (Horner 1985a, Cota et al. 1991, Michel et al. 1996, 2006, Renaud et al. 2007). Therefore, the timing and duration of the growth season and the release of ice algae into the water column in spring are extremely important for pelagic and benthic food webs (Michel et al. 2006). Ice algae are also known to produce exopolymeric substances, which were recently recognized as an important source of organic material (Krembs et al. 2002, Riedel et al. 2007b). These exopolymeric substances contribute significantly to carbon export to the deep waters of the Arctic Ocean (Emerson et al. 1997, Fortier et al. 2002, Riedel et al. 2007b). Thus, ice algae play an important role in polar ecosystems, and the changes recently observed in the Arctic, especially in the reduction of ice and snow cover, increasing precipitation and faster onset of ice-melt, may have a strong impact on these highly productive communities.

Sea-Ice Biota

Uni- and multicellular organisms are distributed throughout the entire ice matrix. Because they colonize different ice horizons, specific names have been given to describe

these various protist communities (Horner 1985a). Three distinct habitats were distinguished by Horner et al. (1992), according to the position of the protists within the ice matrix: surface community, interior community and bottom community (Fig. 1).

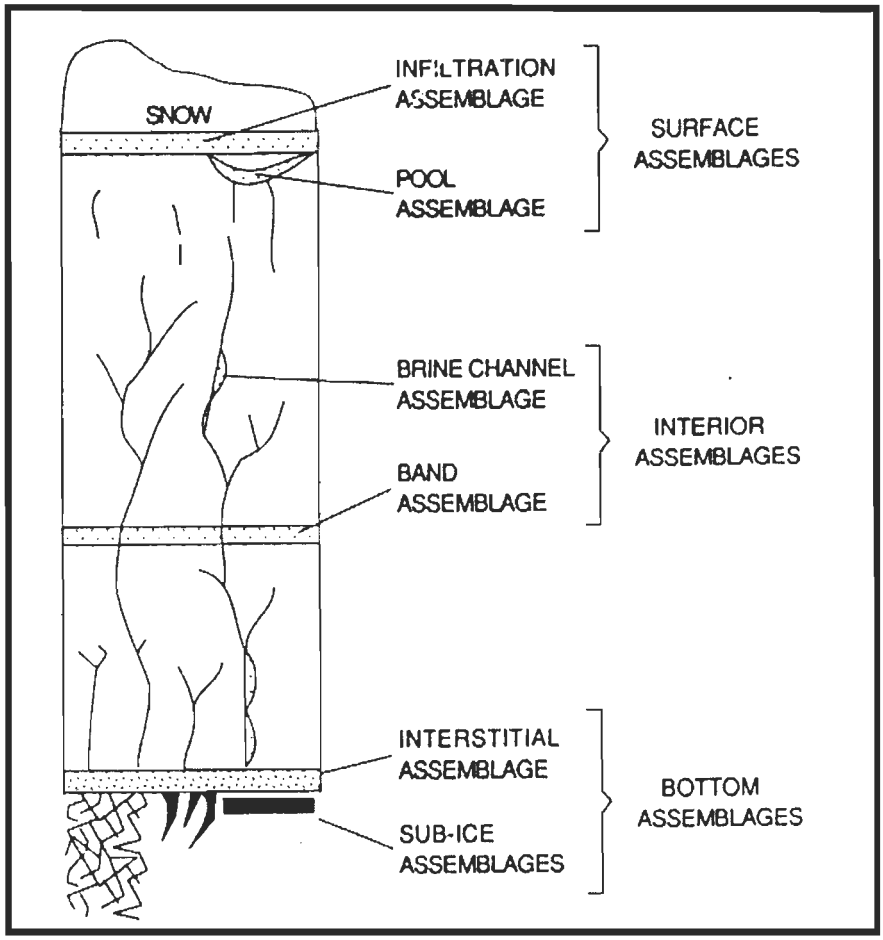

Fig. 1. Schematic description of sea ice and potential habitats for various types of ice protist communities (adapted from Cota et al. 1991)

Surface communities occur at the snow–ice interface and result from the flooding of the ice surface with seawater (Meguro 1962). **Interior communities**, primarily known from the Antarctic, correspond to a remnant assemblage of the previous bloom season

(Ackley et al. 1979). Finally, the **bottom community** develops during the spring in the lowest ice layer (Apollonio 1961, Bunt 1963). The bottom ice biota is further divided into **interstitial** and **sub-ice communities**, the latter consisting of algae floating directly beneath the ice or attached to the underside of the ice and forming strands and mats (Horner et al. 1988). The **interstitial community** occurs in the bottom 2–10 cm of the ice and is usually associated with small ice crystals, brine pockets and a well-developed network of channels and capillaries (Horner et al. 1988, 1992, Arrigo 2003). Surface, interior and bottom ice communities appear to have differing taxonomic composition, growth seasons and physiological requirements (Cota et al. 1991, Arrigo 2003).

The main subject of this thesis focuses on ice algae and other protists, which are defined by Horner et al. (1988) as the microalgae living "either within the ice attached to ice crystals, in the interstitial water between ice crystals, or they may be associated with the undersurface of the ice as floating mats, lumps, or strands that extend downward into the water column." Several names have been used to describe the organisms living in association with the sea ice (Horner 1985a, Horner et al. 1988). Horner et al. (1992) proposed using the term *sympagic community* to describe the group of microorganisms (autotroph and heterotroph) inhabiting the ice. In terms of abundance, the main groups of ice protists are diatoms, flagellates and dinoflagellates. While diatoms are mainly photosynthetic, a large fraction of the flagellated community, including some dinoflagellates, can be heterotrophic.

The occurrence of microorganisms in polar sea ice has been known for more than 165 years (see the review of Horner 1985a). Ehrenberg (1841, 1853) and Hooker (1847)

were the first to report on the presence of diatoms in sea ice from the Northern and Southern hemispheres, respectively. Subsequently, extensive floristic and taxonomic studies were conducted in the Kara Sea, at Cape Wankarem and Franz Josef Land in Russia (Cleve & Grunow 1880, Cleve 1883, Grunow 1884), in Baffin Bay and Davis Strait in Canada and near Spitsbergen, Norway (Cleve 1896, 1899). Also, Østrup (1895) studied diatoms collected from ice floes off East Greenland. For the Antarctic, several taxonomic and floristic reports were published from the first Belgian, French and German Antarctic expeditions (Van Heurck 1909, Peragallo 1921, 1924, Heiden & Kolbe 1928).

Most of the early works on sea-ice algae were taxonomic and floristic in nature. The first ecological studies were published in the 1960s (see the review of Horner 1985a). Several studies described the algal species composition within different ice habitats (Horner 1976, 1985b, Garrison et al. 1982, Horner & Schrader 1982, Syvertsen 1991, Michel et al. 1993, Gleitz et al. 1998, Gradinger 1999, Günther & Dieckmann 2001). The effects of physical and chemical variables (such as light, temperature, salinity, tidal mixing and nutrients) on the biomass and physiological rates of ice algae were investigated in the Arctic (Poulin et al. 1983, Gosselin et al. 1985, 1986, 1990, 1997, Bates & Cota 1986, Maestrini et al. 1986, Cota et al. 1987, Smith et al. 1987, 1989, Barlow et al. 1988, Cota & Horne 1989, Tremblay et al. 1989, Legendre et al. 1992) and the Antarctic (Cota & Sullivan 1990, Garrison 1991, Lizotte & Sullivan 1992).

Temporal variations in the abundance of bottom ice algae were studied in many Arctic regions (Alaskan Beaufort Sea: Horner & Schrader 1982; Barrow Strait: Smith et al. 1988, Welch & Bergmann 1989; Frobisher Bay: Hsiao 1980, 1992, Grainger & Hsiao

1982; Hudson Bay: Poulin et al. 1983, Gosselin et al. 1985, 1990; Canada Basin: Melnikov et al. 2002), but only a few studies have addressed the influence of environmental factors on the taxonomic composition of the bottom ice algae during the community's different growth periods (e.g., Horner & Schrader 1982, Poulin et al. 1983). Similarly, the influence of environmental factors such as snow depth, salinity and nutrient availability on the horizontal distribution of bottom ice algal biomass has been examined (Gosselin et al. 1986, Monti et al. 1996, Robineau et al. 1997, Rysgaard et al. 2001, Mundy et al. 2007b), but the patchy distribution in the taxonomic composition of the community was only rarely investigated (Monti et al. 1996). Furthermore, information is still missing about the biological processes taking place during sea-ice formation in autumn, despite the studies on this topic over the last 15 years (Grossmann & Gleitz 1993, Fritsen et al. 1994, Gradinger & Ikävalko 1998, Tuschling et al. 2000, Riedel et al. 2006). Still being debated are the similarity or difference in the autumn algal taxonomic composition between the newly formed sea ice and the underlying surface water, the selective incorporation in autumn of large cells in sea ice, and the winter survival strategies of algae (Garrison et al. 1983, Gradinger & Ikävalko 1998, Syvertsen 1991, Tuschling et al. 2000, Zhang et al. 2003).

Annual Cycle of the Protist Community in Sea Ice

In autumn, ice crystals start to form in the upper water column when the water temperature drops below –1.86°C (Eicken 2003). In the first steps of freezing, frazil ice crystals float to the water surface and accumulate as grease ice, which consolidates to form nilas and new ice. As the season progresses, various stages in sea-ice development lead to

the formation of annual first-year ice, which may reach up to 2 m in thickness by the end of April in the Canadian Arctic (Weeks & Ackley 1982, Garrison 1991, Manice 2002, Eicken 2003). In the case of first-year sea ice attached to or in association with a landmass, the term landfast ice is used as opposed to that of mobile ice, which is referred to herein as pack ice (Weeks & Ackley 1982, Carmack & Macdonald 2002).

During the initial steps of sea-ice formation, inorganic sediments as well as autotrophic and heterotrophic protists can be entrapped in concentrations nearly exceeding those of the underlying surface waters (Garrison et al. 1983, 1989, Reimnitz et al. 1992, Gradinger & Ikävalko 1998). Almost all biological investigations carried out in the Antarctic have suggested that the entrapment of organisms in newly formed sea ice is purely a random process. In the Arctic, studies on the entrapment of particles in sea ice focused mainly on sediments (e.g., Reimnitz et al. 1993) while biological data were lacking (Gradinger & Ikävalko 1998, Riedel et al. 2006). The main process responsible for protist entrapment in newly formed sea ice is the harvesting or scavenging of particles, including protist cells, by frazil ice crystals that form in the water column and rise up to the water surface. This mechanism is associated with small-scale circulation features (e.g., Langmuir cells) that collect organisms suspended in the water column (Ackley 1982, Garrison et al. 1983, 1989). Cell size and stickiness of the cell surface seem to be important factors during the process of protist entrapment in newly formed sea ice, where a selective incorporation of larger cells has been suggested (Gradinger & Ikävalko 1998, Riedel et al. 2007b).

Microalgae can grow in the ice until November, when the light becomes limiting (Lizotte 2003). The development of these cells is very slow in winter and they are scattered

throughout the ice (Horner et al. 1992, Arrigo 2003). By the end of winter, usually around mid-March, algal cells become concentrated in the bottom few centimetres of the ice, probably because of a combination of brine drainage and active migration of cells through brine channels (Horner & Schrader 1982). The abundance of autotrophic cells increases exponentially in early spring with increasing solar irradiance; cells divide every 3–5 days, and a brown colour is usually visible by early April in the lower ice layer (Horner 1985a, Lizotte 2003). Maximum biomass and abundance generally occur by mid- to late May, prior to the melt period when the snow cover disappears and the ice is at its maximum thickness. The algal bloom rapidly declines in late spring or early summer, coincident with ice-melting (Hsiao 1980, Horner 1985a, Horner et al. 1992). The skeletal layer of the bottom ice that contains microalgae becomes softer and begins to disintegrate. Weak water movements systematically wash away the algal layer until, often by early June, the brown layer is no longer visible (Hsiao 1980, Horner 1985a, Syvertsen 1991, Horner et al. 1992, Lizotte 2003).

Taxonomic Composition

The interstitial bottom ice community of the Canadian High Arctic is composed mainly of diatoms (Bacillariophyta) with a high proportion of pennate taxa chiefly belonging to two families, Naviculaceae and Bacillariaceae. The Naviculaceae are by far the most important group of diatoms in bottom ice algal communities in spring, and they are represented by the genera *Navicula* Bory, *Pinnularia* Ehrenberg, *Pleurosigma* Hassall and *Entomoneis* Ehrenberg (Poulin & Cardinal 1982a, b, 1983, Poulin 1990a). Early in the

season, the bottom ice community is composed mainly of flagellates, with some occurrence of solitary diatom species. As the season progresses, the species dominance changes to colony-forming pennate diatoms, which dominate the community during the bloom period (von Quillfeldt et al. 2003). By the end of the bloom in summer, the dominance of diatoms diminishes and the flagellates again increase in the interstitial ice layer (Hsiao 1980, 1992, Horner & Schrader 1982).

The taxonomic composition of bottom ice algae and other protists differs according to the type of ice (Garrison 1991, Gleitz et al. 1998). The interstitial community of landfast ice in the North Water, northern Baffin Bay, was found to be dominated in spring by diatoms belonging to the genera *Nitzschia* Hassall, *Navicula* and *Pleurosigma*, whereas *Fossula arctica* Hasle, Syvertsen *et* von Quillfeldt, *Fragilariopsis cylindrus* (Grunow) Krieger / *F. oceanica* (Cleve) Hasle, *Pauliella taeniata* (Grunow) Round *et* Basson and *Navicula septentrionalis* (Grunow) Gran were the most abundant species in pack ice (Simard 2003). *Nitzschia frigida* Grunow was the dominant species of bottom ice communities in both landfast and pack ice in early spring. By mid-June, nanoflagellates < 10 µm dominated the interstitial communities in the North Water (Simard 2003). Similar results were obtained in the pack ice of the Greenland Sea and the central Arctic Ocean, where phototrophic flagellates and cysts of unknown origin were the most abundant groups in the melting pack ice in summer (Ikävalko & Gradinger 1997, Gradinger 1999). During the ice melt season, flagellates (mainly chrysophytes and dinoflagellates) were also numerous in Frobisher Bay, contributing up to 78% of the total algal abundance in the upper part of ice floes (Hsiao 1992).

Role of Environmental Factors

Environmental conditions play an important role in the ecology and dynamics of sea-ice algae (Cota et al. 1991). The growth and accumulation of algae in the bottom ice horizon are mainly regulated by *in situ* irradiance (Welch & Bergmann 1989, Gosselin et al. 1990) and nutrient supply (Cota et al. 1990, Gosselin et al. 1990), while their horizontal distribution is mainly related to space availability (Welch & Bergmann 1989, Legendre et al. 1991, Eicken 1992), ice growth rate (Legendre et al. 1991), vertical brine stability (Krembs et al. 2001), and surface water and bottom ice salinity (Poulin et al. 1983, Legendre et al. 1992).

Irradiance, Ice Thickness and Snow Cover

Until recently, solar irradiance was identified as the paramount factor for the growth of bottom ice algae (Horner & Schrader 1982), controlling their biomass and production (Smith et al. 1988). In the Arctic, sea-ice algae start photosynthesizing when *in situ* irradiance reaches 2–9 µmol photons m^{-2} s^{-1} in late winter (Horner & Schrader 1982, Gosselin et al. 1985). Beyond these minimum values, ice algae respond to a seasonal increase in irradiance by altering their photosynthetic characteristics (Gosselin et al. 1985, Rochet et al. 1986, Barlow et al. 1988, Michel et al. 1988, Cota & Horne 1989, Cota et al. 1991, Kirst & Wiencke 1995). Gosselin et al. (1990) suggested that ice algae are limited by light at the beginning of the growth season and become periodically limited by nutrients as the season progresses. The transmission of incident irradiance to the bottom sea-ice horizon

depends on the albedo and the attenuation of the irradiance by the snow, ice, and inorganic and organic particles trapped in the ice sheet (Maykut 1985, Belzile et al. 2000). Horner & Schrader (1982) demonstrated that only 2% of the incident irradiance reached the algal layer through 1.8 m of sea ice when there was no snow present, while the irradiance was reduced to 1% and < 0.1% of the surface level with a snow cover of 3–4 cm and 20 cm, respectively. Furthermore, snow patchiness on the ice surface leads to a high spatial variability of ice algal biomass and production (Gosselin et al. 1986, Welch & Bergmann 1989, Mundy et al. 2005). Similarly, inter-annual variability in the timing of snow and ice melt appears to influence the bottom ice algal biomass (Fortier et al. 2002, Michel et al. 2006).

Nutrients

It has been assumed that nutrients were not limiting ice algal growth because most polar waters are relatively nutrient-rich (Cota et al. 1991, Lizotte 2003). However, for both the Arctic and the Antarctic, several pieces of evidence have suggested that the availability of inorganic nutrients can be limiting for the ice algal communities, particularly at the end of bloom events (Palmisano & Sullivan 1985b, Maestrini et al. 1986, Cota et al. 1987, Cota & Horne 1989, Gosselin et al. 1990, Smith et al. 1990, 1997, Lizotte & Sullivan 1992). Silicic acid was identified as the most limiting nutrient for the growth of ice diatom communities in the Canadian Arctic (Cota et al. 1987, Gosselin et al. 1990, Smith et al. 1990) and the Antarctic (Cota & Sullivan 1990). Similarly, in the Weddell Sea in Antarctica, Dieckmann et al. (1991) concluded that silicic acid was likely limiting for ice

algal production, while nitrogen limitation was reported in the Canadian Arctic's Resolute Passage (Smith et al. 1997) and Hudson Bay (Maestrini et al. 1986, Demers et al. 1989).

Salinity

Bottom ice algae can grow under varying salinity regimes in the underlying surface waters (Grant & Horner 1976, Vargo et al. 1986, Legendre et al. 1992). In Hudson Bay, the algal biomass and number of diatom species in first-year bottom ice increased along an offshore salinity gradient associated with the under-ice plume of the Great Whale River (Poulin et al. 1983, Gosselin et al. 1986). The surface available for protist colonization in the bottom ice increased with surface water salinity (Poulin et al. 1983). Ice salinity may affect the taxonomic composition directly through osmotic or other physiological effects, or indirectly by changes in the physical properties of sea ice (Poulin et al. 1983, Legendre et al. 1992, Ryan et al. 2004, Ralph et al. 2007).

General Objectives

The development of ice algae and other protists has rarely been studied along the continental shelf of the western North American Arctic, except for the works of Hsiao (1980) in Eskimo Lakes, Northwest Territories, and Horner & Schrader (1982) at Point Barrow, Alaska. There have been no studies of sea-ice microalgae in the western part of the Canadian Beaufort Sea. A climate scenario for the next century predicts that the global temperature will increase by 1.8 to 4°C (IPCC 2007). The temperature rise may substantially influence the ice algal community through its effect on the physical and

chemical characteristics of the sea ice and the underlying water column. Furthermore, snow thickness and snowmelt are the primary factors determining the production and release of ice algae to the water column (Cota et al. 1991, Fortier et al. 2002). Thus, on one hand, the faster onset of snowmelt in spring related to higher air temperature would cause shorter ice algal bloom duration, potentially decreasing their production. On the other hand, the shift from multi-year ice to first-year ice presently observed in large areas of the Canadian Archipelago would increase ice algal production, because multi-year ice supports only low ice algal production compared to annual sea ice (Fortier et al. 2002, Michel et al. 2006). Therefore, it is presently difficult, if not impossible, to predict how these changes will influence the development of the sea-ice community in general and the algal taxonomic composition in particular. Better knowledge of the ice algal development cycle is thus needed.

The general objective of this study was to determine how environmental variables govern species composition and development of the bottom ice protist communities in the western Beaufort Sea area. This research was an integral component of project 2.3 (*Light, Nutrients, Primary and Export Pproduction in Ice-Free Waters*) of the Canadian Arctic Shelf Exchange Study (CASES).

The thesis comprises three main chapters supported by a general introduction and conclusion. The three chapters are devoted to the main topic of my thesis project. In the first chapter, I examine whether there was random entrapment of planktonic protists in newly formed sea ice, I compare protist taxonomic composition among different types of newly formed sea ice (new ice, nilas, young ice, thin first-year ice), and I assess the

importance of picoalgae, spores, cysts and potentially harmful algae in sea ice and surface water.

In the second chapter, I examine the seasonal changes in abundance and taxonomic composition of bottom ice diatoms, flagellates and dinoflagellates under two contrasting snow covers from mid-winter to late spring. The specific objectives of this chapter are to assess (1) the role of meteorological and hydrodynamic factors on the temporal variability of the bottom ice protist community, (2) the influence of snow cover on growth rates, cell abundance and taxonomic composition of diatoms and other protists throughout the study period, (3) the role of the nutrient supply on the large-scale horizontal distribution of chlorophyll *a* biomass in the bottom ice, and (4) key species of the bottom ice community during the season and the importance of heterotrophic protists.

In the last chapter, I describe the small-scale (< 25 m) horizontal distribution of bottom ice protists in first-year landfast ice on three occasions in spring. The two main objectives of the study described in this final chapter are to estimate the patchiness of the bottom ice protist community at different periods of the growth season, and to determine which environmental variables best explains the horizontal variability and how this variable influences the taxonomic composition.

CHAPITRE I

PROTIST ENTRAPMENT IN NEWLY FORMED SEA ICE IN THE COASTAL ARCTIC OCEAN

RÉSUMÉ

Une étude a été réalisée dans le secteur canadien de la mer de Beaufort entre le 30 septembre et le 19 novembre 2003 pour établir la composition taxonomique et déterminer l'abondance des protistes de la glace de mer nouvellement formée (i.e. glace nouvelle, nilas, jeune glace et glace mince de première année) ainsi que des eaux de surface sous-jacentes à la glace. Les picoalgues (0.2–2 µm) et les nanoalgues (2–20 µm) ont été comptées par cytométrie de flux, tandis que les protistes photosynthétiques et hétérotrophes de dimension égale ou supérieure à 4 µm ont été identifiés et comptés par microscopie inversée. Des protistes ont été observés dans tous les échantillons de glace de mer et d'eau de surface prélevés au cours de l'étude. Les plus abondants étaient les organismes de taille inférieure à 4 µm. Il y en avait cependant moins dans la glace de mer (418–3051 $\times 10^3$ cellules L^{-1}) que dans les eaux de surface (1393–5373 $\times 10^3$ cellules L^{-1}). En revanche, les gros protistes de dimension égale ou supérieure à 4 µm étaient plus nombreux dans la glace de mer (59–821$\times 10^3$ cellules L^{-1}) que dans les eaux de surface (22–256 $\times 10^3$ cellules L^{-1}). Ces données suggèrent qu'il y a une incorporation sélective des organismes unicellulaires de grande taille dans la glace de mer. Le groupe de protistes de taille supérieure ou égale à 4 µm se composait d'un total de 73 taxons, dont 12 diatomées centriques, 7 diatomées pennées, 11 dinoflagellés et 16 flagellés. La composition taxonomique de la glace au premier stade de sa formation (glace nouvelle) était très semblable à celle des eaux de surface et comprenait une population mixte de nanoflagellés (prasinophycées et prymnésiophycées), de diatomées (surtout le genre *Chaetoceros*) et de dinoflagellés. Aux stades plus avancés (jeune glace et glace mince de première année), elle devenait nettement différente de celle des eaux de surface. Les échantillons de cette glace plus ancienne contenaient relativement moins de prasinophycées et davantage de nanoflagellés non identifiés que la glace plus nouvelle. Les spores de résistance et les kystes de dinoflagellés étaient généralement plus abondants dans la glace de mer que dans les eaux de surface. Il faudra cependant poursuivre la recherche pour établir l'importance de cette stratégie de

survie en hiver dans la glace de mer de l'Arctique. La présente étude montre clairement l'incorporation sélective de gros organismes unicellulaires de taille supérieure ou égale à 4 µm dans la glace de mer nouvellement formée et la modification de la composition taxonomique des protistes entre la glace de mer et les eaux de surface à mesure que l'automne avance.

ABSTRACT

Protist abundance and taxonomic composition were determined in four development stages of newly formed sea ice (new ice, nilas, young ice and thin first-year ice) and in the underlying surface waters of the Canadian Beaufort Sea from 30 September to 19 November 2003. Pico- and nanoalgae were counted by flow cytometry whereas photosynthetic and heterotrophic protists ≥ 4 µm were identified and counted by inverted microscopy. Protists were always present in sea ice and surface water samples throughout the study period. The most abundant protists in sea ice and surface waters were cells < 4 µm. They were less abundant in sea ice (418–3051 x 10^3 cells L^{-1}) than in surface waters (1393–5373 x 10^3 cells L^{-1}). In contrast, larger protists (≥ 4 µm) were more abundant in sea ice (59–821 x 10^3 cells L^{-1}) than in surface waters (22–256 x 10^3 cells L^{-1}). These results suggest a selective incorporation of larger cells into sea ice. The ≥ 4 µm protist assemblage was composed of a total number of 73 taxa, including 12 centric diatom species, 7 pennate diatoms, 11 dinoflagellates and 16 flagellates. The taxonomic composition in the early stage of ice formation (i.e., new ice) was very similar to that observed in surface waters and was composed of a mixed population of nanoflagellates (Prasinophyceae and Prymnesiophyceae), diatoms (mainly *Chaetoceros* species) and dinoflagellates. In older stages of sea ice (i.e., young ice and thin first-year ice), the taxonomic composition became markedly different from that of the surface waters. These older ice samples contained relatively fewer Prasinophyceae and more unidentified nanoflagellates than the younger ice. Diatom resting spores and dinoflagellate cysts were generally more abundant in sea ice than in surface waters. However, further studies are needed to determine the importance of this winter survival strategy in Arctic sea ice. This study clearly shows the selective incorporation of large cells (≥ 4 µm) in newly formed sea ice and the change in the taxonomic composition of protists between sea ice and surface waters as the fall season progresses.

1.1. Introduction

The occurrence of microorganisms in sea ice has been reported for more than 160 years in both polar hemispheres (reviewed by Horner 1985a). However, there are few studies on the biological processes during sea-ice formation in the fall (Grossmann & Gleitz 1993, Fritsen et al. 1994, Hoshiai et al. 1996, Gradinger & Ikävalko 1998, Tuschling et al. 2000, Garrison et al. 2003).

Polar oceans are characterized by the presence of extensive sea-ice coverage that attains its maximum extent at the end of the winter. In the Northern Hemisphere, the extent of the sea-ice cover varies from a minimum of 5.6 x 10^6 km^2 in September to a maximum of 15.5 x 10^6 km^2 in March (Parkinson et al. 1999, Comiso 2003, Serreze et al. 2007). According to the Manice (2002) sea-ice terminology, four stages of sea-ice development can be distinguished in the Arctic: new ice, nilas, young ice and thin first-year ice. New ice is a general term used to define recently formed ice composed of ice crystals that are weakly frozen together and have a definite form only while they are afloat. It includes frazil ice, grease ice, slush and shuga. Nilas consists of a thin elastic crust of ice that easily bends on waves and swells and grows in an interlocking finger-like pattern (finger rafting); it can reach up to 10 cm in thickness. Young ice corresponds to a transition stage between nilas and first-year ice, with a thickness varying between 10 and 30 cm. Finally, young ice develops into first-year ice, which is not more than one winter's growth and is 30 cm and more in thickness. In the fall, ice crystals begin to form in the upper water column when the water temperature drops below the freezing point (Weeks & Ackley 1982). In the first freezing steps, individual unconsolidated frazil ice crystals form in the water column, float

to the surface waters and accumulate as grease ice. As freezing continues, ice crystals consolidate to form nilas under calm sea conditions, after which young ice is formed (Weeks & Ackley 1982, Garrison 1991, Manice 2002). As the season progresses, these various stages in sea-ice development lead to the formation of annual first-year ice, which may reach up to 2 m in thickness in the Canadian Arctic.

Several physical mechanisms have been proposed to explain protist entrapment in newly formed sea ice (Ackley 1982, Weeks & Ackley 1982, Garrison et al. 1983, 1989, Ackley et al. 1987, Shen & Ackermann 1990). A first mechanism refers to the harvesting or scavenging of particles, including protist cells, by frazil ice crystals that form in the water column and rise to the water surface. This mechanism is associated with small-scale circulation features, such as the Langmuir cells, which collect organisms suspended in the water column. During the early stages of ice formation, this mechanism can cause microorganisms to accumulate in sea ice in concentrations nearly exceeding that of the underlying surface waters (Garrison et al. 1983). It has also been reported to concentrate microalgal cells in sea ice in some Antarctic regions (Ackley 1982, Garrison et al. 1983, 1989), and it is probably the best mechanism for concentrating cells in the ice (Garrison et al. 1983). A second mechanism consists of the nucleation of ice particles at the surface of microorganisms with subsequent rise to the water's surface (Ackley 1982). However, this mechanism was rejected by Reimnitz et al. (1993) after experimental observations. A third mechanism is related to a pumping process by which cells are concentrated by wave fields that pump the water through the ice and deposit microorganisms inside the ice (Ackley et al. 1987, Shen & Ackermann 1990).

Almost all biological studies carried out in the Antarctic have suggested that the entrapment of organisms in newly formed sea ice is a random process (Garrison et al. 1983, 1989). In the Arctic, studies on particle entrapment in sea ice have mainly focused on sediments (e.g., Reimnitz et al. 1993), while only a few dealt with biological data (Hegseth 1997, Gradinger & Ikävalko 1998, Tuschling et al. 2000, Riedel et al. 2007b). Based on an enrichment index comparing the abundance of organisms in the water column with different stages of newly formed sea ice, Gradinger & Ikävalko (1998) concluded that diatoms were the most successful colonizers of newly formed sea ice off Greenland in autum while they contribute only a minor fraction to the pelagic community. Autotrophic and heterotrophic flagellates larger than 10 µm exhibited a higher enrichment in sea ice compared to smaller cells. Size selectivity processes due to different incorporation rates of algae and bacteria in Antarctic sea ice were proposed by Penny & Sullivan (1990).

Reports on the taxonomic composition of microalgae in sea ice and the underlying surface waters are contradictory. Some studies (e.g., Tuschling et al. 2000) suggested that ice algal communities consist of species different from those in the water column, whereas others reported the occurrence of similar taxa in both environments (Schandelmeier & Alexander 1981, Horner & Schrader 1982, Garrison et al. 1983, Horner 1985a, Garrison 1991). In the Weddell Sea (Antarctica), some microalgal species occupied both the sea ice and the water column, which can be explained by a cycle during which the algal cells or spores are regularly trapped and survive in the ice and are released back into the water column in spring when ice melts (see Garrison et al. 1983, Horner 1985a, Garrison & Buck 1986). In the Beaufort Sea, Horner & Schrader (1982) showed that the spring

phytoplankton bloom was composed of microalgal species different from those found in the sea ice and the water column during winter.

Under unfavorable environmental conditions, some diatoms and dinoflagellates can produce resting spores or cysts. Hypnozygotes and cysts from dinoflagellate and chrysophyte species have been observed (Buck et al. 1992, Montresor et al. 1999). The formation of resting spores is common in centric diatoms, which are mainly planktonic (Hasle & Syvertsen 1996), but these spores are rather rare in pennate diatoms, which predominate in sea ice (Hargraves & French 1983, Buck et al. 1992). Some ice-associated diatoms (e.g., *Cylindrotheca closterium*) were found to reduce their metabolic rate and increase storage products under unfavorable conditions (Palmisano & Sullivan 1982). Such forms may function as survival stages in the ice (Garrison & Buck 1985). The formation of resting spores has been suggested as an overwintering strategy for sea-ice diatoms in the Antarctic (Palmisano & Sullivan 1985a). Resting spores do not seem to play an important role in the winter survival of Arctic ice algae; rather, facultative heterotrophy and energy storage were suggested as the main processes enabling winter survival in Arctic sea ice (Syvertsen 1991, Zhang et al. 2003).

In the fall of 2003, we investigated the entrapment of protists in different types of newly formed sea ice in the Canadian Beaufort Sea. The main objectives of this study were (1) to compare the protist taxonomic composition among different types of newly formed sea ice (new ice, nilas, young ice, thin first-year ice), (2) to determine if there was random entrapment of planktonic protists in newly formed sea ice, and (3) to assess the importance of picoalgae, spores, cysts and potentially harmful algae in sea ice and surface waters.

1.2. Materials and methods

1.2.1. Study site and sampling

Sampling was carried out in the Beaufort Sea from 30 September to 6 November 2003 on board the research ice-breaker CCGS *Amundsen* during the Canadian Arctic Shelf Exchange Study (CASES) (Fig. 1). Floating ice of different development stages and the underlying surface waters were collected at nine stations. Ice samples consisted of newly formed sea ice (i.e., new ice, nilas, young ice and thin first-year ice).

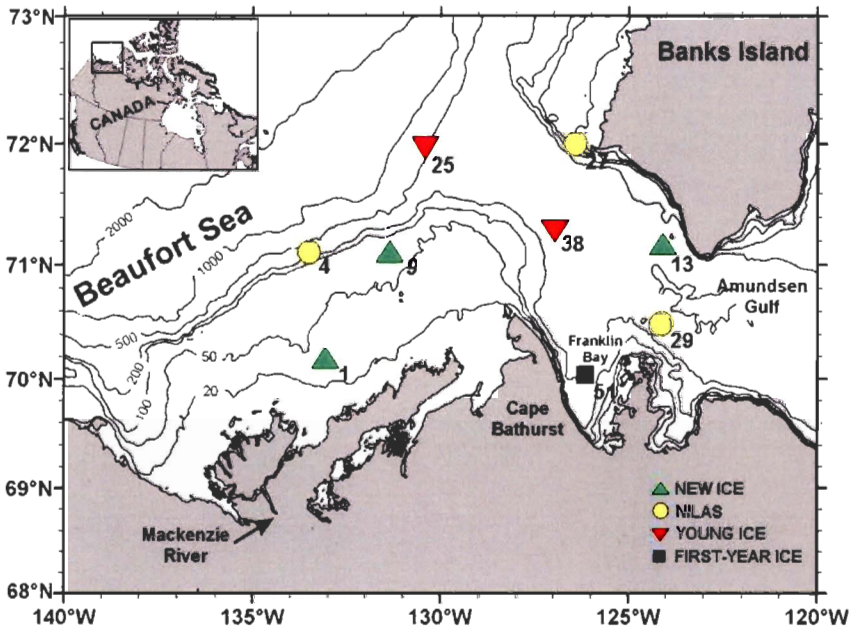

Fig. 1. Location of the sampling stations in the Canadian Beaufort Sea in fall 2003. Depth contours in meters

Newly formed sea ice < 7 cm was sampled with a strainer, whereas sea ice ≥ 7 cm thick was sampled with a manual Mark II ice corer (9 cm internal diameter; Kovacs Enterprises) from a metallic cage lowered from the ship's deck to the ice surface. The bottom 3 cm of the ice core was cut with a stainless steel saw and stored in isothermal plastic containers. Additional ice samples were taken for salinity analysis.

Underlying surface waters were collected with a clean container or Niskin bottle. At each station, we measured snow depth, ice thickness, and air and surface water temperature.

1.2.2. Laboratory analyses

On board the ship's laboratory, ice samples for cell counts were slowly melted in surface seawater filtered through 0.2 µm polycarbonate membranes to avoid any osmotic stress to ice protists (Bates & Cota 1986, Garrison & Buck 1986). Melted ice and surface seawater samples were preserved with acidic Lugol solution (Parsons et al. 1984a) for the enumeration of protists ≥ 4 µm. Cells were identified to the lowest possible taxonomic rank and enumerated using an inverted microscope (WILD Heerbrugg) operating with phase contrast optics (Lund et al. 1958). A minimum of 400 cells were counted for each sample except for the first-year ice sample, where only 233 cells were present in the entire settling chamber. We used the following references for protist identification: Thomsen (1988), Hill (1992), Hill et al. (1992), Moestrup (1992), Daugbjerg & Moestrup (1993), Ikävalko & Gradinger (1997), Throndsen (1997), Jensen & Moestrup (1998) and Bérard-Therriault et al. (1999).

At selected stations, samples were also preserved in 1% paraformaldehyde (Marie et al. 2005) and frozen at –80°C for later counts of pico- (0.2–2 µm) and nanoalgae (2–20 µm) using an Epis-Altra flow cytometer (Beckman-Coulter) equipped with a 488 nm laser (15 mW output). Forward light scatter (FSC), side light scatter (SSC), 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 mesh. The flow rate was set to 100 µL min^{-1} and the acquisition time was at least 20 min. Microspheres measuring 1 µm (Fluoresbrite plain YG, Polysciences) were added to each sample as an internal standard. Pico- and nanoalgae were discriminated based on FSC calibration with polystyrene microspheres of known size (Flow cytometry size calibration kit, Invitrogen). Cyanobacteria were discriminated using the orange fluorescence.

Cell abundance determined from ice samples was corrected for added seawater using a dilution factor ranging from 1.3 to 2.4 (Cota & Sullivan 1990). For simplicity, cells enumerated by inverted light microscopy are referred as protists (including both photosynthetic and heterotrophic cells), whereas algal cells counted by flow cytometry are defined as photosynthetic prokaryotes (cyanobacteria) or eukaryotes in the rest of the paper. Salinity of melted ice and surface water samples was determined with a Guildline (Model 8400B) Autosal laboratory salinometer.

1.2.3. Statistical analyses

To group samples having similar taxonomic compositions, a group-average linkage cluster analysis and a non-metric multidimensional scaling (MDS) ordination of a Bray-

Curtis similarity matrix were performed (Clarke & Warwick 2001) using the PRIMER v5 software (Clarke & Gorley 2001). To reduce double zeros in the data matrix, only taxonomic entries that were present in more than two samples were included in the analyses. Before calculating the similarity matrix, the abundance of protists was standardized (i.e., the abundance of each taxonomic entry was divided by the total protist abundance to obtain a relative value) and log (x+1) transformed to reduce the influence of the most dominant taxonomic entries, as suggested by Clarke & Warwick (2001).

An analysis of similarities (one-way ANOSIM) was conducted on the same similarity matrix to test differences in the taxonomic composition between the groups of samples. The pairwise R value obtained gave us an absolute measure of how separated the groups were on a scale of 0 (indistinguishable) to 1 (all similarities within groups are greater than similarities between groups) (Clarke & Warwick 2001). A breakdown of species similarities (SIMPER) was used to determine which species combination led to the resulting groups (Clarke 1993).

A Kolmogorov–Smirnov two-sample test was used to assess differences in the distribution of cells of different sizes between newly formed sea ice and the underlying surface water samples (Sokal & Rohlf 1995). This statistical test was performed with the Statistica 6 software (StatSoft Inc.).

1.3. Results

The fall season in the Canadian Beaufort Sea brings with it a cooling of atmospheric temperatures, which gradually decreased from 1.6°C at the beginning of the sampling

period to –22.8°C at the end, when first-year ice was forming (Table 1). Day length decreased from about 11 h on 30 September to 3 h on 19 November (Table 1). Surface water temperatures remained relatively constant throughout the season, with values ranging from –0.9°C on the first day of sampling to –1.2°C on the last day. Water depth and surface water salinity ranged from 29 m and 16.7, respectively, in the Mackenzie River plume (station 1) to 810 m and 27.8 offshore (station 25). Bulk ice salinity and ice thickness ranged from 5.9 to 9.0 and from 0.5 cm to 31.4 cm, respectively (Table 1). There was no snow accumulation on the ice surface.

The abundance of protists (≥ 4 µm) ranged from 59 to 821 x 10^3 cells L^{-1} in sea ice and from 22 to 256 x 10^3 cells L^{-1} in the underlying surface waters (Table 1). The average number of protists was almost three times more abundant in sea ice (301 x 10^3 cells L^{-1}) than in the underlying surface waters (105 x 10^3 cells L^{-1}). Since cells < 4 µm cannot be accurately counted using inverted microscopy, flow cytometry was used to determine the abundance of small cells (< 4 µm) (Table 1) and the size spectra of algal cells in the range of 0.2 to 20 µm for sea ice and surface water samples (Fig. 2). In both habitats, photosynthetic eukaryotes < 4 µm were the most abundant cells, with concentrations varying from 418 to 3051 x 10^3 cells L^{-1} in sea ice and from 1393 to 5373 x 10^3 cells L^{-1} in the underlying surface waters (Table 1). Picoeukaryotic algal cells (< 2 µm) dominated the underlying surface water assemblages of new ice and nilas (Fig. 2b). Picocyanobacteria were only observed in the new ice (85 x 10^3 cells L^{-1}) and surface waters (250 x 10^3 cells L^{-1}) of station 1. The abundance of protists ≥ 4 µm from new ice and nilas was

positively correlated with ice thickness (Kendall $\tau = 0.97$, $p < 0.01$). There was no other significant correlation between cell abundance and environmental factors.

Compared to the surface waters, the four development stages of newly formed sea ice contained on average half the number of small cells (< 2 μm) but three times more large cells (> 4 μm) (Fig. 2).

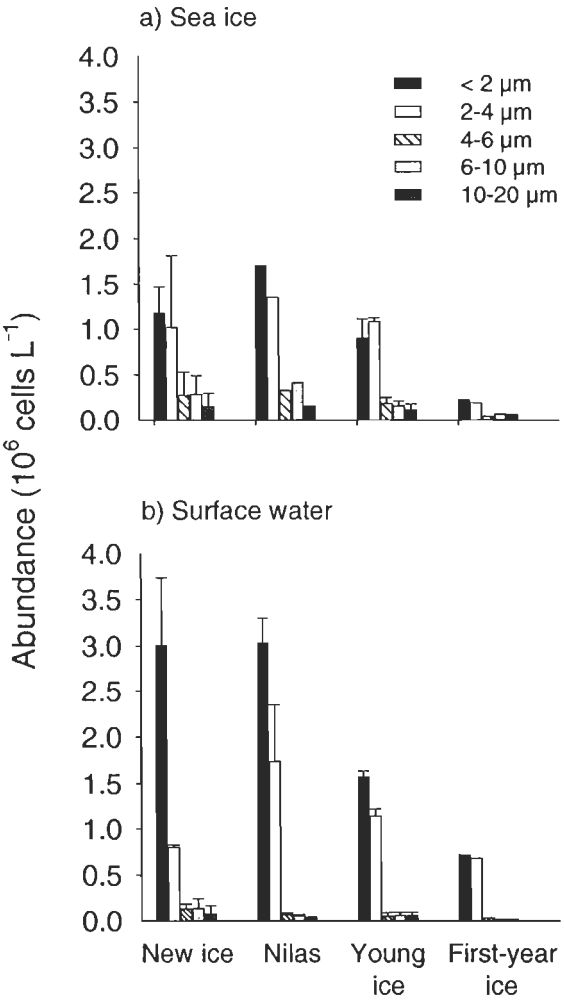

Fig. 2. Abundances of photosynthetic eukaryotes as a function of cell size classes (5 classes ranging from 0.2 to 20 μm) in (a) newly formed sea ice and (b) the underlying surface waters in the Canadian Beaufort Sea in fall 2003. Means and standard deviations are shown for new ice, nilas and young ice (number of stations visited = 2)

Table 1. Physical and biological characteristics in the different stages of newly formed sea ice and the underlying surface waters of the Canadian Beaufort Sea in fall 2003. Cells < 4 μm and ≥ 4 μm were counted by flow cytometry (photosynthetic eukaryotes only) and inverted microscopy, respectively (nd = no data)

Stage of ice development	Date	Station	Day length (h)	Water depth (m)	Air temperature (°C)	Water temperature (°C)	Surface water salinity	Ice salinity	Ice thickness (cm)	Abundance of protists (10^3 cells L^{-1})			
										(< 4 μm)		(≥ 4 μm)	
										Ice	Surface waters	Ice	Surface waters
New ice (NI)	30 Sept.	1	11.3	29	1.6	–0.9	16.7	7.80	3.0	2963	3276	350	256
	8 Oct.	9	10.0	300	–1.0	–1.2	25.9	8.65	2.0	1413	4339	71	132
	12 Oct.	13	9.4	570	–4.0	–0.5	25.4	7.89	0.5	nd	nd	59	22
Nilas (N)	3 Oct.	4	10.8	580	2.3	–1.2	25.8	7.17	3.0	nd	3800	261	77
	26 Oct.	27	6.7	440	–5.4	–1.2	24.6	6.11	7.1	3051	5131	666	92
	28 Oct.	29	6.9	540	–10.0	–1.1	26.7	6.12	8.4	nd	5373	821	142
Young ice (Y)	24 Oct.	25	7.2	810	–5.0	–1.5	27.8	7.01	21.0	1797	2601	82	35
	6 Nov.	38	4.9	372	–5.9	–1.0	27.2	5.99	16.9	2158	2809	317	85
First-year ice (F)	19 Nov.	51	3.1	167	–22.8	–1.2	27.5	9.01	31.4	418	1393	77	104

To seek for differences in the size distribution of cells between newly formed sea ice and the underlying surface waters, Kolmogorov–Smirnov two-sample tests were performed. For protists, the relative abundance of small cells (< 4 μm) was significantly lower ($p < 0.05$) in newly formed sea ice (mean 89%) than in the underlying surface waters (mean 96.5%), whereas the relative abundance of large cells (≥ 4 μm) was significantly higher ($p < 0.05$) in newly formed sea ice (mean 11%) than in the underlying surface waters (mean 3.5%) (Table 2). Photosynthetic eukaryotes showed the same pattern as protists, with a lower relative abundance of small cells (< 2 μm) and a higher relative abundance of large cells (≥ 4 μm) in newly formed sea ice than in the underlying surface waters (Table 2).

Table 2. Mean (SD) relative abundance of protists and photosynthetic eukaryotes of different size classes in newly formed sea ice and the underlying surface waters. Significant differences (> or <) between sea ice and surface waters were tested with Kolmogorov–Smirnov two-sample test (*: $p < 0.05$; **: $p < 0.01$)

Organism	Size class (μm)	Relative abundance (%)		
		Sea ice		Surface waters
Protists	< 4	89.0 (5.6)	<*	96.5 (2.3)
	≥ 4	11.0 (5.6)	>*	3.5 (2.3)
Photosynthetic eukaryotes	< 2	40.9 (8.5)	<*	61.2 (9.5)
	2–4	36.9 (7.4)	=	33.5 (10.5)
	4–6	7.9 (2.0)	>**	2.0 (1.2)
	6–10	8.9 (2.4)	>*	1.9 (1.6)
	10–20	5.4 (2.9)	>*	1.3 (1.3)

Protist assemblages observed in the newly formed sea ice and underlying surface waters were composed of a total of 73 taxa, including 15 centric diatom species, 7 pennate diatoms, 11 dinoflagellates and 16 flagellates (Table 3). All protists observed in sea ice were present in the underlying surface waters, except for *Nitzschia longissima* and Cryptophyceae 11–15 µm (Table 3). On the other hand, some surface water species, such as *Chaetoceros convolutus* f. *trisetosa, Chaetoceros* sp. 6, *Amphidinium sphenoides*, four species of *Gymnodinium*, two species of *Gyrodinium, Protoperidinium bipes, Pterosperma marginatum* and *Meringosphaera mediterranea* were not detected in sea ice (Table 3). There were five times fewer species in thin first-year ice (7 species) than in the other newly formed sea ice (34 species) (Table 3). Based on the combined protist abundance from both habitats (data not shown), the assemblages over the sampling period were mainly represented by unidentified flagellates (32%), centric and pennate diatoms (20%), Prasinophyceae (16%), Prymnesiophyceae (11%), Dinophyceae (11%) and Cryptophyceae (7%).

The relative abundances of the different protist groups in newly formed sea ice and the underlying surface waters are presented in Fig. 3. In new ice, Prasinophyceae and Prymnesiophyceae were numerous compared to other protists in both habitats (Fig. 3a). However, the relative abundance of Prasinophyceae was higher in surface waters. Centric and pennate diatoms and Chlorophyceae were mostly observed in new ice, while the Choanoflagellidea and ciliates were mainly present in surface waters.

Table 3. Occurrence of protists in the different development stages of newly formed sea ice and the underlying surface waters in the Canadian Beaufort Sea in fall 2003

Protists	New ice	Nilas	Young ice	First-year ice	Surface waters
COSCINODISCOPHYCEAE					
Attheya septentrionalis (Østrup) Crawford	X	X	X		X
Attheya / Chaetoceros complex	X	X	X		X
Chaetoceros convolutus/concavicornis	X				X
Chaetoceros convolutus f. *trisetosa* Brunel					X
Chaetoceros cf. *diadema* (Ehrenberg) Gran	X	X			X
Chaetoceros ingolfianus Ostenfeld		X			X
Chaetoceros similis Cleve		X	X		X
Chaetoceros simplex Ostenfeld	X	X	X		X
Chaetoceros subtilis Cleve		X			X
Chaetoceros wighamii Brightwell	X		X	X	X
Chaetoceros sp. 2	X		X		X
Chaetoceros sp. 6					X
Chaetoceros sp. 9	X				X
Chaetoceros spp.		X	X		X
Melosira arctica Dickie	X	X		X	X
Thalassiosira / Porosira complex	X	X	X	X	X
FRAGILARIOPHYCEAE					
Thalassionema nitzschioides (Grunow) Grunow ex Hustedt		X	X		X
BACILLARIOPHYCEAE					
Cylindrotheca closterium (Ehrenberg) Reimann & Lewin	X	X	X	X	X
Entomoneis spp.		X	X	X	X
Fragilariopsis cylindrus (Grunow) Krieger	X	X	X	X	X
Navicula directa Grunow	X		X	X	X
Navicula spp.	X		X		X
Nitzschia frigida Grunow	X			X	X
Nitzschia longissima (Brébisson) Ralfs		X	X		
Pseudo-nitzschia cf. *pseudodelicatissima* (Hasle) Hasle	X	X	X		X
Pennates < 30 µm			X		X
Pennates ≥ 30 µm	X	X		X	X

Table 3 – Continued

DINOPHYCEAE					
Amphidinium cf. *sphenoides* Wülff					X
Amphidinium spp.		X			X
Dinophysis cf. *acuminata* Claparède & Lachmann		X			X
Gymnodinium cf. *galeatum* Larsen					X
Gymnodinium cf. *parvum* Larsen					X
Gymnodinium cf. *pygmaeum* Lebour	X	X	X		X
Gymnodinium sp. 1 *sensu* Bérard-Therriault et al.					X
Gyrodinium cf. *biconicum* Kofoid & Swezy					X
Gyrodinium flagellare Schiller					X
Gymnodinium / Gyrodinium sp. 2					X
Gymnodinium / Gyrodinium ≤ 20 µm		X			X
Heterocapsa arctica Horiguchi		X	X		X
Pronoctiluca pelagica Fabre-Domergue	X	X			X
Protoperidinium bipes (Paulsen) Balech					X
Dinophyceae ≤ 20 µm	X	X	X		X
Thecate dinophyceae spp.	X	X			X
CHLOROPHYCEAE					
Monoraphidium arcuatum (Korshikov) Hindák	X				X
CHOANOFLAGELLIDEA					
Choanoflagellidea spp.	X	X	X		X
CRYPTOPHYCEAE					
Plagioselmis prolonga var. *nordica* Novarino, Lucas & Morrall	X	X			X
Teleaulax amphioxeia (Conrad) Hill	X				X
Cryptophyceae spp.	X	X	X	X	X
Cryptophyceae ≤ 5 µm	X	X			X
Cryptophyceae 6–10 µm	X	X			X
Cryptophyceae 11–15 µm		X	X		
DICTYOCHOPHYCEAE					
Apedinella spinifera (Throndsen) Throndsen		X			X
Dictyocha speculum Ehrenberg	X	X	X		X
EUGLENOPHYCEAE					
Euglenophyceae spp.	X	X			X

Table 3 – Continued

PRASINOPHYCEAE					
Pterosperma marginatum Gaarder					X
Pterosperma undulatum Ostenfeld			X		X
Pyramimonas nansenii Braarud	X	X	X	X	X
Pyramimonas virginica Pennick	X	X			X
Pyramimonas spp.	X	X			X
PRYMNESIOPHYCEAE					
Prymnesiophyceae sp. 1	X	X	X		X
Prymnesiophyceae spp.	X	X			X
UNIDENTIFIED FLAGELLATES					
Flagellate sp. 1	X				X
Flagellate sp. 2		X			X
Flagellate sp. 3	X	X	X		X
Flagellate sp. 4	X	X			X
Nanoflagellates ≤ 5 µm	X	X	X	X	X
Nanoflagellates 6–10 µm	X	X	X	X	X
Flagellates 11–20 µm	X	X	X	X	X
CILIATES					
Mesodinium rubrum Leegaard	X	X			X
Strombidium spp.		X	X		X
Unidentified ciliates	X	X		X	X
HETEROTROPHIC ORGANISMS					
Meringosphaera mediterranea Lohmann					X
Telonema spp.				X	X
SPORES					
Chaetoceros cf. *contortus* Schütt		X	X	X	X
Chaetoceros furcillatus Bailey	X	X	X		X
Chaetoceros ingolfianus Ostenfeld	X	X	X		X
Melosira arctica Dickie	X	X			X
Dinoflagellate cysts	X	X	X		X
Unidentified spores	X	X	X		X
Number of species (excluding spores)	**25**	**26**	**18**	**7**	**45**
Number of taxa (excluding spores)	**43**	**48**	**32**	**16**	**71**

In nilas, the relative abundance of protists was more or less identical in both habitats. The exceptions were the Prymnesiophyceae, which mostly occurred in newly formed sea ice, and the Choanoflagellidea, which were mainly present in surface waters (Fig. 3b). Unidentified flagellated cells made up a large part of the protist assemblages in both habitats; however, they showed higher abundance in surface waters. Diatoms and Dinophyceae were slightly more abundant in nilas than in surface waters.

In young ice, unidentified flagellates and pennate diatoms were numerous in both habitats (Fig. 3c). However, unidentified flagellates were more abundant in surface waters than in young ice whereas the opposite was observed for pennate diatoms. Cryptophyceae, Prasinophyceae, Prymnesiophyceae and spores were mostly observed in young ice, while Choanoflagellidea and other heterotrophic groups were mainly present in surface waters. Dinophyceae were slightly more abundant in surface waters than in young ice.

In the single sample of thin first-year ice, unidentified flagellates strongly dominated the protist assemblages of both habitats, being more abundant in surface waters (Fig. 3d). Spores and other groups of protists such as Cryptophyceae, centric and pennate diatoms, ciliates, and Prasinophyceae all characterized the thin first-year ice, while Dinophyceae and Choanoflagellidea, which were absent from the bottom ice, occurred mostly in surface waters. Pennate diatoms were much more abundant in the bottom layers of young ice and thin first-year ice than in surface waters, and they outnumbered centric diatoms.

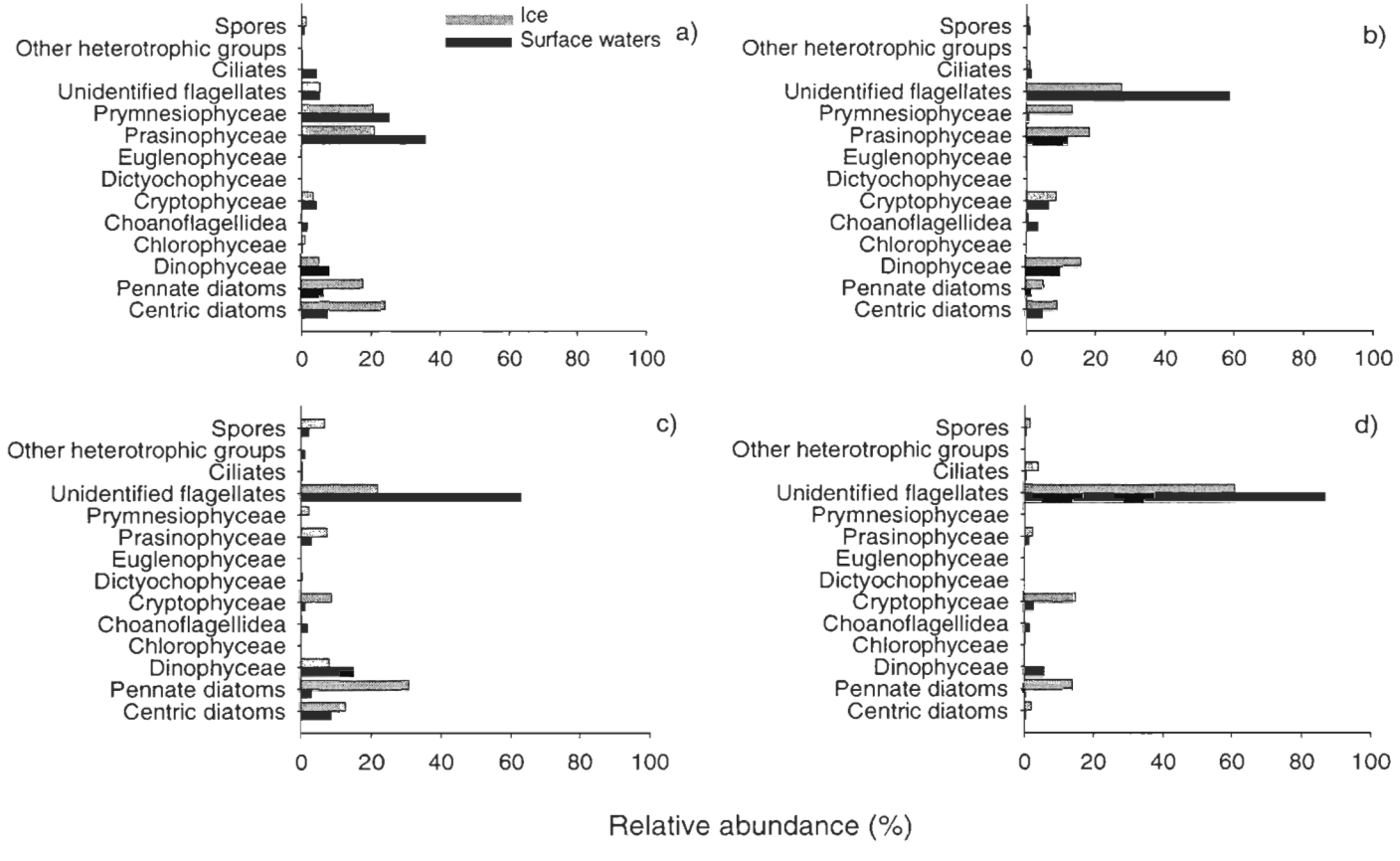

Fig. 3. Relative abundance of protist groups and spores in newly formed sea ice from four different ice types and the underlying surface waters for (a) new ice, (b) nilas, (c) young ice and (d) thin first-year ice in the Canadian Beaufort Sea in fall 2003

The cluster analysis based on the similarity matrix identified four groups of taxonomically similar protists in the Canadian Beaufort Sea. The graphic representation of the clusters on a two-dimensional MDS plot showed the relative distances between the four groups (Fig. 4). According to the global one-way ANOSIM test, there were significant differences between the four groups (global $R = 0.884$, $p \leq 0.001$). A pairwise test of the one-way ANOSIM indicated that Groups II, III and IV were significantly different ($p \leq 0.05$). Group I consisted of only one young ice sample (station 25); Group II was characterized by mixed samples of new ice and their underlying surface waters from stations 1 and 13. Group III contained exclusively surface water samples from stations 4, 9, 25, 27, 29, 38 and 51, while Group IV consisted of mixed types of newly formed ice samples from stations 4, 9, 27, 29 38, and 51 (Fig. 4). The main protists contributing to each group were as follows: Group I: *Nitzschia longissima*, *Pseudo-nitzschia* cf. *pseudodelicatissima* and *Cylindrotheca closterium,* which are all planktonic pennate diatoms from a single sample of young ice collected at the deepest station of the continental slope (810 m; Table 1); Group II: *Pyramimonas nansenii*, Prymnesiophyceae sp. 1 and *Thalassiosira/Porosira* complex; Group III: nanoflagellates ≤ 5 µm, which characterize surface waters; and Group IV: nanoflagellates ≤ 10 µm and *Pyramimonas nansenii,* which characterize only ice samples. More details of the group compositions are shown in Table 4.

Table 4. Breakdown of similarities within groups into contributions from each taxonomic entity (Clarke 1993). Protists are ordered by decreasing average contribution (Cont. %) to a total of more than 70%

Group I Average similarity: 100 (only one sample)	Cont. (%)
Nitzschia longissima	30
Pseudo-nitzschia cf. *pseudodelicatissima*	17
Cylindrotheca closterium	9
Nitzschia frigida	6
Chaetoceros wighamii	4
Gymnodinium cf. *pygmaeum*	3

Group II Average similarity: 28	Cont. (%)
Pyramimonas nansenii	28
Prymnesiophyceae sp. 1	22
Thalassiosira/Porosira complex	15
Pseudo-nitzschia cf. *pseudodelicatissima*	7

Group III Average similarity: 45	Cont. (%)
Nanoflagellates ≤ 5 µm	62
Nanoflagellates 6–10 µm	7
Flagellate sp. 1	7
Choanoflagellidea spp.	4
Gymnodinium / Gyrodinium < 20 µm	3

Group IV Average similarity: 37	Cont. (%)
Nanoflagellates 6–10 µm	27
Nanoflagellates ≤ 5 µm	26
Pyramimonas nansenii	10
Fragilariopsis cylindrus	5

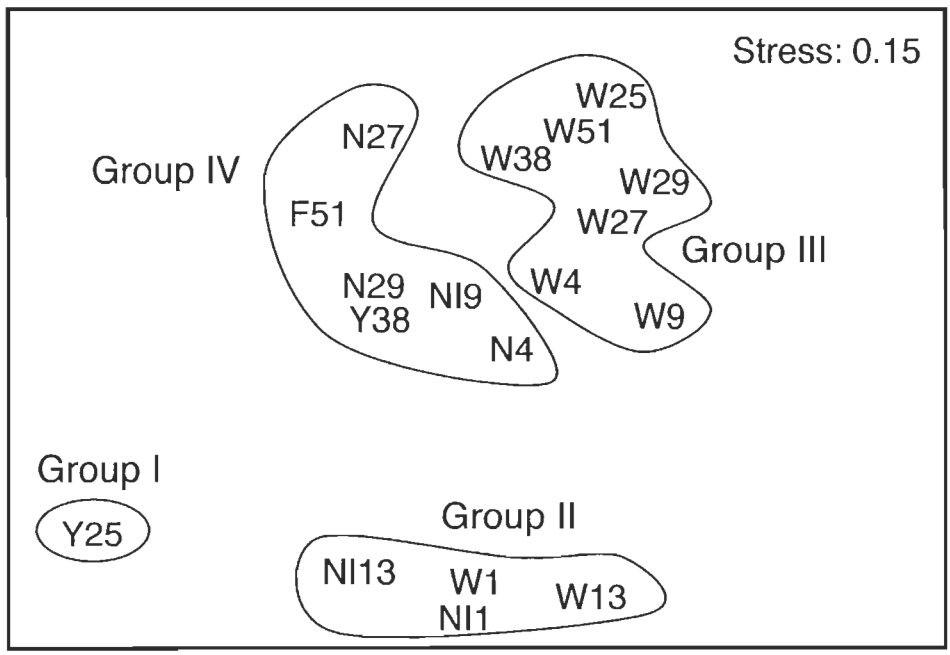

Fig. 4. Two-dimensional non-metric multidimensional scaling (MDS) of 18 protist samples collected at nine stations in the Canadian Beaufort Sea. The four groups of samples with taxonomically similar protists assessed with the group-average clustering are superposed to the MDS. The similarity matrix was created on the log (x+1) transformed relative abundance of protists. Each sample is identified by a letter (NI: new ice; N: nilas; Y: young ice; F: thin first-year ice; W: underlying surface waters) followed by the station number

Spores composed a minor fraction of all analyzed samples and represented only 1.8% of the combined protist assemblage, with abundances ranging from 1.2 to 13.6 x 10^3 cells L^{-1} in sea ice and from 0.5 to 1.4 x 10^3 cells L^{-1} in the underlying surface waters. Four species forming spores belonging to *Chaetoceros* and *Melosira* were identified, and we also recognized some dinoflagellate cysts and a group of unidentified spores (Fig. 5). Spores of *Chaetoceros* cf. *contortus* and *Melosira arctica* were mainly represented in the underlying surface waters while spores of *Chaetoceros ingolfianus* and unknown spores were usually recorded in newly formed sea ice. Thin first-year ice and its underlying surface waters had

only one species of spore, *Chaetoceros* cf. *contortus*, while other samples were characterized by a mixed spore composition (Fig. 5).

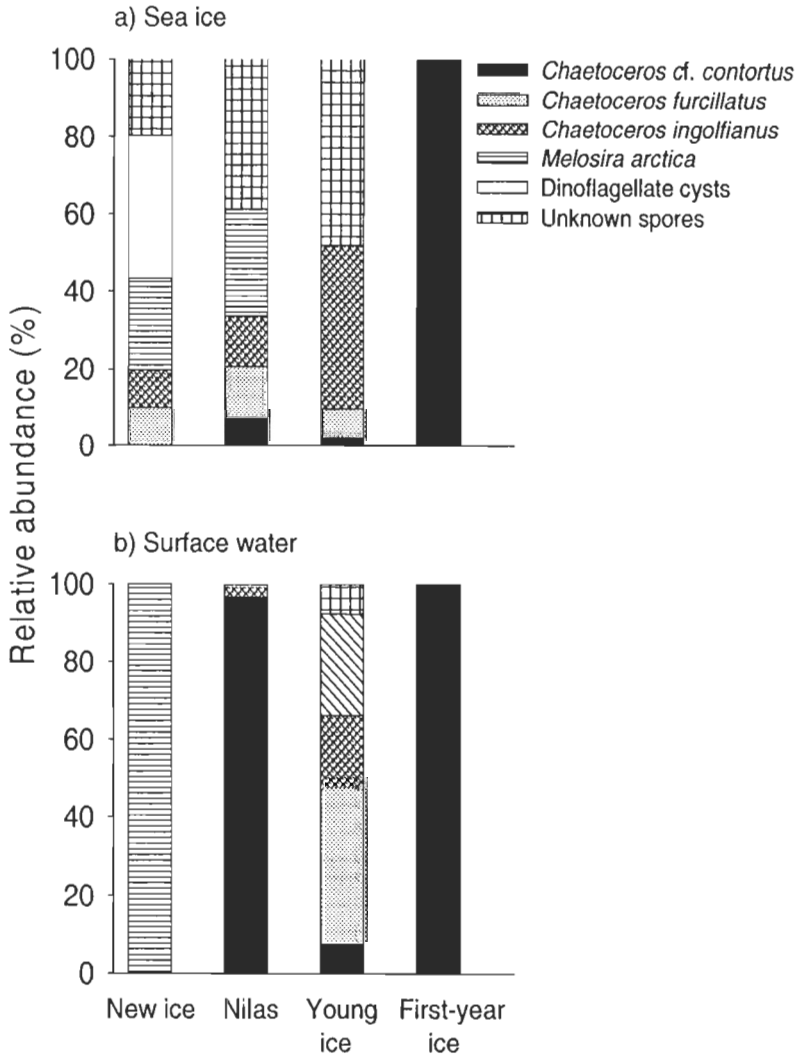

Fig. 5. Cumulative abundance of centric diatom spores (four species), dinoflagellate cysts and unknown spores in (a) newly formed sea ice and (b) the underlying surface waters in the Canadian Beaufort Sea in fall 2003

1.4. Discussion

In the Canadian Beaufort Sea, photosynthetic and heterotrophic protists are incorporated into sea ice during its formation in the fall. Similar results have been reported elsewhere in the Arctic (Stefansson Sound, Beaufort Sea: Horner & Schrader 1982; Frobisher Bay: Hsiao 1992; Greenland Sea: Gradinger & Ikävalko 1998; Laptev Sea: Tuschling et al. 2000) and in Antarctica (Weddell Sea: Garrison et al. 1983, Ross Sea: Garrison et al. 2003). Our paper describes for the first time changes in the taxonomic composition of protists during four development stages of sea ice in the western Arctic. In the next sections, we will discuss the temporal change in taxonomic composition of large cells, their selective incorporation into sea ice, the numerical and ecological importance of small cells, and the survival strategies of protists in newly formed sea ice of the Canadian Beaufort Sea.

1.4.1. Temporal change in the taxonomic composition of large cells

From September to November 2003, 73 taxa and 46 species of protists were recorded in newly formed sea ice and surface waters of the Canadian Beaufort Sea (Table 3). Similar numbers (81 taxa and 71 species) were reported during the fall freeze-up in the Laptev Sea (Tuschling et al. 2000). In newly formed sea ice, we observed two times more protist taxa (61) and species (35) than in the Laptev Sea (32 taxa and 25 species: Tuschling et al. 2000) and Stefansson Sound in November (24 taxa and 18 species: Horner & Schrader 1982).

During our study, the assemblage of the newly formed sea ice was composed of flagellates, diatoms and dinoflagellates. Similar taxonomic compositions were observed in the Laptev Sea (Tuschling et al. 2000) and Greenland Sea (Gradinger & Ikävalko 1998) in early fall. However, the sea-ice assemblage was numerically dominated by pennate diatoms in Stefansson Sound (Horner & Schrader 1982). In the surface waters, we found that unidentified flagellates were the most common group of protists. Similarly, the surface water assemblage was dominated by unidentified flagellates < 6 μm in Stefansson Sound (Horner & Schrader 1982) and by pico- and nanoflagellates in Greenland Sea (Gradinger & Ikävalko 1998).

In the present study, almost all species observed in surface waters were present in the newly formed sea ice while only a few (e.g., *Chaetoceros convolutus* f. *trisetosa*, *Chaetoceros* sp. 6, *Pterosperma marginatum*, *Meringosphaera mediterranea* and eight species of Dinophyceae) were found exclusively in the water column (Table 3). In the Laptev Sea, in contrast, few algal species (i.e., *Attheya septentrionalis, Chaetoceros wighamii, Cylindrotheca closterium, Navicula directa, Nitzschia frigida*, thecate dinoflagellates and unidentified flagellates) were found in both habitats and two-thirds of those reported in sea ice (eleven diatom species, four dinoflagellates and one chlorophyte) were not observed in the water column (Tuschling et al. 2000). The shallow waters of the Laptev Sea (ca. 46 m), compared to the greater depths of the Canadian Beaufort Sea (up to 810 m, Table 1), seem to have favored the entrapment of benthic species in the newly formed sea ice.

In the early ice formation stage (i.e., new ice) in the Canadian Beaufort Sea, protist abundance and composition were generally very similar to those observed in the underlying surface waters; they were mainly characterized by a mixed assemblage of prasinophytes, prymnesiophytes, diatoms and dinoflagellates. Similarly, in the Weddell Sea (Antarctica), the taxonomic composition was essentially identical between new sea ice and the underlying surface waters in early fall (Garrison et al. 1983, Garrison & Buck 1985). During the initial stages of ice formation, planktonic protists were probably physically concentrated within sea ice by the scavenging of frazil ice crystals rising to the surface (Ackley 1982, Garrison et al. 1983, 1989). In this process, protists adhere to individual ice crystals that develop in the water column up to a depth of 25–30 m and subsequently accumulate as grease ice at the sea surface (Weeks & Ackley 1982, Garrison et al. 1983). Alternatively, protists may be concentrated by wave fields pumping water through the new ice, causing cells to become attached to, or trapped between, ice crystals (Ackley et al. 1987, Weissenberger & Grossmann 1998). These mechanisms may explain the random, non-selective incorporation of protists into new sea ice in both polar environments.

As the season progressed, we observed a lower number of protist species in young ice (18 species) and thin first-year ice (7 species) than the more diverse assemblages initially captured in new ice (25 species) and nilas (26 species). The two older stages of ice were characterized by large nanoflagellates (6–10 μm) and pennate diatoms while the underlying surface waters consisted mainly of small nanoflagellates (≤ 5 μm) and dinoflagellates (Table 4). The early stages of sea ice are likely to have significant fraction of frazil ice, whereas the lower few centimeters of older ice could be entirely columnar ice.

In columnar ice, the main processes responsible for the incorporation of protists into the sea ice (i.e., scavenging and the wave fields) do not take place (Spindler 1990). The change in the taxonomic composition between sea ice and surface waters and the decrease in the number of sea-ice protists as the season progresses may be explained by a combination of factors, such as (1) the restricted space availability in the brine channels, (2) mechanical damage of cells (Gleitz & Thomas 1993, Grossmann & Gleitz 1993), (3) different survival rates among the protists incorporated into sea ice, and (4) species succession (Lizotte 2003).

Another point of interest is the occurrence of the potentially toxic diatom *Pseudo-nitzschia* cf. *pseudodelicatissima* in newly formed sea ice (on average 5.6 x 10^3 cells L^{-1}) and the underlying surface waters (10 x 10^3 cells L^{-1}). Species belonging to the genus *Pseudo-nitzschia* H. Peragallo are known to produce domoic acid, a neurotoxic amino acid responsible for Amnesic Shellfish Poisoning (ASP) in humans (Bates et al. 1998) and for extensive seabird (Work et al. 1993) and marine mammal (Scholin et al. 2000) deaths in temperate coastal waters. In the Arctic, this species is common in surface waters (e.g., Barents Sea, Svalbard area, Denmark Strait, west coast of Greenland, Northeast Water polynya, Hudson Strait, Barrow Strait and Resolute Bay: Hasle 1965, Booth & Horner 1997, von Quillfeldt 2000) and in sea ice (e.g., Northeast Water polynya, Narwhal Island in the Beaufort Sea, east Siberian Sea and central Arctic Ocean: Horner & Schrader 1982, Okolodkov 1993, Booth & Horner 1997, von Quillfeldt 1997). Further studies are needed to determine the dynamics of these potentially harmful algae in the changing Arctic environment.

1.4.2. Selective incorporation of large cells in sea ice

The average abundance of protists ≥ 4 µm was almost three times higher in newly formed sea ice than in the underlying surface waters in the Canadian Beaufort Sea. In addition, photosynthetic eukaryotes showed the same distribution as protists, with a lower relative abundance of small cells (< 2 µm) and a higher relative abundance of large cells (≥ 4 µm) in newly formed sea ice than in the underlying surface waters (Table 2). This indicates a selective incorporation of larger cells, mainly pennate diatoms (Fig. 2), in newly formed sea ice. The selective incorporation of large protists in sea ice has also been demonstrated using an enrichment index for diatoms and autotrophic and heterotrophic flagellated cells > 10 µm in newly formed sea ice off Greenland (Gradinger & Ikävalko 1998). Using the same index as Gradinger & Ikävalko (1998), Riedel et al. (2007b) showed that the newly formed sea ice of the Canadian Beaufort Sea was significantly enriched in large photosynthetic cells (≥ 5 µm) in the fall. They proposed that the clear selection for the large photosynthetic cells is likely due to cell size and the presence of exopolymeric substances, which greatly enhance the stickiness of cell surfaces.

Some species that were incorporated in the newly formed sea ice in the fall of 2003 were present in the bottom landfast ice in Franklin Bay (Fig. 1) in the late winter and spring of 2004. These species were mainly pennate diatoms (*Cylindrotheca closterium, Entomoneis* spp., *Fragilariopsis cylindrus, Navicula directa, Nitzschia frigida, N. longissima* and *Pseudo-nitzschia* cf. *pseudodelicatissima*), Dinophyceae (*Amphidinium* cf. *sphenoides*, *Dinophysis* cf. *acuminata, Heterocapsa arctica*) and Cryptophyceae

(*Plagioselmis prolonga*) (Różańska, unpublished data). These species are commonly observed at the bottom surface of the sea ice in many regions of the Arctic during the spring and summer (Hsiao 1980, Horner & Schrader 1982, Poulin 1990a, Okolodkow 1992, 1993, Booth & Horner 1997). The only centric diatoms present in the sea ice during both fall and spring were *Attheya septentrionalis, Melosira arctica* and the *Thalassiosira/Porosira* complex. These taxa are frequently observed in Arctic and subarctic sea ice and can dominate the assemblages in the bottom of sea ice (*Thalassiosira/Porosira*: Booth & Horner 1997, Lee et al. 2001, Booth et al. 2002, Lovejoy et al. 2002), at the ice–water interface (*M. arctica*: Booth & Horner 1997, Gosselin et al. 1997) or in various habitats, including sea ice, under-ice and the open water column (*A. septentrionalis*: Booth & Horner 1997) in spring or early summer. These results indicate that some algal species can overwinter in sea ice without being structurally or physiologically damaged during ice growth.

1.4.3. Ecological importance of small cells

Recent studies conducted in the Arctic Ocean and adjacent seas have shown that algal abundance, biomass and production in sea ice and surface waters can be dominated by pico- (0.2–2 μm) and nanoalgal (2–20 μm) cells at different periods of the year (e.g., Gosselin et al. 1997, Lovejoy et al. 2002, 2006, Sherr et al. 2003). These small cells are known to be an active component of the microbial food web within the sea ice (Riedel et al. 2007a, 2008) and in the upper water column (Sherr et al. 2003), despite low ambient temperatures.

Small-sized algae (< 4 μm) were the most abundant cells in sea ice and the underlying surface waters of the Canadian Beaufort Sea in the fall; however, they were less numerous in sea ice (418–3051 x 10^3 cells L^{-1}) than in surface waters (1393–5373 x 10^3 cells L^{-1}). Not et al. (2005) reported photosynthetic picoeukaryote abundances almost twice as high in the Barents Sea in late summer (2600–10,200 x 10^3 cells L^{-1}). However, we were unable to identify the small photosynthetic eukaryotes. Pigment analyses on samples collected in the same area revealed the recurrent predominance of eukaryotic picoalgae from the Prasinophyceae, a class of green algae, in the surface waters throughout the year (Lovejoy et al. 2007). Since the most abundant autotrophic cells were *Micromonas*-like picoprasinophytes, it is possible that this taxon also dominated in our samples.

Flow cytometry analyses allowed us to distinguish between photosynthetic eukaryotes and prokaryotes (cyanobacteria) based on the presence of the phycoerythrin pigment. In this study, all enumerated algae were eukaryotes except at the brackish water (salinity of 16.2) station 1 located in the Mackenzie River plume (Fig. 1). At this station, photosynthetic prokaryotic cells ≤ 2 μm made up 0.6% and 0.8% of all cells < 20 μm in new ice and underlying surface waters, respectively. Their average abundance was three times higher in the underlying surface waters (250 x 10^3 cells L^{-1}) than in sea ice (85 x 10^3 cells L^{-1}). To our knowledge, this is the first report of the occurrence of photosynthetic prokaryotes in the sea ice of the western Arctic Ocean. The surface abundance of a *Synechococcus*-like picocyanobacteria was 3503–6713 x 10^3 cells L^{-1} in the Mackenzie River and an order of magnitude lower (225–560 x 10^3 cells L^{-1}) at offshore stations near the Arctic pack ice in fall (Waleron et al. 2007). According to Waleron et al. (2007), the

picocyanobacteria population observed in the Canadian Arctic Ocean is largely derived from allochthonous inputs of microbiota from the Mackenzie River and other nearby inflows. Hence, picocyanobacteria are probably not a permanent resident of sea ice. However, our results clearly show that small photosynthetic eukaryotic cells $< 4\ \mu m$ dominate protist assemblages in both newly formed sea ice and the underlying surface waters of the Arctic Ocean during the fall.

1.4.4. Survival strategies of protists in sea ice

Newly formed sea ice provides a unique habitat for planktonic organisms, albeit one exerting drastic abiotic changes (Gleitz & Thomas 1992). At the end of the summer growth season, some phytoplankton species can survive entrapment in newly formed sea ice by continuing to be metabolically active (Gleitz & Thomas 1992, Gradinger & Ikävalko 1998), while others may form resting spores or cysts, using the ice as an overwintering platform (Garrison & Buck 1985). Cyst formation is well-known in Antarctic regions (Garrison & Buck 1989, Buck et al. 1992, Stoecker et al. 1992, 1997, Montresor et al. 1999), but records from the Arctic are very scarce (Ikävalko & Gradinger 1997, Okolodkov 1998).

In the fall, the protist assemblages trapped in newly formed sea ice were still active, as shown by their active uptake of dissolved silicon and nitrate and production of ammonium (Riedel et al. 2007a). In addition to living cells, the newly formed sea-ice assemblage was composed of diatom resting spores and dinoflagellate cysts. These accounted for only a very small proportion (1.8%) of the total protist assemblages, and the

majority belonged to different *Chaetoceros* species. Similar results were obtained by Zhang et al. (2003) from dark survival experiments conducted over a five-month period on ice algae from the autumnal community off Greenland. These authors observed spore/cyst formation in less than 4.5% of all cells, and only for *Chaetoceros* spp. and dinoflagellates. We can conclude that the formation of spores and cysts is a minor survival strategy for Arctic sea-ice protists.

1.5. Conclusion

The incorporation of protists in newly formed sea ice in the Canadian Beaufort Sea begins during the first stages of ice formation in autumn. The abundance and taxonomic composition of protists changed throughout the season. Small algae (< 4 µm) were the most abundant cells in the newly formed sea ice and underlying surface waters, but they were less abundant in sea ice than in surface waters. In contrast, large algae (≥ 4 µm) were more abundant in sea ice than in surface waters. These results suggest a selective incorporation of large protists in the sea ice. In new ice, the taxonomic composition was very similar to that observed in the underlying water column, and we observed a random, non-selective incorporation of protists, probably due to scavenging or harvesting of the large protists by frazil ice crystals that form in the water column and rise to the surface. However, as the ice develops to form nilas, young ice and thin first-year ice, the taxonomic composition in the sea ice becomes markedly different from that in the underlying water column. The decrease in the number of protist taxa within the sea ice as the season progresses may be explained by a restricted space availability in the brine channels, mechanical damage of cells,

different survival rates among protist taxa incorporated in sea ice and species succession. Finally, diatom resting spores and dinoflagellate cysts were generally more abundant in sea ice than in surface waters, but they accounted for only a small proportion of the total protist abundance. Hence, spore and cyst formation is a minor survival strategy for arctic sea-ice protists.

CHAPITRE II

INFLUENCE OF ENVIRONMENTAL FACTORS ON THE DEVELOPMENT OF BOTTOM ICE PROTIST COMMUNITIES DURING THE WINTER–SPRING TRANSITION

RÉSUMÉ

Les changements saisonniers de l'abondance et de la composition taxonomique des diatomées, des flagellés et des dinoflagellés présents dans le niveau inférieur de la glace de mer ont été déterminés dans la banquise côtière de première année de la baie Franklin (secteur canadien de la mer de Beaufort) entre le 24 février et le 20 juin 2004. Chaque jour d'échantillonnage, des protistes présents dans le niveau inférieur de la glace de mer ont été prélevés à des endroits où la couverture de neige était épaisse (> 10 cm) et mince (< 10 cm). L'accumulation de protistes a commencé dès la fin février. Les taux de croissance nets observés chez les diatomées et les nanoflagellés étaient significativement plus élevés avant (24 février–25 mars) que pendant (3 avril–23 mai) la période de floraison sous une courveture de neige mince. Toutefois, aucune différence significative n'a été détectée sous une couverture de neige épaisse. En revanche, les taux de croissance nets observés chez les dinoflagellés ont été relativement constants avant et pendant la période de floraison sous les deux couvertures de neige. Ces résultats suggèrent que les diatomées, les flagellés et les dinoflagellés répondent différemment aux changements du régime lumineux pendant la période de croissance. Le déclin de la communauté de protistes après la période de floraison est expliqué par une combinaison de facteurs, dont une carence en azote et les processus de fonte. Avant la floraison, les cellules flagellées, qui étaient vraisemblablement hétérotrophes, prédominaient sous la couverture de neige épaisse, tandis que les protistes autotrophes, surtout les diatomées solitaires, prévalaient sous la neige mince. Durant la période de floraison, les diatomées coloniales comme *Nitzschia frigida*, *N. promare*, *Navicula* sp. 6, *N. pelagica* et *Fragilariopsis cylindrus* étaient les plus abondantes du niveau inférieur de la glace de mer, indépendamment de l'épaisseur de la neige, bien qu'elles aient été plus nombreuses sous la couverture neigeuse épaisse que sous la mince. La diatomée *Nitzschia frigida*, qui vit en colonies arborescentes, a été la microalgue la plus

abondante du niveau inférieur de la glace de mer tout au long de la saison. Elle peut être considérée comme une espèce endémique clé de la banquise côtière des régions circumarctiques. Pendant toute la période suivant la floraison, l'abondance des diatomées coloniales et solitaires a diminué plus rapidement que celle des nanoflagellés, ce qui semble indiquer que ces derniers, sans doute des hétérotrophes, sont mieux adaptés aux conditions de fonte de la glace de mer. Enfin, nos résultats révèlent que la disponibilité de l'azote dans les eaux de surface limite l'accumulation de la biomasse algale dans le niveau inférieur de la glace de mer durant la floraison des algues de glace au printemps.

ABSTRACT

Seasonal changes in the abundance and taxonomic composition of bottom ice protists (i.e., diatoms, flagellates and dinoflagellates) were assessed in the first-year landfast ice of Franklin Bay (Canadian Beaufort Sea) from 24 February to 20 June 2004. On each sampling day, bottom sea-ice protists were collected at sites of high (>10 cm) and low (<10 cm) snow cover. The accumulation of protists started as early as the end of February. The net observed growth rates of diatoms and nanoflagellates were significantly higher during the pre-bloom (24 February–25 March) than the bloom (ca. 3 April–23 May) period under the low snow cover sites but not statistically different under high snow cover sites. In contrast, dinoflagellates showed relatively constant net observed growth rate before and during the bloom period under both snow covers. These results indicate that the three protist groups responded differently to changes in the light regime during the growth period. The decline of the protist community after the bloom period was related to a combination of factors including nitrogen deficiency and melting processes. Prior to the bloom, flagellated cells, which were presumably heterotrophic, dominated numerically under high snow cover, whereas autotrophic protists, especially solitary diatoms, prevailed under low snow cover. During the bloom period, colonial diatoms such as *Nitzschia frigida*, *N. promare*, *Navicula* sp. 6, *N. pelagica* and *Fragilariopsis cylindrus* dominated the bottom ice community irrespective of snow depth, although abundances were higher under low snow cover. The arborescent colonial *Nitzschia frigida* was the most abundant bottom ice algal diatom throughout the entire season. *Nitzschia frigida* can be considered a key species of landfast ice across circumarctic regions. During the post-bloom period, colonial and solitary diatom numbers declined more rapidly than nanoflagellates, suggesting that nanoflagellates, presumably heterotrophic, were better adapted to melting sea-ice conditions. Finally, our results demonstrated that the availability of nitrate in the surface water limits the accumulation of algal biomass in the bottom horizon of Arctic landfast ice during the vernal growth season.

2.1. Introduction

Sea ice plays a significant role in the biology and ecology of polar marine ecosystems, supporting a productive community of ice algae (e.g., Horner 1985a, Gosselin et al. 1997) and a high diversity of heterotrophic organisms ranging from bacteria (Laurion et al. 1995, Riedel et al. 2007a, 2008) to metazoans (reviewed by Schnack-Schiel 2003). The sea-ice cover in the Arctic Ocean affects the amount of heat and gas exchange between the atmosphere and the ocean surface (Gosink et al. 1976, Delille et al. 2007). Ice thickness and snow cover strongly influence the transmission of photosynthetically active radiation (PAR) through the sea ice, therefore affecting the growth, production and biomass of the bottom ice algal communities (Arrigo 2003, Mundy et al. 2005). It has been estimated that ice algae contribute up to ca. 57% of the total primary production in the central Arctic Ocean (Gosselin et al. 1997), and between 3 and 25% in Arctic shelf regions (Legendre et al. 1992). However, considering the reduction in sea-ice thickness and extent over the Arctic Ocean reported over the last ten years (Comiso et al. 2008), the contribution of ice algae to total primary production may have changed.

Ice algal communities play an important role in polar ecosystems and have a major influence on various trophic levels of Arctic marine food webs (e.g., Runge & Ingram 1988, Vézina et al. 1997, Fortier et al. 2002). They serve as a main food source for sympagic (ice-associated) and pelagic herbivorous protists (Sime-Ngando et al. 1997, Michel et al. 2002) and metazoans (Runge & Ingram 1988, Tremblay et al. 1989, Nozais et al. 2001), contributing significantly to carbon cycling in Arctic regions (Michel et al. 2006).

The incorporation of protists in sea ice starts during fall at the time of ice formation (Gradinger & Ikävalko 1998, Riedel et al. 2006, Różańska et al. 2008). The development of these cells in the bottom ice is very slow in winter but their numbers increase exponentially in early spring with increasing solar irradiance and air temperature, and decreasing brine salinity to reach a maximum prior to the melt period, and then decline rapidly in late spring or early summer with ice melting (Hsiao 1980, Horner 1985a, Lavoie et al. 2005).

Historically, taxonomic studies have emphasized bottom ice diatoms, neglecting the identification and enumeration of flagellated cells (e.g., Hsiao 1980, Horner & Schrader 1982, Booth 1984, Horner 1985b). This may be partly explained by the loss of delicate flagellated cells due to osmotic stress during ice sample thawing (Garrison & Buck 1986). To prevent cell lysis, Garrison & Buck (1986) recommended melting ice core samples in filtered seawater. Since the introduction of this procedure, it has been shown that the total protist carbon biomass in the bottom horizon of Arctic sea ice is dominated by phototrophs (Riedel et al. 2007a, 2008), whereas the total dinoflagellate carbon biomass is dominated by heterotrophs (Gosselin et al. 1997, Michel et al. 2002). In newly formed sea ice, phototrophic flagellates were generally more abundant than heterotrophic ones (Gradinger & Ikävalko 1998, Riedel et al. 2007b).

Temporal variations in the abundance of bottom ice diatoms and other protists were studied in many Arctic regions (Chukchi Sea: Clasby et al. 1976; Alaskan Beaufort Sea: Horner 1976, Horner & Schrader 1982; Barrow Strait: Smith et al. 1988, Welch & Bergmann 1989; Frobisher Bay: Hsiao 1980, 1992, Grainger & Hsiao 1982; Hudson Bay: Poulin et al. 1983, Gosselin et al. 1985, 1990; Canada Basin: Melnikov et al. 2002);

however, few studies have addressed the influence of environmental factors on the taxonomic composition of the bottom ice protist community during the pre-bloom, bloom and post-bloom periods (but see Horner & Schrader 1982, Poulin et al. 1983).

The overwintering of the CCGS *Amundsen* during the Canadian Arctic Shelf Exchange Study (CASES) expedition in the Canadian Beaufort Sea provided a unique opportunity to observe the seasonal variations of bottom landfast ice protist communities in relation to changes in environmental conditions. The aim of this study was to examine seasonal changes in abundance and taxonomic composition of bottom ice diatoms, flagellates and dinoflagellates under two contrasting snow covers from mid-winter to late spring. This investigation provides key insights for comparison with previous data collected three decades ago in the Canadian (Hsiao 1980) and Alaskan (Horner & Schrader 1982) Beaufort Sea.

2.2. Materials and methods

2.2.1. Sampling and laboratory analyses

Sampling was conducted on 27 occasions from 24 February to 20 June 2004 at a field station located on first-year landfast ice in Franklin Bay (70°04' N, 126°26' W; water depth ca. 250 m), southeastern Beaufort Sea, Northwest Territories, Canada (Fig. 1). The station was located 1.5 km northeast of the overwintering site of the research icebreaker CCGS *Amundsen* as part of CASES. In Franklin Bay, landfast ice begins to grow by mid-November (Barber & Hanesiak 2004), reaching a thickness of ca. 2 m by early May (Riedel

et al. 2006). Melting of the sea ice usually starts toward the end of April or in early May and ice breakup occurs in early June (Barber & Hanesiak 2004).

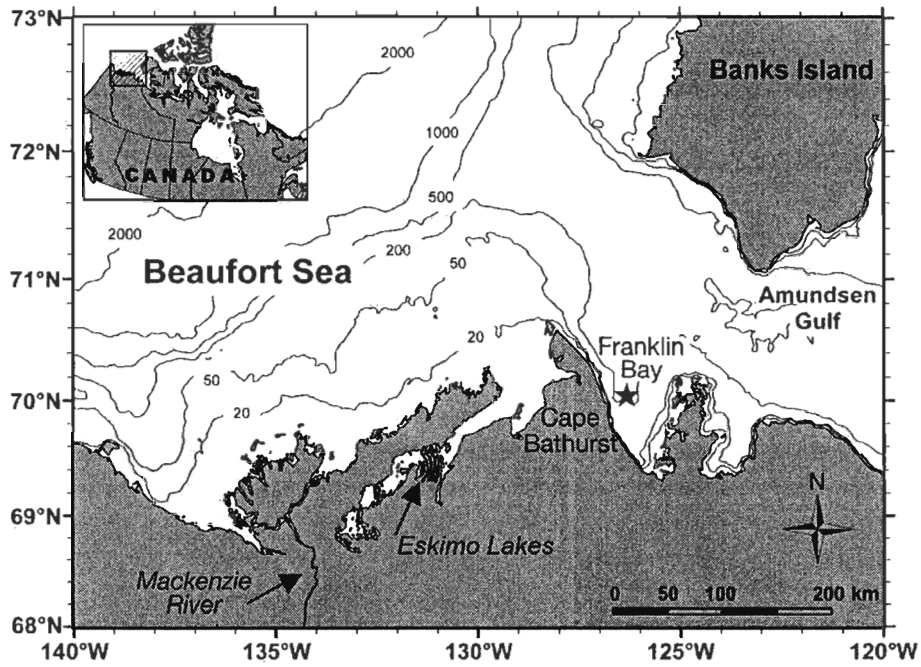

Fig. 1. Map of the Canadian Beaufort Sea showing the location of the overwintering sampling site in Franklin Bay (indicated by star). For comparison, the location of the sampling station of Hsiao (1980) in Eskimo Lakes is shown. Water depth is in metres

Routine ice sampling was performed at high (>10 cm) and low (<10 cm) snow cover sites. On the last sampling day (20 June), only the low snow cover site remained and was sampled. On each sampling day, three to six ice cores were collected with a Mark II ice corer (9 cm internal diameter, Kovacs Enterprises) at each snow site. The ice cores were collected within an area of approximately 25 m^2 to account for horizontal patchiness in the sea-ice algal biomass (Gosselin et al. 1986, Rysgaard et al. 2001). The bottom 4 cm of each ice core was cut off with a stainless steel saw and stored in isothermal plastic containers for

subsequent analyses. Bottom ice cores were combined for each snow site. At each snow site, an additional ice core was collected and kept separately in a sterile plastic bag for salinity determination. On each sampling day, surface water samples were collected with a hand-pump system for salinity and nutrient determination. Snow depth and ice thickness were measured on each sampling day, whereas incident and sub-ice irradiances were measured using Li-Cor 2 π PAR sensors (LI-190SA quantum and LI-192SA underwater quantum sensors, respectively) on 18 March and on 13 occasions between 8 April and 28 May. Incident downwelling irradiance was also recorded with a Li-Cor PAR 2 π sensor every 10 min from 24 February to 23 May and air temperature was measured every 2–6 h throughout the study period.

In the ship's laboratory, the ice core samples were slowly melted in a known volume of filtered (0.2 µm polycarbonate membrane) surface seawater to avoid osmotic stress to ice protists (Bates & Cota 1986, Garrison & Buck 1986). Duplicate subsamples were filtered through Whatman GF/F glass fiber filters for chlorophyll *a* (chl *a*) determination. Chl *a* concentrations were determined on board using a Turner Designs 10-AU fluorometer after 24 h extraction in 10 ml of 90% acetone at 5°C in the dark (Parsons et al. 1984a). Duplicate subsamples for particulate organic carbon (POC) and nitrogen (PON) were filtered on pre-combusted (450°C for 5 h) Whatman GF/F filters, stored at –80°C and later analyzed with a Perkin-Elmer Model 2400 CHN analyzer (Knap et al. 1996). For the identification and enumeration of protists, melted ice subsamples were preserved with acidic Lugol's solution (Parsons et al. 1984a). Cells ≥4 µm were identified to the lowest possible taxonomic rank and enumerated under an inverted microscope (WILD Heerbrugg)

equipped with phase contrast optics (Lund et al. 1958). A minimum of 400 cells was counted in each settling chamber, except for four samples in February and early March when cell abundances were low. For these samples, 100–150 ml of subsample were sedimented and between 50 and 300 cells were counted throughout the entire settling chamber. The following references were used for ice protist identification: Poulin & Cardinal (1982a, b, 1983), Medlin & Round (1986), Medlin & Hasle (1990), Medlin & Priddle (1990), Poulin (1990a, b, 1991, 1993), Hill et al. (1992), Moestrup (1992), Hasle et al. (1994, 1996), Hasle & Syvertsen (1996), von Quillfeldt (1997, 2001) and Witkowski et al. (2000). Chl *a* and POC concentrations and protist abundances were corrected for the dilution effect of added seawater as described in Cota & Sullivan (1990). In the present study, we use the term "nanoflagellates" since flagellates >20 µm accounted, on average, for only 5.8% of the total flagellate abundance. These large flagellates (20–80 µm) belonged to the class Euglenophyceae or were unidentified flagellates >20 µm.

The surface water sample was filtered (<13 Pa) through pre-combusted Whatman GF/F filters and the filtrate was immediately frozen at –80°C in acid-cleaned polypropylene cryogenic vials for the analysis of nitrate+nitrite (NO_3+NO_2), nitrite (NO_2), phosphate (PO_4) and silicic acid ($Si(OH)_4$) using an Alpkem FSIII nutrient autoanalyzer (adapted from Grasshoff et al. 1999). The salinity of both undiluted ice cores and surface water was determined with a Guildline 8400B Autosal Lab salinometer (Knap et al. 1996).

2.2.2. Statistical analyses

Kendall's coefficients of rank correlation (τ) and Wilcoxon's signed-ranks tests were computed to infer relationships between two variables and to compare paired variates from the low and high snow cover sites, respectively (Sokal & Rohlf 1995). The net specific accumulation rates of diatoms, nanoflagellates and dinoflagellates in the bottom ice were estimated using model I linear regressions between the natural logarithm (ln) of cell abundances and different time periods in day (i.e., prior, during or following the ice algal bloom). The regression slope, hereafter referred to as the net observed growth rate (r_n), represents a conservative estimate of the specific growth rate (μ) of protists because losses (e.g., natural mortality, grazing, sinking) from the bottom ice are not accounted for (Landry 1993). Regression slopes were compared using analysis of covariance (ANCOVA) (Sokal & Rolf 1995). A Monod-type equation (Monod 1942) relating the $\log_{10}$ of maximum bottom ice chl *a* biomasses (B) to the mean NO_3 concentrations in the surface water or the upper water column (S) was fitted to the data compiled from the present study and other Arctic sampling stations by nonlinear regression using the Gauss-Newton algorithm. The equation used was:

$$B = B_{max} * S / (K_m + S) \quad (1)$$

where K_m is the NO_3 concentration at half the maximal biomass (B_{max}). Statistical tests and regressions were performed using StatSoft Statistica 6.

2.3. Results

Physico-chemical variables showed a large temporal variability in Franklin Bay during the study period (Figs. 2 & 3, Table 1). The incident irradiance increased gradually

from 0.3 mol photons m^{-2} d^{-1} on 24 February to 57.3 mol photons m^{-2} d^{-1} on 23 May (Fig. 2a) in parallel with the sunlight period, which steadily increased from 8.3 h at the beginning of the sampling to 24 h on 8 May and remained at this value for the rest of the study. Air temperature increased from –35°C to 1.3°C during the study (Fig. 2b). Seasonally averaged snow depth at the high and low snow sites was 15.6 and 3.8 cm, respectively (Table 1).

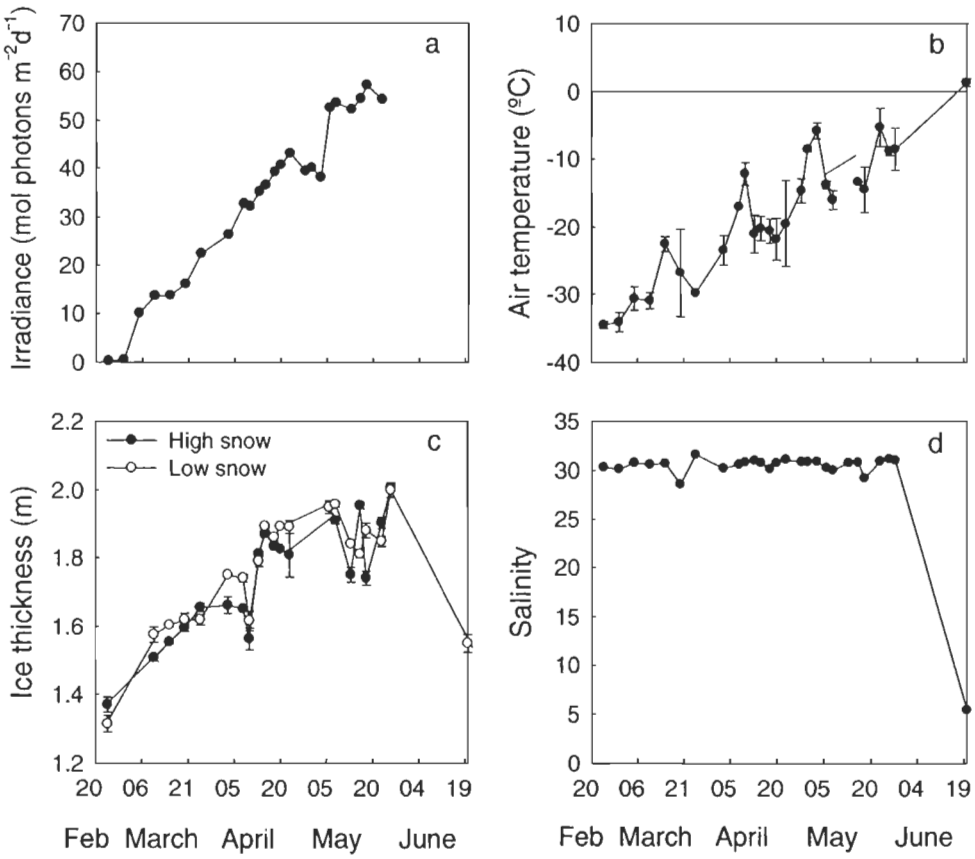

Fig. 2. Temporal variations of (a) incident irradiance, (b) air temperature, (c) ice thickness, and (d) surface water salinity in Franklin Bay from February to June 2004. In (b) and (c), mean values ± SD are shown

Sea-ice thickness under both snow covers increased from 1.32 m on 24 February to maximum of 2.01 m on 26 May, and decreased thereafter to reach 1.55 m on 20 June (Fig. 2c). There was no significant difference in ice thickness between the two snow sites (Table 1). Surface water salinity remained relatively constant at 29.6, on average, until 29 May, after which it decreased to reach 5.4 on 20 June (Fig. 2d). Bottom ice salinity ranged from 5.9 to 12.8 throughout the sampling period and was not significantly different between the two snow sites (Table 1). The salinity of the diluted ice cores ranged from 20 to 24.5, except on 20 June when it was ca. 5.

Sub-ice irradiance was 2.6 and 5.8 µmol photons m^{-2} s^{-1} under high and low snow cover, respectively, corresponding to 0.5% and 1.1% of the incident irradiance on 18 March under 1.67 m of ice. When the sea ice was thicker from 8 April to 28 May, sub-ice irradiance ranged from 0.2 to 4.0 µmol photons m^{-2} s^{-1} under high snow cover and from 2.9 to 26.0 µmol photons m^{-2} s^{-1} under low snow cover (Table 1). The transmitted irradiance through the snow, ice and algal layer varied between 0.03 and 0.5% and between 0.3 and 2.3% of incident PAR under high and low snow cover, respectively (Table 1). Sub-ice and percent transmitted irradiances were significantly lower under high snow than low snow cover and did not show any seasonal trend (Table 1).

Surface water NO_3+NO_2 and $Si(OH)_4$ concentrations decreased from 3.0 to 0.2 µmol l^{-1} and 9.8 to 2.4 µmol l^{-1}, respectively, throughout the sampling period and were both negatively correlated with the time of year ($\tau = -0.51$, $p < 0.001$ and $\tau = -0.32$, $p < 0.05$, respectively; Fig. 3a, c). Surface water NO_2 and PO_4 concentrations ranged from

≤0.05 (i.e., the detection limit) to 0.14 μmol l^{-1} and 0.23 to 2.18 μmol l^{-1}, respectively, and did not show any temporal trend. The $(NO_3+NO_2):PO_4$ and $(NO_3+NO_2):Si(OH)_4$ molar ratios decreased throughout the sampling season ($\tau = -0.42$, $p < 0.01$ and $\tau = -0.47$, $p < 0.001$, respectively; Fig. 3b, d) and were always lower than the critical Redfield values of 16 for $[NO_3+NO_2]:PO_4$ and 1.1 for $[NO_3+NO_2]:Si(OH)_4$ (Redfield et al. 1963). This indicates that dissolved nitrogen was potentially the limiting nutrient for bottom ice algal growth.

Table 1. Descriptive statistics of environmental and biological variables measured under high and low snow cover on landfast ice in Franklin Bay from 24 February to 20 June 2004. Significant differences between snow cover sites were tested with Wilcoxon's signed-ranks test. n: number of observations; nd: not detected; ns: not significant

	High snow site					Low snow site					Probability
Variable	Min	Mean	Max	SD	n	Min	Mean	Max	SD	n	
Snow depth (cm)	7.8	15.6	21.9	3.4	24	0	3.8	9.3	2.3	26	<0.001
Ice thickness (m)	1.37	1.75	2.01	0.17	20	1.32	1.76	2.00	0.17	21	ns
Ice salinity	5.9	9.2	12.8	1.6	24	7.5	9.7	12.0	1.4	24	ns
Sub-ice irradiance (μmol photons m^{-2} s^{-1})	0.2	2.2	4.0	1.3	14	2.9	8.9	26.0	6.1	14	<0.001
Sub-ice irradiance (%)	0.03	0.23	0.52	0.16	13	0.30	0.94	2.26	0.57	13	<0.01
Chlorophyll *a* (mg m^{-2})	0.01	5.9	28.6	8.5	26	0.02	8.9	30.9	9.0	27	<0.01
Total protists (10^9 cells m^{-2})	0.003	0.62	3.87	0.97	26	0.001	1.11	3.23	1.02	27	<0.001
Pennate diatoms (10^9 cells m^{-2})	0.001	0.47	3.58	0.85	26	0.001	0.92	2.58	0.84	27	<0.001
Centric diatoms (10^9 cells m^{-2})	nd	0.01	0.09	0.02	26	nd	0.02	0.07	0.02	27	<0.001
Solitary diatoms (10^9 cells m^{-2})	0.001	0.06	0.34	0.08	26	0.001	0.14	0.56	0.15	27	<0.001
Colonial diatoms (10^9 cells m^{-2})	0.0004	0.41	3.32	0.79	26	0.0002	0.80	2.26	0.74	27	<0.001
Dinoflagellates (10^9 cells m^{-2})	nd	0.001	0.01	0.003	26	nd	0.001	0.01	0.002	27	ns
Nanoflagellates (10^9 cells m^{-2})	0.0005	0.14	0.73	0.19	26	0.0004	0.17	0.79	0.20	27	ns
Chl *a*:protist abundance (pg $cell^{-1}$)	0.4	10.9	25.5	7.9	26	1.4	13.4	48.5	11.3	27	ns
POC:chl *a* (g:g)	16	215	2509	532	22	20	91	1001	194	25	ns

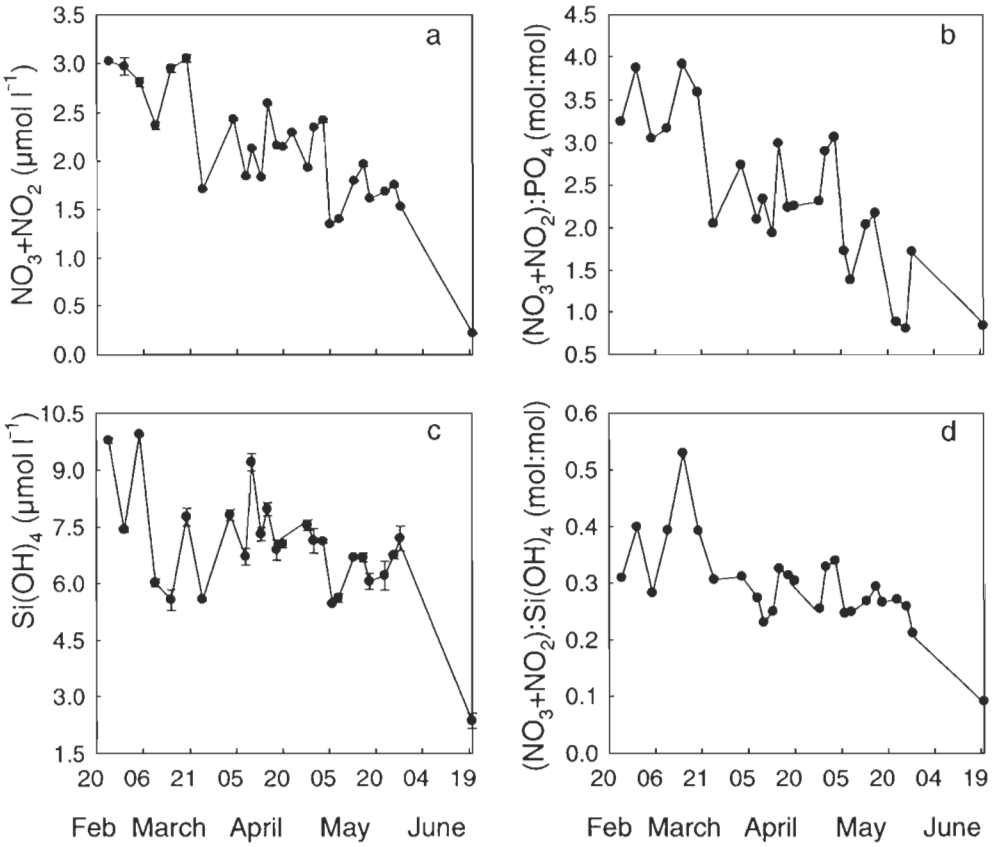

Fig. 3. Temporal variations of (a) nitrate+nitrite (NO_3+NO_2) concentration, (b) ratio of NO_3+NO_2 to phosphate (PO_4), (c) silicic acid ($Si(OH)_4$) concentration, and (d) ratio of NO_3+NO_2 to $Si(OH)_4$ in the surface water in Franklin Bay from February to June 2004. In (a) and (c), mean values ± SD are shown

Chl *a* concentrations were <1.16 mg m^{-2} in sea ice under both snow covers prior to the bloom period (ca. 3 April–23 May) and were barely detectable (<0.02 mg m^{-2}) at the beginning of the sampling in late February. Bottom ice chl *a* concentration started to increase in early March under low snow cover and one week later under high snow cover (Fig. 4a). A steady increase in chl *a* concentrations was observed afterward, with maximum values of 28.6 mg m^{-2} on 23 May and 30.9 mg m^{-2} on 16 May under high and low snow

cover, respectively. The bloom period was followed by a sharp decline in chl *a* concentrations to a minimum value of 0.72 mg m^{-2} on 20 June (Fig. 4a). Bottom ice protist abundances paralleled the seasonal trends in chl *a* over the entire sampling period (Fig. 4a, b). Total protist abundances were $<0.01 \times 10^9$ cells m^{-2} in late February and reached maximum values of 3.87×10^9 cells m^{-2} on 6 May and 3.23×10^9 cells m^{-2} on 18 May under high and low snow cover, respectively (Fig. 4b). The decline in protist abundance was observed after 23 May under both snow covers (Fig. 4b). Chl *a* concentrations and protist abundances were significantly lower and more variable under high snow compared to low snow cover (Table 1, Fig. 4a, b).

The ratio of chl *a* to protist abundance ranged from 0.4 to 25.5 pg $cell^{-1}$ and 1.4 to 48.5 pg $cell^{-1}$ under high and low snow cover, respectively (Fig. 4c). During the pre-bloom period, the chl *a*:protist abundance ratios (pg chl *a*:cell) were significantly lower in sea ice under high snow than low snow cover (Wilcoxon's signed-ranks test, $p < 0.05$). This situation was reversed during the bloom and post-bloom periods, when the ratio was higher in sea ice under high snow than low snow cover (Wilcoxon's signed-ranks test, $p < 0.01$) (Fig. 4c). The POC:chl *a* ratio (g:g) varied between 16 and 2509 g:g and 20 and 1001 g:g in sea ice under high and low snow cover, respectively (Fig. 4d). The ratio was significantly higher under high snow (mean of 215) than low snow (mean of 91) cover during the pre-bloom period (Wilcoxon's signed-ranks test, $p < 0.05$), while there was no statistical difference in the POC:chl *a* ratio for the rest of the season under both snow covers (mean of 45; Wilcoxon's signed-ranks test, $p = 0.76$)

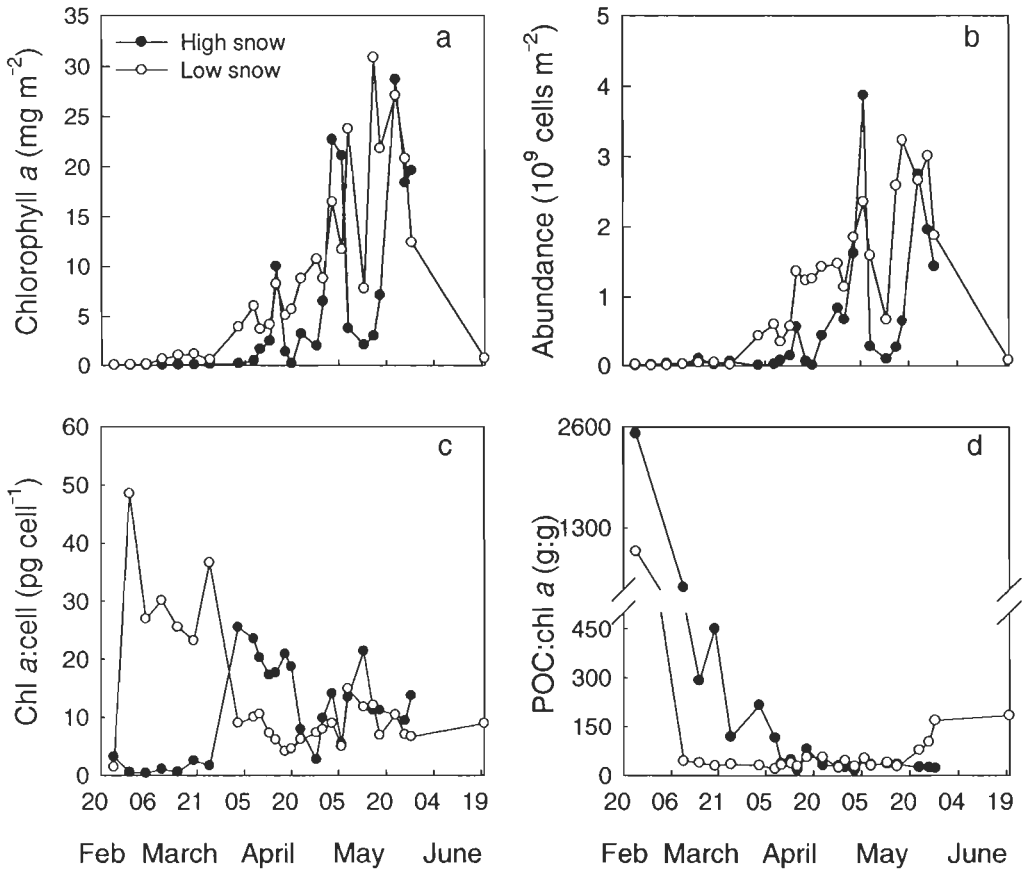

Fig. 4. Temporal variations of (a) chlorophyll *a* (chl *a*) concentration, (b) total cell abundance (i.e., diatoms + flagellates + dinoflagellates), (c) ratio of chl *a* to total protist abundance, and (d) ratio of particulate organic carbon (POC) to chl *a* in the bottom ice under high and low snow cover in Franklin Bay from February to June 2004

The abundances of diatoms, nanoflagellates and dinoflagellates increased progressively until 23 May under both snow covers (Fig. 5a, c). Diatoms and nanoflagellates were always more abundant than dinoflagellates. However, pennate and centric diatoms were significantly less abundant in sea ice under high snow than low snow cover, while nanoflagellate and dinoflagellate abundances were not significantly different between the two snow covers for the entire sampling period (Table 1). Prior to the bloom,

diatom and nanoflagellate abundances were not significantly different in sea ice under high snow cover ($p = 0.24$), whereas diatoms were almost 4 times more abundant than nanoflagellates under low snow cover ($p < 0.05$) (Fig. 5a, c). In contrast during the bloom period, diatoms were significantly more abundant than nanoflagellates in sea ice under high snow cover (diatom numbers twice higher; $p < 0.01$) and under low snow cover (diatom numbers ca. 5 times higher; $p < 0.001$).

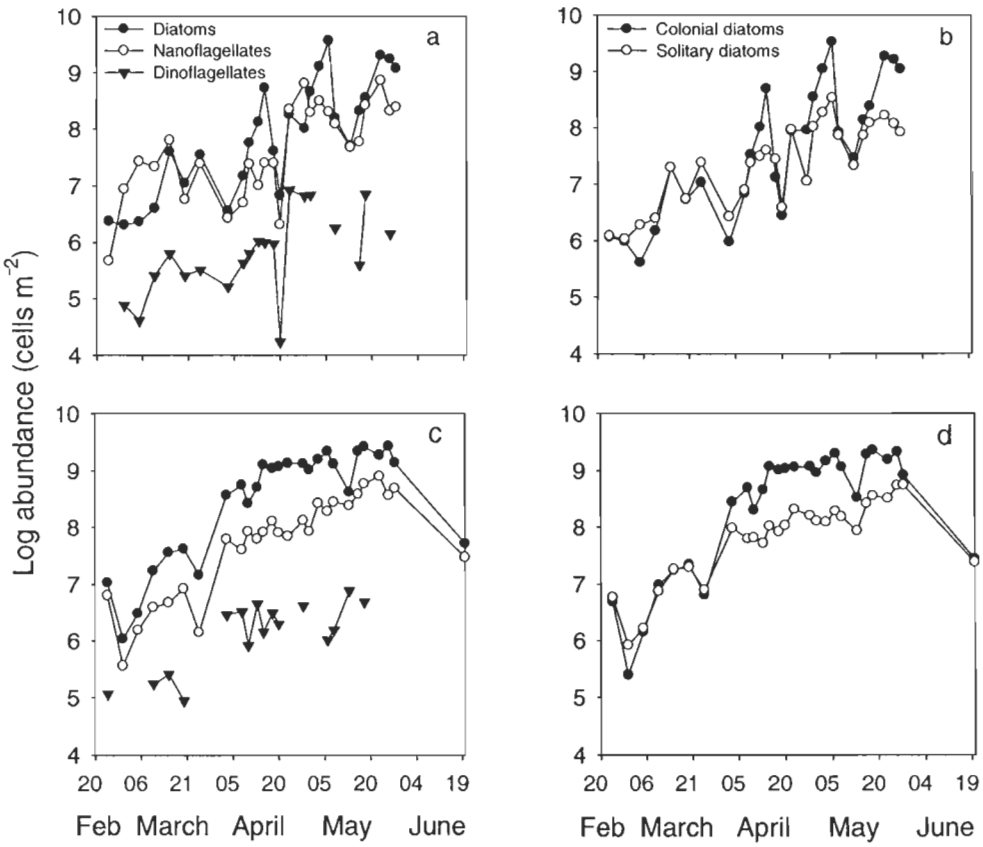

Fig. 5. Temporal variations of the abundances of (a, c) diatoms, nanoflagellates and dinoflagellates, and (b, d) solitary and colonial diatoms in the bottom ice under (a, b) high and (c, d) low snow cover in Franklin Bay from February to June 2004. In (a) and (c), the discontinuous line indicates that dinoflagellates were not detected

Colonial and solitary diatom abundances increased steadily until 23 May (Fig. 5b, d). Prior to the bloom, the colony-forming diatoms were significantly less abundant than solitary diatoms in sea ice under high snow cover (Wilcoxon's signed-ranks test, $p < 0.05$), while the abundances of colonial and solitary diatoms were not significantly different under low snow cover (Wilcoxon's signed-ranks test, $p = 0.31$). During the bloom period, the colony-forming diatoms were significantly more abundant than solitary diatoms in sea ice under high (diatom numbers ca. 5 times higher, $p < 0.01$) and low (diatom numbers ca. 6 times higher, $p < 0.001$) snow cover, respectively (Fig. 5b, d). The percentage of empty diatom cells increased throughout the study under both snow covers (Table 2).

Table 2. Average percent numbers of empty diatom cells and estimated (standard error) net observed growth rate (r_n) of diatoms and nanoflagellates under high and low snow cover during the bottom ice algal pre-bloom (24 February–25 March), bloom (ca. 3 April–23 May) and post-bloom (high snow: 23–28 May; low snow: 23 May–20 June) periods. Negative r_n values indicate a decline in cell abundances. All rates were significantly different from zero ($p \leq 0.05$), except values in italics; na: data not available

Variable	Snow site	Pre-bloom	Bloom	Post-bloom
Empty diatoms (%)	High	4.9	14.4	29.9
	Low	3.5	18.9	60.1
Total diatom r_n (d^{-1})	High	0.101 (0.028)	0.078 (0.025)	na
	Low	0.196 (0.032)	0.030 (0.009)	*–0.151* (0.012)
Colonial diatom r_n (d^{-1})	High	0.100 (0.038)	0.091 (0.030)	na
	Low	0.230 (0.044)	0.031 (0.009)	*–0.163* (0.022)
Solitary diatom r_n (d^{-1})	High	0.104 (0.025)	0.060 (0.025)	na
	Low	0.175 (0.027)	0.030 (0.006)	*–0.130* (0.010)
Nanoflagellate r_n (d^{-1})	High	*0.085* (0.054)	0.089 (0.022)	na
	Low	0.149 (0.028)	0.052 (0.006)	*–0.110* (0.018)

The net observed growth rates of diatoms and nanoflagellates were significantly higher during the pre-bloom than the bloom period under the low snow cover sites (ANCOVAs, $p < 0.001$) but not statistically different under high snow cover sites (ANCOVAs, $p > 0.05$, Table 2). In addition, the net observed growth rates of diatoms and nanoflagellates were lower in sea ice under high snow compared to low snow cover prior to the bloom, whereas they were higher under high than low snow cover during the bloom (Table 2). However, these differences were not statistically significant (ANCOVAs, $p > 0.05$). Due to the large variability in cell counts, the net observed growth rates of dinoflagellates during the pre-bloom and bloom periods were not significantly different from zero under both snow covers (Model I regressions, $p > 0.05$). However, the estimated net observed growth rates of dinoflagellates from 24 February to 23 May were 0.043 d^{-1} (SE = 0.010) under high snow cover and 0.047 d^{-1} (SE = 0.009) under low snow cover (Model I regressions, $p < 0.001$); these two rates were not significantly different (ANCOVA, $p = 0.78$).

During this study, a total of 149 and 140 bottom ice protist taxa representing 119 and 112 species in twelve algal classes were recorded for high and low snow cover, respectively (Table 4). The bottom ice protist community was composed of 106 pennate diatom taxa, 8 centric diatoms, 29 flagellates and 10 dinoflagellates, with diatoms representing 75% of the total protist taxa. The highest numbers of diatom taxa were recorded in the genera *Navicula* Bory and *Nitzschia* Hassall. The arborescent colonial diatom *Nitzschia frigida* was the most abundant diatom during our sampling period

(Table 4). Dinoflagellate cysts were observed in only one sample collected under high snow cover, with an average abundance of 5×10^3 cells m^{-2}.

The taxonomic composition of the bottom ice protist community varied seasonally and differed under high and low snow cover. During the pre-bloom period, unidentified flagellates (<10 μm) were the most abundant along with *Nitzschia frigida*, *N. arctica* and *Cylindrotheca closterium* under high snow cover, whereas *N. frigida* was the most abundant species along with *C. closterium*, *Fragilariopsis cylindrus* and unidentified flagellates (<10 μm) under low snow cover. During the bloom period, high snow cover sites were characterized by a higher number of protist taxa, with a predominance of colony-forming diatoms of the genera *Nitzschia* and *Navicula* followed by unidentified flagellates (<10 μm) along with scattered solitary diatom cells. Under low snow cover sites, the community was characterized by a strong predominance of colonial diatoms belonging to *Nitzschia frigida*, *N. promare*, *Navicula* sp. 6 and *N. pelagica*. During the post-bloom period, the same colonial diatom species were still making up the bottom ice community, with the predominance of *Nitzschia frigida* along with *Navicula* sp. 6, *N. pelagica* and *Nitzschia promare*, except in a higher proportion under high snow than low snow cover. In addition, the abundance of unidentified flagellate (<10 μm) was higher under low snow cover.

Under both snow covers, chl *a* concentrations and diatom and nanoflagellate abundances were positively correlated with time of year, incident irradiance, air temperature and ice thickness, and negatively correlated with surface water NO_3+NO_2 (Table 3). In contrast to the other biological variables, dinoflagellate abundance was not

correlated with ice thickness under neither snow cover nor to air temperature under low snow cover (Table 3). Chl *a* concentrations and diatom and nanoflagellate abundances were not significantly correlated with the other environmental variables (e.g., surface water $Si(OH)_4$ and PO_4). Surface water NO_3+NO_2, $Si(OH)_4$ and PO_4 concentrations were not significantly correlated with surface salinity.

Table 3. Kendall's coefficients of rank correlation (τ) between environmental and biological variables under high and low snow cover. Pairwise deletion of missing data; * $0.01 < p \leq 0.05$; ** $0.001 < p \leq 0.01$; *** $p \leq 0.001$; ns: not significant

	Chl *a*	Diatoms	Nanoflagellates	Dinoflagellates
HIGH SNOW				
Time of year	0.74***	0.66***	0.51**	0.53*
Incident irradiance	0.67***	0.59***	0.44**	0.52*
Air temperature	0.65***	0.59***	0.49**	0.38*
Ice thickness	0.63***	0.57**	0.38*	0.23^{ns}
Surface NO_3+NO_2	–0.46*	–0.43*	–0.33*	–0.34*
Surface $Si(OH)_4$	-0.16^{ns}	-0.22^{ns}	-0.18^{ns}	-0.03^{ns}
LOW SNOW				
Time of year	0.71***	0.66***	0.73***	0.52*
Incident irradiance	0.80***	0.77***	0.74***	0.48*
Air temperature	0.57***	0.57***	0.56***	0.24^{ns}
Ice thickness	0.62***	0.67***	0.55**	0.30^{ns}
Surface NO_3+NO_2	–0.40*	–0.35*	–0.40*	–0.52*
Surface $Si(OH)_4$	-0.21^{ns}	-0.15^{ns}	-0.17^{ns}	-0.15^{ns}

Table 4. List of protists recorded under high and low snow cover on landfast ice in Franklin Bay from 24 February to 20 June 2004. A: mean abundance (10^6 cells m^{-2}); A_{max}: maximum abundance (10^6 cells m^{-2}); A (%): mean relative abundance (%); Occ. (%): number of samples in which the taxon occurred in percent (maximum of 26 and 27 samples for high and low snow depth, respectively); nd: taxon not detected; *: indicates colonial diatoms

Ice protist	High snow				Low snow			
	A	A_{max}	A (%)	Occ. (%)	A	A_{max}	A (%)	Occ. (%)
COSCINODISCOPHYCEAE								
Attheya decora West	0.001	0.02	0.01	4	0.004	0.09	0.04	7
A. longicornis Crawford & Gardner	1.8	17	0.18	27	1.9	17	0.10	26
A. septentrionalis (Østrup) Crawford	4.7	74	0.23	46	14	67	0.83	74
Chaetoceros sp. 2	0.04	0.62	0.09	23	0.01	0.25	0.02	7
Melosira arctica Dickie*	0.11	1.1	0.89	35	1.7	37	0.20	22
Porosira glacialis (Grunow) Jørgensen	0.01	0.16	0.03	8	nd	nd	nd	0
Thalassiosira spp.	0.06	0.64	0.05	23	0.01	0.16	0.03	7
Unidentified centric cells	0.49	9.0	0.24	46	0.13	2.1	0.05	19
FRAGILARIOPHYCEAE								
Synedropsis hyperborea (Grunow) Hasle, Medlin & Syvertsen*	4.4	70	0.33	69	10	82	0.74	78
BACILLARIOPHYCEAE								
Amphora laevis var. *laevissima* (Gregory) Cleve	0.65	3.8	0.36	73	0.27	2.5	0.16	41
Bacillaria paxillifer var. *tumidula* Hustedt	0.42	2.4	0.31	69	0.14	1.0	0.09	41
Biremis ambigua (Cleve) Mann	0.003	0.08	< 0.01	4	0.02	0.41	< 0.01	4
Craspedopleura kryophila (Cleve) Poulin	0.10	1.4	0.04	27	0.07	1.1	0.03	22
Cylindrotheca closterium (Ehrenberg) Reimann & Lewin	1.9	2.0	12.7	88	2.2	2.9	16	93
Diploneis litoralis var. *arctica* Cleve	1.3	7.6	0.51	19	0.58	2.9	0.39	4
D. litoralis var. *clathrata* (Østrup) Cleve	0.08	0.75	0.06	77	0.01	0.21	< 0.01	52
Entomoneis gigantea var. *septentrionalis* (Grunow) Poulin & Cardinal	0.41	4.8	0.08	42	0.57	4.2	0.05	41
E. kjellmanii (Cleve) Poulin & Cardinal*	4.7	49	0.73	96	8.4	55	0.66	93
E. kjellmanii var. *kariana* (Grunow) Poulin & Cardinal*	2.1	17	0.26	54	6.2	24	0.50	81
E. kjellmanii var. *subtilis* (Grunow) Poulin & Cardinal	0.07	1.0	0.03	12	0.12	1.2	0.03	19
E. paludosa (W. Smith) Poulin & Cardinal	0.005	0.12	< 0.01	4	0.08	2.1	0.01	4
E. paludosa var. *hyperborea* (Grunow) Poulin & Cardinal	0.64	4.0	0.12	54	0.49	4.2	0.08	48
Entomoneis spp.	0.67	4.2	0.23	46	0.63	4.1	0.10	41

Table 4 – Continued

Fallacia forcipata var. *densestriata* (Schmidt) Stickle & Mann	0.15	1.1	0.07	38	0.09	1.6	0.06	19
Fragilariopsis cylindrus (Grunow) Krieger*	8.4	48	3.0	81	11	56	2.7	78
F. oceanica (Cleve) Hasle*	0.72	12	0.14	12	1.0	15	0.06	7
Gyrosigma concilians (Cleve) Okolodkov	0.74	3.0	0.52	81	0.51	2.3	0.27	48
G. hudsonii Poulin & Cardinal	0.24	2.2	0.03	27	0.14	2.0	0.03	22
G. tenuissimum var. *hyperborea* (Grunow) Cleve	0.51	3.2	0.44	65	0.36	2.0	0.28	52
Gyrosigma / Pleurosigma complex	0.57	3.1	0.38	65	0.46	2.3	0.14	52
Haslea crucigeroides (Hustedt) Simonsen	0.74	2.8	0.46	81	1.0	4.2	0.37	74
H. kjellmanii (Cleve) Simonsen	0.32	3.3	0.03	23	0.19	2.1	0.01	15
H. spicula (Hickie) Lange-Bertalot	0.52	3.3	0.28	54	0.48	4.2	0.22	41
H. vitrea (Cleve) Simonsen	0.09	2.2	0.01	12	0.02	0.41	0.02	7
Kurpiszia kryokonites (Cleve) Witkowski, Lange-Bertalot & Metzeltin	0.27	2.1	0.18	46	0.30	4.2	0.16	30
K. subprotracta (Cleve) Witkowski, Lange-Bertalot & Metzeltin	0.03	0.54	0.02	15	0.02	0.41	0.04	11
Manguinia rigida (M. Peragallo) Paddock	0.07	1.1	0.03	19	0.45	5.2	0.05	19
Meuniera membranacea (Cleve) Silva	0.78	5.2	0.25	69	0.61	2.9	0.18	59
Navicula algida Grunow	0.22	2.2	0.07	35	0.27	2.0	0.04	37
N. directa (W. Smith) Ralfs	2.2	11	1.2	88	2.2	13	0.89	74
N. gelida Grunow	0.27	2.3	0.23	38	0.23	1.6	0.20	37
N. gelida var. *manitounukensis* Poulin & Cardinal	0.01	0.38	0.01	4	nd	nd	nd	0
N. gelida var. *radissonii* Poulin & Cardinal	2.1	9.1	1.4	88	1.3	5.6	0.60	67
N. cf. *impexa* Hustedt *sensu* Poulin & Cardinal	0.16	1.6	0.19	38	0.13	1.0	0.10	33
N. kariana Grunow	0.001	0.02	0.01	4	0.02	0.4	< 0.01	7
N. kariana var. *detersa* Grunow	0.76	4.3	0.15	58	0.34	2.1	0.18	44
N. kariana var. *frigida* (Grunow) Cleve	0.01	0.28	0.02	15	0.02	0.41	< 0.01	4
N. lineola var. *perlepida* (Grunow) Cleve	0.01	0.20	< 0.01	4	0.03	0.82	0.02	7
N. pelagica Cleve*	25.5	195	2.8	77	30	152	3.2	93
N. pellucidula Hustedt	0.39	2.4	0.14	50	0.20	1.4	0.06	37
N. recurvata Gran	0.01	0.17	0.01	8	0.10	2.0	0.01	11
N. septentrionalis (Grunow) Gran*	20.5	178	1.6	62	40	316	2.0	63
N. superba Cleve	0.09	1.0	0.03	23	0.01	0.21	0.01	7
N. superba var. *elliptica* Cleve	0.02	0.38	0.02	8	0.02	0.41	< 0.01	4
N. superba var. *subacuta* Gran	0.02	0.38	0.01	8	nd	nd	nd	0
N. superba group	nd	nd	nd	0	0.04	1.0	0.01	7
N. transitans Cleve	0.13	1.3	0.08	31	0.20	2.3	0.13	30
N. transitans var. *derasa* (Grunow) Cleve	0.45	2.8	0.25	58	0.18	2.9	0.09	22
N. transitans var. *derasa* f. *delicatula* Heimdal	0.07	1.4	0.03	19	0.03	0.62	0.02	11

Table 4 – Continued

N. transitans / kariana complex	0.06	0.54	0.04	27	0.002	0.04	0.01	4
N. transitans group	0.65	2.8	0.47	69	0.13	2.1	0.16	26
N. trigonocephala Cleve	0.09	0.64	0.04	35	0.10	2.1	0.06	22
N. trigonocephala var. *depressa* Østrup	0.10	1.0	0.04	23	0.06	0.98	0.01	15
N. valida Cleve & Grunow	0.06	0.80	0.02	19	0.04	0.83	0.01	11
N. valida var. *minuta* Cleve	0.10	1.4	0.05	31	0.04	0.41	0.04	15
N. vanhoeffenii Gran*	3.9	92	0.28	19	3.0	37	0.23	22
Navicula sp. 1	0.08	1.3	0.21	12	0.12	2.1	0.12	11
Navicula sp. 2	3.8	76	0.63	54	2.2	15.3	0.65	48
Navicula sp. 5	0.65	7.0	0.13	38	1.2	9.2	0.18	37
Navicula sp. 6*	53.1	325	4.6	50	93	493	5.5	81
Navicula sp. 12	0.70	4.4	0.38	46	1.4	10	0.22	56
Navicula spp.	2.2	20	0.83	92	3.6	28	0.45	85
Nitzschia angularis W. Smith	0.09	2.2	0.02	12	0.21	4.2	0.08	26
N. arctica Cleve*	4.4	39	1.8	69	7.6	32	1.7	78
N. brebissonii var. *borealis* Grunow ex Cleve	0.09	1.4	0.03	15	0.11	1.5	0.01	11
N. distans var. *erratica* Cleve*	0.08	1.3	0.23	23	0.05	0.42	0.10	19
N. frigida Grunow*	236	2562	17	92	465	1326	35	100
N. laevissima Grunow	0.29	3.3	0.05	27	1.6	29	0.08	33
N. lanceolata var. *pygmaea* Cleve	0.01	0.16	< 0.01	8	0.08	2.1	0.01	4
N. longissima (Brébisson) Ralfs	1.8	23	0.64	73	0.89	4.5	0.77	52
N. neofrigida Medlin*	5.8	50	0.38	54	13	43	0.97	67
N. promare Medlin*	30.1	167	3.4	81	84	300	6.0	85
N. scabra Cleve	0.26	4.2	0.09	35	0.14	2.1	0.03	22
Nitzschia sp. 1	0.02	0.32	0.02	12	0.41	10	0.02	7
Nitzschia spp.	2.4	20.9	0.52	73	9.4	66	0.64	81
Pauliella taeniata (Grunow) Round & Basson*	3.7	75	0.45	19	8.3	78	0.53	30
Petroneis glacialis (Cleve) Witkowski, Lange-Bertalot & Metzeltin	0.16	2.1	0.11	38	0.08	1.2	0.05	19
Pinnularia quadratarea (Schmidt) Cleve	0.21	2.8	0.06	23	0.03	0.83	0.01	4
P. quadratarea var. *bicontracta* (Østrup) Heiden	0.09	1.4	0.04	23	0.002	0.06	0.01	4
P. quadratarea var. *capitata* Heiden	0.005	0.1	< 0.01	4	0.002	0.03	0.01	4
P. quadratarea var. *constricta* (Østrup) Heiden	0.13	1.3	0.04	19	0.02	0.42	0.01	7
P. quadratarea var. *densestriata* Cleve	0.35	2.2	0.28	62	0.09	0.83	0.14	33
P. quadratarea var. *maxima* (Østrup) Boyer	0.05	0.80	0.02	15	nd	nd	nd	0
P. quadratarea group	0.06	0.77	0.09	12	0.002	0.06	0.01	4
P. semiinflata (Østrup) Gran	0.07	0.80	0.01	12	0.11	2.1	0.07	19

Table 4 – Continued

Plagiotropis spp.	0.17	2.2	0.03	27	0.54	6.1	0.06	26
Pleurosigma clevei Grunow	0.02	0.49	0.01	8	0.03	0.41	0.01	11
P. stuxbergii Cleve & Grunow	0.23	1.6	0.06	35	0.17	0.98	0.06	41
P. stuxbergii var. *rhomboides* (Cleve) Cleve	0.09	0.86	0.08	35	0.25	2.1	0.07	41
Pseudogomphonema arcticum (Grunow) Medlin*	3.6	31	0.36	81	3.8	17	0.29	78
P. groenlandicum (Østrup) Medlin	0.02	0.64	< 0.01	4	0.21	2.1	0.02	19
Pseudo-nitzschia delicatissima (Cleve) Heiden*	0.01	0.25	0.03	12	0.13	3.0	0.01	7
P. cf. *pseudodelicatissima* (Hasle) Hasle*	7.2	45	1.2	85	21	105	1.5	85
P. pungens (Grunow ex Cleve) Hasle*	0.11	2.8	< 0.01	4	0.11	2.1	< 0.01	7
P. seriata (Cleve) H. Peragallo*	0.56	5.8	0.17	38	0.21	2.5	0.03	15
P. turgidula (Hustedt) Hasle*	0.10	1.0	0.02	12	0.23	6.2	0.01	4
Pseudo-nitzschia spp.*	1.7	15	0.18	58	3.0	25	0.15	52
Stauroneis radissonii Poulin & Cardinal	0.67	5.2	0.18	69	0.47	2.9	0.16	52
Stenoneis inconspicua var. *baculus* (Cleve) Cleve*	0.47	7.0	0.08	15	0.56	6.2	0.07	22
S. obtuserostrata (Hustedt) Poulin	0.73	3.2	0.41	81	0.84	6.2	0.29	63
Pennate sp. 1	0.16	3.2	0.04	19	0.28	3.3	0.07	22
Pennate sp. 2	0.02	0.6	< 0.01	4	0.01	0.09	0.02	7
Pennate sp. 8	0.11	1.2	0.10	31	0.16	3.1	0.05	19
Unidentified pennate cells	14.3	93	4.2	100	71	448	7.1	100
DINOPHYCEAE								
Amphidinium sphenoides Wülff	0.001	0.02	0.01	4	0.02	0.41	< 0.01	4
Dinophysis acuminata Claparède & Lachmann	0.005	0.08	0.02	8	nd	nd	nd	0
Gymnodinium sp. 1 *sensu* Bérard-Therriault et al.	0.003	0.08	< 0.01	4	nd	nd	nd	0
Gymnodinium / Gyrodinium complex	0.54	6.8	0.24	50	0.33	5.0	0.06	26
Heterocapsa arctica Horiguchi	0.14	1.1	0.05	31	0.20	1.0	0.04	33
Heterocapsa spp.	0.11	1.4	0.03	15	0.21	3.9	0.02	19
Peridiniella catenata (Levander) Balech	0.36	6.5	0.07	15	0.13	2.1	0.02	7
Protoperidinium spp.	0.02	0.63	< 0.01	4	nd	nd	nd	0
Dinophyceae spp.	0.26	3.1	0.25	46	0.37	3.7	0.09	26
Thecate dinophyceae	0.01	0.30	0.02	12	0.16	4.1	0.02	7
CHRYSOPHYCEAE								
Dinobryon faculiferum (Willén) Willén	0.41	4.3	0.07	27	1.4	8.2	0.18	63
Chrysophyceae sp. 1 *sensu* Bérard-Therriault et al.	nd	nd	nd	0	0.06	1.5	< 0.01	4
Chrysophyceae spp.	0.01	0.25	0.01	4	nd	nd	nd	0
CHOANOFLAGELLIDEA								
Monosiga marina Grøntved	nd	nd	nd	0	0.08	1.6	0.01	7

Table 4 – Continued

Choanoflagellidea sp. 1	3.8	52	0.21	12	nd	nd	nd	0
Choanoflagellidea spp.	4.4	31	0.34	38	5.5	70	0.23	33
CRYPTOPHYCEAE								
Hemiselmis virescens Droop	0.17	2.5	0.14	23	0.05	0.75	0.03	15
Plagioselmis prolonga Butcher ex Novarino, Lucas & Morrall	0.03	0.85	0.01	8	nd	nd	nd	0
Rhodomonas maculata Butcher ex Hill & Wetherbee	0.28	2.6	0.20	31	0.15	2.1	0.04	19
Teleaulax spp.	0.06	1.3	0.03	15	nd	nd	nd	0
Cryptophyceae spp.	5.7	34	2.2	88	5.5	30	0.97	85
DICTYOCHOPHYCEAE								
Apedinella spinifera (Throndsen) Throndsen	0.005	0.13	0.01	4	nd	nd	nd	0
Dictyocha speculum Ehrenberg	0.005	0.13	0.01	4	nd	nd	nd	0
EUGLENOPHYCEAE								
Eutreptia spp.	0.001	0.04	0.01	4	0.002	0.06	0.01	4
Eutreptiella braarudii Throndsen	0.12	1.8	0.07	23	0.02	0.49	< 0.01	4
Euglenophyceae spp.	0.56	4.2	0.14	50	0.50	5.5	0.05	30
PRASINOPHYCEAE								
Pyramimonas cf. *nansenii* Braarud	0.42	6.5	0.08	12	0.02	0.41	< 0.01	4
P. virginica Pennick	0.01	0.17	0.08	8	0.14	3.9	< 0.01	4
Pyramimonas spp.	0.81	13	0.19	38	0.45	4.9	0.06	30
Prasinophyceae spp.	0.60	7.1	0.14	38	0.36	4.6	0.12	41
PRYMNESIOPHYCEAE								
Prymnesiophyceae spp.	0.13	2.3	0.04	15	0.30	4.6	0.02	15
CHLOROPHYCEAE								
Chlainomonas cf. *rubrum* (Stein & Brooke) Honam	0.88	5.4	0.50	69	0.92	7.0	0.57	52
Chlorophyceae sp. 1	nd	nd	nd	0	0.004	0.01	0.03	4
Chlorophyceae spp.	1.5	16	0.32	46	2.0	14	0.15	41
HETEROTROPHIC FLAGELLATES								
Telonema subtilis Griessmann	1.1	13	0.25	35	0.42	7.8	0.03	19
UNIDENTIFIED FLAGELLATES								
Flagellate sp. 2	0.1	2.5	0.05	15	0.002	0.06	0.01	4
Flagellates ≤5 µm	60.5	398	16	100	76	381	7.1	100
Flagellates 6–10 µm	47.7	350	14	96	61	394	6.3	100
Flagellates >10 µm	6.0	47	2.3	88	9.8	60	1.3	93
Number of species				119				112
Number of taxa				149				140

2.4. Discussion

The dynamics of algae and heterotrophic protists in sea ice has only rarely been investigated in the Arctic during the winter–spring transition period (e.g., Riedel et al. 2006, 2007a, 2008). This study reports one of the most complete seasonal time series on the taxonomic composition and abundance of bottom ice diatoms, nanoflagellates and dinoflagellates in the Arctic under two contrasting irradiance conditions. In this section, we will discuss: (1) the role of meteorological and hydrodynamic factors with respect to the temporal variability of the protist community, (2) the influence of snow cover on the net observed growth rates, cell abundance and taxonomic composition of diatoms and other protists throughout the study period, (3) the importance of improving our knowledge on the ecology of heterotrophic protists and key ice species, and (4) the significance of nutrient supply for the large-scale horizontal distribution of chl *a* biomass in the bottom ice.

2.4.1. Seasonal and short-term variability

During the present study, the chl *a* biomass and protist abundance in the bottom landfast ice horizon increased gradually from the end of February to the end of May, in parallel with seasonal increases in incident irradiance, air temperature and ice thickness (Figs. 2a–c & 4a, b, Table 1). The protist community then declined rapidly during the melt period, following the increase in air temperature and decreases in ice thickness and surface water salinity.

As the season progressed, there is evidence that surface water NO_3 concentration decreased gradually as a result of its consumption by algae (Figs. 3a & 4a, b). This is

supported by the negative correlations between surface NO_3 concentration and bottom ice chl *a* biomass and protist abundances under both snow covers (Table 3). This is also supported by estimates of the depletion time of dissolved inorganic nitrogen (DIN) (i.e., the ratio of DIN concentration to net daily accumulation rate of PON) by bottom ice algae during the bloom period, using data from the same sampling sites published in Riedel et al. (2008). Based on the net daily accumulation rates of POC in the bottom ice, the POC:PON molar ratio of 7.0 and the median DIN concentrations in the bottom ice for the bloom period, we calculated a depletion time of DIN of 0.6–1.0 d. Hence, without replenishment from the water column, DIN at the ice–water interface would have been rapidly depleted by ice algal consumption.

From the seasonal pattern observed, three periods in the bottom ice protist development were distinguished. Based on trends under low snow cover, these periods were: (1) a pre-bloom period (24 February–25 March) characterized by low chl *a* biomass and cell abundance but high net observed growth rates, (2) a bloom period (3 April–23 May) defined by a rapid increase in chl *a* biomass and cell concentrations and lower net observed growth rates, and (3) a declining phase (post-bloom, after 23 May) that coincided with the start of the ice melt (Fig. 4a, b). A similar pattern was also observed under high snow cover, however, the bloom at these sites was delayed by one week and the net observed growth rates did not decrease during the bloom period. In addition, the chl *a* biomass and total protist abundance were generally lower under the high snow cover, as discussed in the next section. The seasonal pattern observed is typical for the bottom

landfast ice community reported throughout the Arctic (Gosselin et al. 1990, Welch et al. 1991, Michel et al. 1996).

During the bloom period, the ice protist community also showed short-term variability superimposed on the seasonal trend. The decrease in bottom ice chl *a* biomass and protist abundance from 6 to 13 May (Fig. 4a, b) under both snow covers coincided with an increase in biogenic silica sinking fluxes in the upper 25 m of the water column (Juul-Pedersen et al. 2008). Since this event occurred during the spring tide, we hypothesize that part of the bottom ice community was washed away by stronger tidal currents. In addition, relatively elevated bottom ice chl *a* biomass and protist abundance compared to the general trend were measured under high snow cover on 13 April, 3–6 May and 23 May (Fig. 4a, b). These values were similar to those determined under low snow cover at this time of the year. This suggests that sites sampled on these days were likely covered by little (or less) snow prior to sampling. Hence, the patchy distribution of the bottom ice protist communities under the high snow cover can be attributed to shifting snowdrifts and new snow. These results support the hypothesis that meteorological and hydrodynamic forcings affect the temporal and horizontal variability of the bottom ice protist community in southeastern Beaufort Sea, as has been shown in other Arctic environments by Gosselin et al. (1985, 1986), Cota et al. (1987), Welch et al. (1991) and Mundy et al. (2007).

2.4.2. Snow cover effect on net observed growth rate, cell abundance and taxonomic composition of ice protists

Throughout the sampling period, the net observed growth rate, abundance and taxonomic composition of the bottom ice photosynthetic protists were influenced by snow cover depth, which strongly influences light transmission through the ice sheet (Maykut 1985, Perovich 1990, Belzile et al. 2000). Indeed, diatom abundance was significantly lower under high snow cover, while nanoflagellates and dinoflagellates showed no differences between the two snow depths (Table 1). In addition, the bottom ice algal bloom, which was mostly composed of pennate diatoms, was delayed by one week under high snow cover (Figs. 4a, b & 5), as mentioned previously. These results indicate that diatoms were more affected by light conditions than nanoflagellates and dinoflagellates. These latter two groups were composed of photosynthetic and heterotrophic organisms, as discussed in the next section.

By the end of February, the bottom ice irradiance was sufficient to allow diatom growth under low snow cover (Fig. 5c). Unfortunately, sub-ice irradiance was measured only on one occasion prior to the bloom period. On 18 March, the sub-ice irradiance was 2.6 and 5.8 μmol photons m^{-2} s^{-1} under high and low snow cover, respectively. These values are within the range of irradiance sufficient to trigger the growth of autotrophic protists in the bottom ice horizon (i.e., 2–9 μmol photons m^{-2} s^{-1}: Horner & Schrader 1982, Gosselin et al. 1985).

Under low snow cover sites, the net observed growth rates of diatoms and nanoflagellates were significantly higher before (0.15–0.23 d^{-1}) than during (0.03–0.09 d^{-1}) the bloom period (Table 2). This seasonal decrease in net observed growth rates was also observed for algae determined by epifluorescence microscopy from the same sampling site

(Riedel et al. 2008). This general pattern of decreasing net observed growth rate, as the biomass of protists accumulates in the environment, is similar to that observed during phytoplankton development in a stratified water column (Parsons et al. 1984b). The smaller net observed growth rates later in the season may result from losses of bottom ice protist cells by sinking, grazing, viral lysis and/or ablation.

In contrast to sites under low snow cover, the net observed growth rates of diatoms and nanoflagellates under high snow cover remained relatively constant during the pre-bloom and bloom periods. This difference in net observed growth rates between the two snow cover sites may be explained by earlier nutrient limitation under low snow sites due to the higher algal biomass (Gosselin et al. 1990, Smith et al. 1997) or, alternatively, by less intense grazing pressure on the protist community by copepods and other metazoans (Nozais et al. 2001, Seuthe et al. 2007) under the high snow cover site due to the lower food availability. It is interesting to note that the net observed growth rate of dinoflagellates was relatively constant during the pre-bloom and bloom periods under both snow covers (i.e., 0.04–0.05 d^{-1}). This result suggests that this group, which was not affected by the light regime, was mainly composed of heterotrophic organisms, as discussed in the next section.

The decline of the bottom ice community under both snow covers after 23 May was related to a combination of factors including nutrient deficiency, as suggested by the sudden increase in POC:chl *a* ratios from ca. 41 to 184 g:g after 23 May, and melting processes, as indicated by the thinning of the sea ice and the freshening of the surface water.

The taxonomic composition was also affected by the snow cover depth throughout the study. Colonial and solitary diatom taxa were more abundant under low snow than high snow cover (Table 1). Among the colonial pennate diatoms, *Nitzschia frigida*, *Navicula* sp. 6, *Nitzschia promare*, *Navicula septentrionalis*, *Pseudo-nitzschia* cf. *pseudodelicatissima*, *Nitzschia neofrigida*, *Entomoneis kjellmanii*, *Nitzschia arctica*, *Synedropsis hyperborea*, *Pauliella taeniata* and *Entomoneis kjellmanii* var. *kariana* were at least two to three times more abundant under low snow than high snow cover, whereas the centric diatom *Melosira arctica* was 16 times more abundant (Table 4). The only solitary centric diatom showing higher abundances under low snow cover was the epiphytic species *Attheya septentrionalis*, which was mainly attached to *Nitzschia frigida*, as previously reported by von Quillfeldt (1997). Even though the total abundance of nanoflagellates was not affected by snow depth, the colonial species *Dinobryon faculiferum* and flagellates >10 µm were two to three times more abundant under low snow than high snow cover, while the heterotrophic species *Telonema subtilis* (Shalchian-Tabrizi et al. 2006) was two times more abundant under high snow cover (Table 4). Hence, snow cover depth is a key factor influencing the composition of the bottom ice protist community from late winter to the end of spring.

2.4.3. Heterotrophic organisms

There is evidence showing that the flagellate community was dominated by heterotrophic organisms prior to the bloom period under high snow cover. First, the low chl *a*:protist abundance ratio (<3.15 pg cell^{-1}) and high POC:chl *a* ratio (>118 g:g) under

high snow compared to low snow cover (Fig. 4c, d) indicate a predominance of heterotrophic biomass in the bottom ice prior to 3 April. Secondly, these observations are supported by direct enumeration of heterotrophic bacteria and protists using epifluorescence microscopy by Riedel et al. (2007a). This is also supported by a carbon budget indicating that heterotrophs represented 72% of the total carbon biomass (i.e., heterotrophic protists + bacteria + algae) under high snow cover compared to 15% under low snow cover during the pre-bloom period (Riedel et al. 2008).

The occurrence of phagotrophic taxa such as *Telonema subtilis*, choanoflagellates, and unidentified *Gymnodinium/Gyrodinium* indicates that heterotrophic protists were present under both snow covers throughout the study (Table 4). Furthermore, microscopic observations of diatom cells ingested by dinoflagellates and Euglenophyceae indicate that phagotrophic activity was occurring during the bloom period, as observed by Riedel et al. (2007a). As reported by these authors, heterotrophic flagellates were probably using dissolved organic carbon, exopolymeric substances, bacteria and/or small algae to satisfy their energy requirements. Hence, bottom ice flagellates and dinoflagellates are composed of a mixed community of autotrophic, heterotrophic and mixotrophic protists, which needs to be studied in more detail.

2.4.4. Key species

Regardless of the snow thickness on sea ice during the study, the taxonomic composition of the bottom ice diatom community was comparable to that reported in other Arctic landfast ice regions (Hsiao 1980, 1992, Horner & Schrader 1982, Poulin et al. 1983,

Okodlokov 1992, Ratkova & Wassmann 2005). All these studies showed that pennate diatoms dominated over centric diatoms, except in White Sea landfast and pack ice (Ratkova & Wassmann 2005). We recorded a total of 95 pennate and 6 centric diatom taxa in Franklin Bay, which is comparable to the values ranging from 91 to 139 pennate and 7 to 16 centric diatoms reported from Eskimo Lakes, Eclipse Sound and Frobisher Bay (Hsiao 1980), southeastern Hudson Bay (Poulin et al. 1983), and the Laptev, East Siberian and Chukchi seas (Okolodkov 1992). However, these numbers are low compared to the 233 diatom taxa recorded from two cores collected on first-year pack ice of the Chukchi Sea by von Quillfeldt et al. (2003).

The arborescent colonial species *Nitzschia frigida* was the most abundant diatom during this study. However, *Fragilariopsis cylindrus* (formerly *Nitzschia cylindrus* (Grunow) Hasle) was reported as the most abundant diatom species in the Alaskan Beaufort Sea during the bottom ice algal bloom (Horner & Schrader 1982). In Franklin Bay, this species never represented more than 1.4% of the total diatom abundance. *Nitzschia frigida* has been frequently observed in many other circumarctic regions, such as the Chukchi Sea (Okolodkov 1992, von Quillfeldt et al. 2003), Eskimo Lakes (Hsiao 1980), Resolute Passage (Sime-Ngando et al. 1997), Eclipse Sound and Frobisher Bay (Hsiao 1980), Northeast Water off Greenland (von Quillfeldt 1997), the Barents Sea (Syvertsen 1991), the White Sea (Ratkova & Wassmann 2005), and the Laptev and East Siberian seas (Okolodkov 1992) as well as in the central Arctic Ocean (Booth & Horner 1997, Gosselin et al. 1997). The consistent occurrence of *N. frigida* in bottom sea ice throughout the Arctic can be explained by the fact that this species is extremely well-adapted to a wide range of

light regimes. Indeed, Hegseth (1992) showed in the laboratory that this species can grow well at a constant temperature of –0.5°C under irradiances varying from 10 to 400 µmol photons m^{-2} s^{-1}, maintaining a maximum growth rate at irradiances from 50 to 400 µmol photons m^{-2} s^{-1}. The physiological characteristics of *N. frigida* make it the most frequent and most abundant species of the Arctic sea-ice habitat.

During the present study, 3 classes of diatoms and 9 classes of flagellated cells were found in the bottom ice of Franklin Bay (Table 4). These numbers are comparable to the 7 and 12 non-diatom algal classes reported in the sea ice of the North Water (northern Baffin Bay) by Simard (2003) and the Barents and White seas by Ratkova & Wassmann (2005), respectively, during spring. In Arctic sea-ice studies, the importance of pico-, nano- and microflagellates has been largely overlooked, due in part to methodological problems inherent to the melting process of sea-ice samples (Garrison & Buck 1986). Some chrysophytes and dinoflagellates have been previously recognized at the species level, but very often these non-diatom cells have simply been grouped together and listed as unidentified flagellates (e.g., Hsiao 1980, Horner & Schrader 1982, Poulin et al. 1983, Okodlokov 1992). However, working with non-preserved samples, Ikävalko & Gradinger (1997) identified 40 and 43 flagellate taxa belonging to 10 classes in newly formed sea ice and multi-year ice floes, respectively. Therefore, when the aim is to identify flagellated cells or other delicate protists, it is highly recommended to adequately prepare melted sea-ice samples in the field following the method of Garrison & Buck (1986) or collect brine samples (Stoecker et al. 1997) and to identify live cells with light or electron microscopy,

to maintain cultures, or to use current molecular tools (Lovejoy et al. 2006). This will improve our knowledge of this understudied protist group.

2.4.5. Influence of nutrient supply on the large-scale horizontal distribution of bottom ice algae

The maximum bottom ice chl *a* concentration of 31 mg m^{-2} recorded during this study is similar to concentrations reported for Barrow, Alaska (27 mg m^{-2}; Lee et al. 2008), the Alaskan Beaufort Sea (27 mg m^{-2}; Horner & Schrader 1982), Jones Sound (23 mg m^{-2}; Apollonio 1965), Frobisher Bay (30 mg m^{-2}; Hsiao 1980) and southeastern Hudson Bay (25–40 mg m^{-2}; Gosselin et al. 1986, 1990), but two to ten times lower than the values recorded for northwestern Hudson Bay (170 mg m^{-2}; Welch et al. 1991) and Resolute Passage (77–325 mg m^{-2}; Smith et al. 1988, Michel et al. 1996).

Since the sunlight period and snow conditions are comparable in all these Arctic regions, the differences in bottom ice algal biomass are probably related to the water column dynamics and nutrient supply. In Franklin Bay, surface water NO_3 was low compared to PO_4 and $Si(OH)_4$ (Fig. 3) and could have limited the accumulation of algal biomass in the bottom ice horizon. In this study, surface water NO_3 concentrations (0.2–3.1 µmol l^{-1}) were similar to those reported for southeastern Hudson Bay (0.2–3.3 µmol l^{-1}; Gosselin et al. 1985, 1990) but several times lower than those from the Alaskan Beaufort Sea (6–9 µmol l^{-1}; Horner & Schrader 1982) and Barrow Strait (2–10 µmol l^{-1}; Cota et al. 1990). Carmack et al. (2004) proposed that low NO_3 availability in the upper water column of the Canadian Beaufort Sea result from the formation of a strong halocline at the base of

the winter mixed layer, which restricts nutrient-rich waters of Pacific origin from entering the euphotic zone. As the maximum biomass attained in the bottom ice can be limited by nutrient supply (Maestrini et al. 1986, Welch et al. 1991), it is plausible that the NO_3 availability is responsible for the relatively low ice algal biomass reached during the bloom period in the Canadian Beaufort Sea and possibly in other Arctic regions.

In order to test this hypothesis, maximum bottom ice chl *a* concentrations reported from different studies conducted on Arctic first-year landfast ice were plotted against mean surface water NO_3 concentrations observed during the vernal growth season (Fig. 6). The data show a Monod-type relationship between the two variables, with chl *a* concentrations up to 320 mg m^{-2} at NO_3 concentrations $\geq$6 µmol l^{-1} (Fig. 6).

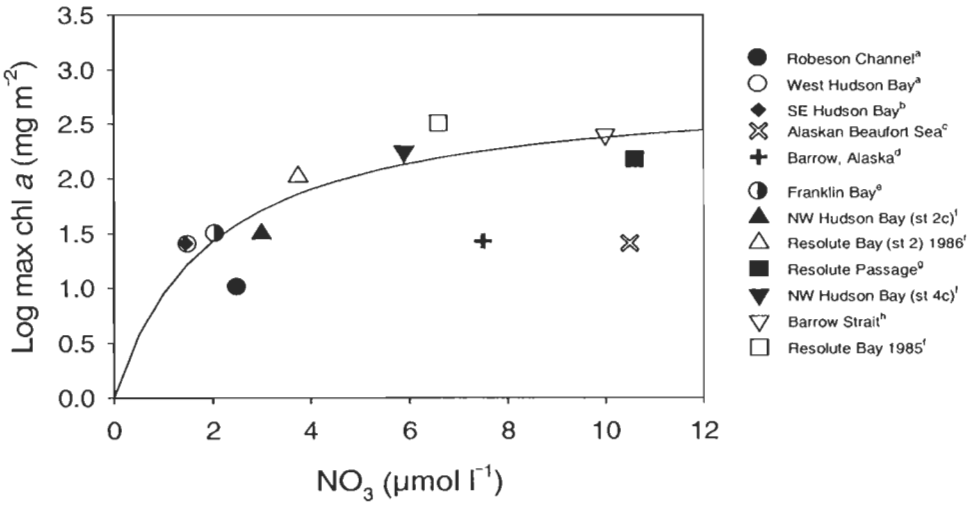

Fig. 6. Relationship between maximum bottom ice chlorophyll *a* (chl *a*) concentrations and NO_3 concentrations in the surface water from different studies conducted on Arctic first-year landfast ice: [a] Dunbar & Acreman (1980), [b] Gosselin et al. (1990), [c] Horner & Schrader (1982), [d] Lee et al. (2008), [e] present study, [f] Welch et al. (1991), [g] Levasseur et al. (1994) and [h] Smith et al. (1990). In Welch et al. (1991), NO_3 concentrations were measured in the upper water column. Note log scale on Y-axis. The curve is calculated using eq. (1): $B_{max} = 2.85$, $K_m = 1.99$ µmol l^{-1}, $r^2 = 0.91$). The encircled data were excluded from the regression

This equation fits the data very well ($r^2 = 0.91$). These results indicate that the availability of NO_3 in the surface water can be limiting for the accumulation of bottom ice algae during the spring bloom in Arctic waters. In nitrate-rich waters (e.g., >12 $\mu mol\ l^{-1}$), however, dense algal populations may experience some degree of light limitation from self-shading toward the bottom of the algal horizon (Cota & Horne 1989).

In the Alaskan Beaufort Sea (Horner & Schrader 1982) and at Barrow, Alaska (Lee et al. 2008), the maximum chl *a* concentration is one order of magnitude lower than values from other stations with similar surface water NO_3 concentrations (Fig. 6). Disruption of the bottom ice skeletal layer by strong currents and tides (see Lee et al. 2008), reduced light transmission to the bottom ice caused by sediments entrapped in the top sea-ice layer, nutrient deficiency by an element other than nitrogen, viral lysis or intense grazing pressure may have limited the accumulation of algae in the bottom ice at these shallow Alaskan coastal sites (i.e., 4–7 m) in spring.

Our overall results indicate that the small-scale horizontal variability in ice algal biomass and composition is controlled by snow distribution, whereas the large-scale distribution may be governed by nutrient supply from the water column. This supports the early model of bottom ice dynamics proposed by Gosselin et al. (1985) and Welch et al. (1991), in which the production of ice algal biomass is controlled not only from above, by the seasonal changes in irradiance, but also from below, by the vertical mixing that replenishes the ice–water interface with nutrients, and as recently shown by Lavoie et al. (2005) in a coupled sea-ice model of ice algal growth and decline.

2.5. Conclusion

In the Canadian Beaufort Sea, the accumulation of algae and other protists in the bottom horizon of first-year landfast ice starts as early as the end of February, with higher net observed growth rates of diatoms and nanoflagellates during the pre-bloom than during the bloom period under low snow cover. In contrast, the net observed growth rate of dinoflagellates did not change during the bloom period under both snow covers. These results show the differential response of the bottom ice protist communities to changes in the light regime during the winter–spring transition.

Flagellated cells represented, on average, 28% of the total protist abundance. Past studies have underestimated the occurrence and abundance of this group in Arctic sea ice. Prior to the bloom, flagellated cells, which were presumably heterotrophic, dominated under high snow cover whereas autotrophic protists, especially solitary diatoms, prevailed under low snow cover. During the bloom period, colonial diatoms dominated in the bottom ice community irrespective of the snow depth, although higher abundances were observed under low snow cover. Moreover, the arborescent colonial diatom *Nitzschia frigida* was the most abundant bottom ice algal species throughout the entire season. *Nitzschia frigida* can be considered a key species of landfast ice across circumarctic regions. During the post-bloom period, the decline of colonial and solitary diatom abundances was faster than that of nanoflagellates, suggesting that nanoflagellates, presumably heterotrophic (Riedel et al. 2008), can survive under melting sea-ice conditions.

Finally, our study indicates that the maximum bottom ice algal biomass attained during the vernal growth season may depend on nitrate supply from the upper water

column. Hence, the amount of nutrients available in the surface water column at the end of the winter is an important factor determining the magnitude of the ice algal spring bloom, as recently shown by the sea-ice algal model of Lavoie et al. (2005, 2009).

CHAPITRE III

SMALL-SCALE HORIZONTAL DISTRIBUTION OF BOTTOM ICE PROTISTS DURING THE VERNAL SEASON IN THE WESTERN CANADIAN ARCTIC

RÉSUMÉ

Les facteurs qui contrôlent la répartition à petite échelle (< 25 m) des algues et des autres protistes du niveau inférieur de la glace de mer ont été étudiés dans la baie Franklin, au sud-est de la mer de Beaufort à trois reprises entre le 26 avril et le 29 mai 2004. À chaque reprise, des carottes de glace ont été recueillies à 36 sites répartis également au sein d'une grille rectangulaire de 15 m par 25 m. À chaque site, nous avons déterminé la biomasse chlorophyllienne, l'abondance et la composition taxonomique des protistes, et la salinité à la base de la glace ainsi que l'épaisseur de neige, l'épaisseur de la glace, la hauteur du *freeboard* et l'irradiance à l'interface glace–eau. Les protistes de glace, en termes de biomasse chlorophyllienne et d'abondance, se répartissent en taches dont le diamètre varie entre 6 et 12 m. En général, les flagellés étaient très nombreux par rapport à l'abondance totale des protistes aux sites sous couvert de neige épais alors que les diatomées étaient très abondantes aux sites sous couvert de neige mince. La répartition horizontale des taxons de diatomées peut s'expliquer, entre autres, par les variations de l'épaisseur du couvert de neige à la fin avril et par les variations de la salinité de la glace et de l'épaisseur du couvert de neige à la fin mai. En revanche, la répartition des taxons de cellules flagellées est attribuable à une combinaison de facteurs du milieu au début de l'étude et à l'épaisseur du couvert de neige et à la salinité de la glace à la fin de l'étude. Les variations de l'épaisseur de la glace n'ont joué aucun rôle sur la répartition horizontale des taxons pendant toute l'étude. Les diatomées les plus abondantes (i.e., *Nitzschia frigida*, *Navicula* sp. 6 et *Fragilariopsis cylindrus*) ont diminué en nombre après la mi-mai tandis que *Navicula pelagica*, *N. septentrionalis*, *N. vanhoeffenii*, *Attheya septentrionalis*, *Synedropsis hyperborea* et des flagellés (6–10 µm) ont augmenté progressivement entre la

fin avril et la fin mai. Cette succession d'espèces était sans doute liée à l'augmentation saisonnière de l'irradiance atteignant la base de la glace.

ABSTRACT

Environmental factors controlling the small-scale (< 25 m) distribution of bottom ice algae and other protists were studied on three occasions between 26 April and 29 May 2004 in Franklin Bay, southeastern Beaufort Sea. Ice cores were collected at 36 sites evenly distributed in a rectangular grid of 15 by 25 m. Snow depth, ice thickness, ice freeboard height, bottom ice salinity and sub-ice irradiance were measured at each sampling site, as well as chlorophyll *a* (chl *a*) biomass, cell abundance and taxonomic composition of bottom ice protists. The bottom ice chl *a* biomass and protist abundance showed distribution in small patches (6–12 m in diameter). Flagellated taxa were usually highly numerous in proportion to the total protist abundance at high snow sites, while diatoms were very abundant at low snow sites. The horizontal distribution of diatom taxa can result from variations in the snow depth at the end of April and variations in the bottom ice salinity and snow depth at the end of May. On the other hand, the distribution of flagellated taxa could be explained by a combination of environmental factors at the beginning of the study and by snow depth and bottom ice salinity at the end of the sampling period. The variations in ice thickness were not important in the horizontal distribution of bottom ice protists in this small-scale study. The most abundant diatoms, i.e., *Nitzschia frigida*, *Navicula* sp. 6 and *Fragilariopsis cylindrus* decreased in number after mid-May, whereas *Navicula pelagica*, *N. septentrionalis*, *N. vanhoeffenii*, *Attheya septentrionalis*, *Synedropsis hyperborea* and the flagellates (6–10 µm) steadily increased from the end of April to the end of May. This species succession was most likely related to surface water nutrient depletion and the seasonal increased in irradiance reaching the bottom ice horizon.

3.1. Introduction

The spatial distribution of microalgae in aquatic and marine system is heterogeneous (Denman & Platt 1976, Denman et al. 1977, Antoine et al. 2005). This heterogeneity is due to an equilibrium state between physical and biological processes. On one hand, physical processes such as upwelling, wind or tidal mixing tend to homogenize aquatic ecosystems. On the other side, biological processes such as algal growth promote heterogeneities in the biomass (Denman & Platt 1976, Denman et al. 1977, Gosselin et al. 1986). The horizontal distribution of bottom ice algal biomass is also reported to be patchy (Gosselin et al. 1986, Robineau et al. 1997, Rysgaard et al. 2001, Granskog et al. 2005, Mundy et al. 2007b), however, only a few studies investigated the horizontal distribution of algae and other protist taxa in the bottom ice horizon (e.g., Poulin et al. 1983, Legendre et al. 1991, Monti et al. 1996). At large scales (> 10 km), the horizontal distribution of sea-ice algae is attributed to latitude (i.e., variation in short wave insulation), surface water salinity, ice formation processes and nutrient availability (Garrison et al. 1983, Poulin et al. 1983, Booth 1984, Clarke & Ackley 1984, Gosselin et al. 1986, 1990, Granskog et al. 2005, Chapitre II). At the mesoscale (0.1–10 km), ice salinity and growth rate (Poulin et al. 1983, Legendre et al. 1991) and the hydrographic regime of the underlying water column (e.g., currents, stratification, surface water salinity) (Robineau et al. 1997, Granskog et al. 2005) can be responsible for the variability in ice algal biomass. At the marginal ice zone, the mesoscale distribution of bottom ice algae may be influenced by krill grazing (Schnack-Schiel 2003). At the small scale (1–100 m), the spatial distribution of the bottom ice algal biomass is most often influenced by snow distribution over the ice surface, which controls

the irradiance transmitted to the bottom ice layer (Horner & Schrader 1982, Gosselin et al. 1986, Rysgaard et al. 2001, Mundy et al. 2005). Recently Mundy et al. (2007b), using *in situ* photographic techniques, investigated the microscale (0.01–1 m) variability in the bottom ice algal biomass in relation to the bottom ice morphology. They showed a higher accumulation of algal biomass along crystal lamellae and brine channels.

At present, only a few studies have assessed the factors controlling the horizontal distribution of bottom ice algal taxa. In southeastern Hudson Bay, the number of diatom taxa in the bottom ice increased along an inshore-offshore salinity gradient associated with an under-ice river plume (Poulin et al. 1983, Legendre et al. 1991, Monti et al. 1996). It was suggested that the salinity gradient was affecting the taxonomic composition of ice diatoms directly through osmotic or other physiological effects, or indirectly by changing the physical properties of sea ice (Poulin et al. 1983, Legendre et al. 1992). However, to our knowledge, the spatial heterogeneity of diatom and other protistan taxa in the bottom ice was never studied at a small scale.

The main objectives of this study were to estimate the patchiness of the bottom ice protist community at different periods of the vernal growth season and to determine which environmental variables best explain the horizontal variability, and how it influences the taxonomic composition, in first-year landfast ice.

3.2. Materials and methods

3.2.1 Study site and sampling

Sampling was carried out on first-year landfast ice in Franklin Bay, southeastern Beaufort Sea, Northwest Territories (Fig. 1) on three occasions (26 April, 10 May and 29 May 2004). The station was located 1.5 km northeast of the overwintering location of the research icebreaker CCGS *Amundsen* as part of CASES.

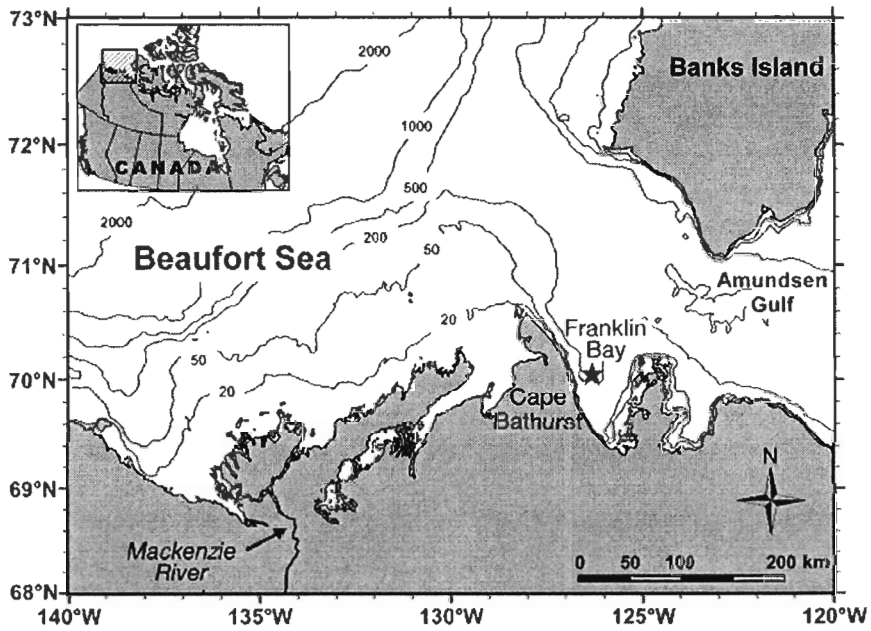

Fig. 1. Location of the sampling station (*) in Franklin Bay. Water depth in m

On each sampling day, ice cores were collected at 36 sites evenly distributed in a rectangular grid of 15 by 25 m. Ice cores were sampled with a Mark II ice corer (9 cm internal diameter, Kovacs Enterprises). The bottom 4 cm of each ice core was cut with a stainless steel saw and stored in separate isothermal plastic containers for subsequent biological analyses. Snow depth, ice thickness and ice freeboard height were measured at each sampling site. At selected sites (ca. 6 for each grid), sub-ice irradiance was measured with a Li-Cor LI-192SA underwater quantum sensor. Under-ice water samples were

collected with a hand-pump system for surface water salinity determination. During the sampling, downwelling incident irradiance (LI-190SA quantum sensor) and air temperature were monitored every 10 min and 2–6 h, respectively.

3.2.2. Laboratory analyses

In the ship's laboratory, the ice core samples from each site were slowly melted in 500 ml of surface seawater filtered on 0.2 µm polycarbonate membrane filters to minimize osmotic stress on the ice protists (Bates & Cota 1986, Garrison & Buck 1986). Duplicate subsamples were filtered through Whatman GF/F glass fiber filters and 5 µm polycarbonate Nuclepore membrane filters for chlorophyll *a* (chl *a*) determination. Chl *a* concentrations were determined using a Turner Designs 10-AU fluorometer after 24 h extraction in 10 ml of 90% acetone at 5°C in the dark (Parsons et al. 1984a). For the identification and enumeration of diatoms, flagellates and dinoflagellates, melted ice subsamples were preserved in acidic Lugol solution (Parsons et al. 1984a). Cells > 4 µm were identified to the lowest possible taxonomic rank and counted using an inverted microscope (WILD Heerbrugg) operating with phase contrast optics (Lund et al. 1958). A minimum of 400 cells was counted in each settling chamber. The following references were used for ice protist identification: Poulin & Cardinal (1982a, b, 1983), Medlin & Hasle (1990), Medlin & Priddle (1990), Thomsen (1992), Hasle et al. (1994), Tomas (1996), von Quillfeldt (1997, 2001), Bérard-Therriault et al. (1999) and Horner (2002). The concentration of chl *a* and abundance of protists were corrected for the dilution effect of added seawater as described in Cota & Sullivan (1990). The salinity of the diluted ice cores and the under-ice

water samples was determined with a portable Orion salinometer and Guildline 8400B Autosal Lab salinometer, respectively. The salinity of the ice cores was calculated using the following equation which is based on the conservation law:

$$C_{ICE} = (C_T V_T - C_{SW} V_{SW}) / (V_T - V_{SW}) \quad (1)$$

where: C_{ICE} is the ice core salinity, C_T is the salinity of the melted ice core with added surface seawater, V_T is the total volume of the melted ice core with added surface seawater (l), C_{SW} is the salinity of the added surface seawater, and V_{SW} is the volume of the added surface seawater (l).

3.2.3. Statistical analyses

To test the hypothesis that sites from the three sampling grids had a similar taxonomic composition, a group-average linkage cluster analysis of a Bray-Curtis similarity matrix was performed, as in Różańska et al. (2008). Only taxonomic entries present in more than four samples were included in the analyses in order to reduce double zeros in the data matrix. Before calculating the similarity matrix, the abundance of protists was standardized to obtain a relative value and log (x+1) transformed to reduce the influence of the most dominant taxonomic entries, as suggested by Clarke & Warwick (2001). An analysis of similarities (one-way ANOSIM) was conducted on the same similarity matrix to test differences in the taxonomic composition between the groups of samples. The pairwise R values obtained gave an absolute measure of how separated the groups were on a scale of 0 (indistinguishable) to 1 (all similarities within groups are greater than similarities between

groups) (Clarke & Warwick 2001). A breakdown of species similarities (SIMPER) was used to determine which species combination led to the resulting groups (Clarke 1993).

The heterogeneity in the horizontal distribution of environmental and biological variables over the three grids was analyzed by spatial autocorrelation (Cliff & Ord 1981, Legendre & Legendre 1998) using Moran's (1950) *I* coefficient. When Moran's *I* exceeds the critical value (positive or negative), the null hypothesis of a random spatial distribution was rejected at the specific level of significance. A two-tailed test of significance was used since we did not have any *a priori* information on the sign of the spatial autocorrelation. A significance level of $p < 0.05$ was used. Statistical tests were performed with the R software 4.1 (Legendre & Vaudor 1991).

The links between environmental variables (i.e., snow depth, ice thickness, ice freeboard height and ice salinity) and the observed abundance of diatom and flagellated cell (i.e., flagellates and dinoflagellates) taxa were quantified using Partial Canonical Correspondence Analyses (PCCA: ter Braak 1988, Borcard et al. 1992, Legendre & Legendre 1998). This method allows identifying which environmental variable contributes most to the relationship controlling for the effect of space. Only those taxonomic entries present in more than three samples were included in the analyses. The principal coordinates of neighbor matrices (PCNM) method was used to obtain the spatial predictor in PCCA (Hill 1973, ter Braak 1985, 1986a, b, Legendre & Legendre 1998, Borcard et al. 2004). Taxa and environmental variables were plotted in the same bidimensional space defined by the chi-square distance. In the ordination plots, taxa were represented by dots and environmental variables by vectors. The total variation of taxon data was partitioned into

four fractions: (a) non-spatial environmental variation in the taxon data, (b) spatial structuring in the taxon data that is shared by the environmental data, (c) spatial patterns in the taxon data that are not shared by the environmental data, and (d) the fraction of the taxon variation explained neither by spatial coordinates nor by environmental data (Borcard et al. 1992). All analyses were performed with the R software 2.6.1 (R Development Core Team 2008).

For each variable, significant differences between the three sampling periods were tested using Kruskal–Wallis one-way analyses of variance (Sokal & Rohlf 1995). This statistical analysis was carried out using StatSoft Statistica 6. Figures 2–5 were produced with the Ocean-Data-View Software (Schlitzer 2007).

3.3. Results

3.3.1. Temporal variability

During this study, the environmental and biological variables showed significant temporal (Table 1) and spatial variability (see below). From 26 April to 29 May, the incident irradiance and average daily air temperature increased, whereas surface water salinity remained relatively constant (Table 1). Snow depth and relative abundance of flagellates were significantly lower on 29 May than during the two previous sampling dates. Ice thickness, sub-ice irradiance, chl *a* concentration, total protist abundance, abundance of diatoms, flagellates, dinoflagellates, and relative abundance of diatoms, dinoflagellates and empty diatom frustules were significantly higher during the two last sampling dates than on 26 April. Average values in bottom ice salinity, ice freeboard height

and relative contribution of large algal cells (> 5 μm) to total chl *a* concentration did not change throughout the season.

During the study, diatoms, flagellates and dinoflagellates made up, on average, 76.3–84.4%, 14.4–23.1% and 0.5–1.2 % of the total protist abundance, respectively (Table 1). The bottom ice diatom community was always dominated by colonial pennate taxa, such as *Nitzschia frigida*, *Navicula pelagica* and *Navicula* sp. 6, in addition to an important contribution of non-diatom cells < 10 μm, which were composed of unidentified flagellates (Table 2). The spatial variations of these three colonial diatom taxa and nanoflagellates < 10 μm in terms of cell abundances during the three sampling days are presented in Fig. 4. The abundance of *Nitzschia frigida* was significantly ($p \leq 0.05$) higher on the last two sampling days in May than on 26 April (Fig. 4a, e, l). The abundances of *Navicula pelagica* and nanoflagellates < 10 μm increased significantly ($p \leq 0.05$) throughout the season (Fig. 4b, d, f, h, j, l), whereas the maximum cell number of *Navicula* sp. 6 was observed on 10 May (Fig. 4c, g, k).

Table 1. Range and mean values of environmental and biological variables measured in three grids carried out 26 April, 10 and 29 May 2004 on first-year landfast ice in Franklin Bay. *: significant differences ($p \leq 0.05$) between 26 April, 10 and 29 May represented by [a], [b] and [c], respectively. Sub-ice irradiance was measured at selected sites; na: not available

	26 April	10 May	29 May
Variable	Min (Mean) Max	Min (Mean) Max	Min (Mean) Max
Incident irradiance (mol photons m^{-2} d^{-1})	44.8	54.6	na
Surface water salinity	31.1	30.8	31.0
Air temperature (°C)	–22 (–18) –14	–12 (–11) –10	–10 (–4.6) –0.6
Snow depth (cm)	5.5 (14.7) 26.5	3.0 (12.7) 37.0	0.5 (7.7) 23.0*[a,b]
Ice freeboard height (cm)	10.5 (14.7) 19.5	12.5 (14.3) 16.0*[c]	13.5 (16.8) 22.0
Ice thickness (m)	1.67 (1.83) 1.92*[b, c]	1.85 (1.94) 2.00	1.87 (1.97) 2.05
Ice salinity	2.7 (5.7) 9.1	4.4 (6.5) 8.8	4.3 (6.9) 9.5
Sub-ice irradiance (µmol photons m^{-2} s^{-1})	0.7 (2.9) 4.9*[b, c]	0.7 (9.0) 23.2	6.2 (13.2) 19.4
Chlorophyll *a* (mg m^{-2})	0.3 (6.5) 16.5*[b, c]	3.3 (15.5) 28.1	2.2 (12.5) 25.6
Chlorophyll *a* > 5 µm (%)	49.9 (94.4) 100	49.9 (95.4) 100	84.0 (96.6) 100
Total protists (10^9 cells m^{-2})	0.02 (0.74) 2.09*[b, c]	0.34 (2.56) 5.01	0.33 (2.58) 7.16
Diatoms (10^9 cells m^{-2})	0.01 (0.61) 1.85*[b, c]	0.21 (2.11) 4.48	0.19 (2.30) 6.52
Flagellates (10^9 cells m^{-2})	0.01 (0.12) 0.31*[b, c]	0.11 (0.43) 0.81*[c]	0.06 (0.26) 0.61
Dinoflagellates (10^9 cells m^{-2})	0 (0.003) 0.01*[b, c]	0.002 (0.02) 0.04	0.004 (0.02) 0.05
Diatoms (%)	39.4 (76.3) 92.8*[c]	53.8 (79.2) 89.4*[c]	57.9 (84.4) 96.1
Flagellates (%)	7.1 (23.1) 59.8	10.0 (19.9) 44.5	3.42 (14.4) 37.9*[a,b]
Dinoflagellates (%)	0.0 (0.5) 2.1*[b, c]	0.2 (0.9) 4.2	0.1 (1.2) 7.23
Empty diatom frustules (%)	7.8 (16.1) 25.6*[b, c]	10.0 (19.9) 44.5	17.4 (32.3) 53.2

The cluster analysis based on the similarity matrix identified four groups of taxonomically similar protist community from the 108 sites sampled on 26 April, 10 and 29 May (Fig. 5). The global one-way ANOSIM test revealed significant differences between the four groups (global $R = 0.78$, $p \leq 0.001$). A pairwise test of the one-way ANOSIM indicated that Group II was significantly different from Group I, III and IV ($R = 0.70$, 0.72, 0.86, $p \leq 0.001$, respectively). Group III was significantly different from Group I ($R = 0.94$, $p \leq 0.001$) and Group IV ($R = 0.65$, $p \leq 0.001$), while Group IV was significantly different from Group I with the lowest R value ($R = 0.54$, $p \leq 0.001$). Group I was composed of five ice core samples collected on 29 May; Group II contained the highest number of ice samples covering the three sampling dates; Group III was characterized by 13 ice core samples collected mostly on 26 April; Group IV consisted of ice core samples mainly collected on 29 May (Fig. 5).

The main protist taxa contributing to each group consisted of: Group I: *Navicula pelagica*, *Nitzschia frigida*, flagellates 6–10 µm, unidentified pennates, *Navicula* sp. 6 and *Nitzschia promare*, which all represent highly abundant ice-associated colonial diatoms; Group II: *N frigida*, *N. pelagica*, flagellates ≤ 5 µm, unidentified pennates and *Nitzschia neofrigida*, which represent the highest cell numbers for these ice-related colonial diatoms; Group III: flagellates ≤ 5 µm, unidentified pennates, *N. frigida* and *N. pelagica*, with the lowest cell numbers; and Group IV: unidentified pennates, *N. pelagica*, flagellates ≤ 10 µm, *N. frigida* and *Cylindrotheca closterium*.

3.3.2. Horizontal variability

Spatial autocorrelations revealed that all variables showed heterogeneous horizontal distributions during the three sampling dates. On 26 April, ice thickness and ice freeboard height showed significant gradients with increasing values from the northwest to the southeast corner of the grid (Fig. 2b, c). In contrast, snow depth, bottom ice salinity, chl *a* concentration, total protist, diatom and flagellate abundances showed a patchy distribution (Figs. 2a, d & 3a-d). The patch size of snow depth, chl *a* concentration, total protist and diatom abundance ranged from 5.8 to 17.5 m, whereas the patch size of bottom ice salinity and total flagellate abundance varied between 5.8 and 11.7 m. On 10 May, the only variable showing a gradient was the ice freeboard height with increasing values from the southeast to the northwest corner of the grid (Fig. 2g). All other variables showed a patchy distribution with the patch size ranging from 5.8 to 11.7 m, except for the ice thickness reaching up 17.5 m (Figs. 2e, f, h & 3e-h). On 29 May, the bottom ice salinity was the only variable showing a gradient with increasing value from the southeast to the northwest corner of the grid (Fig. 2l). All other variables showed a patchy distribution with the patch size ranging from 5.8 to 11.7 m for chl *a* concentration and total protist abundance, from 5.8 to 17.5 m for ice thickness and total flagellate abundance, and from 17.5 to 23.3 m for ice freeboard height (Figs. 2i-k & 3i-l).

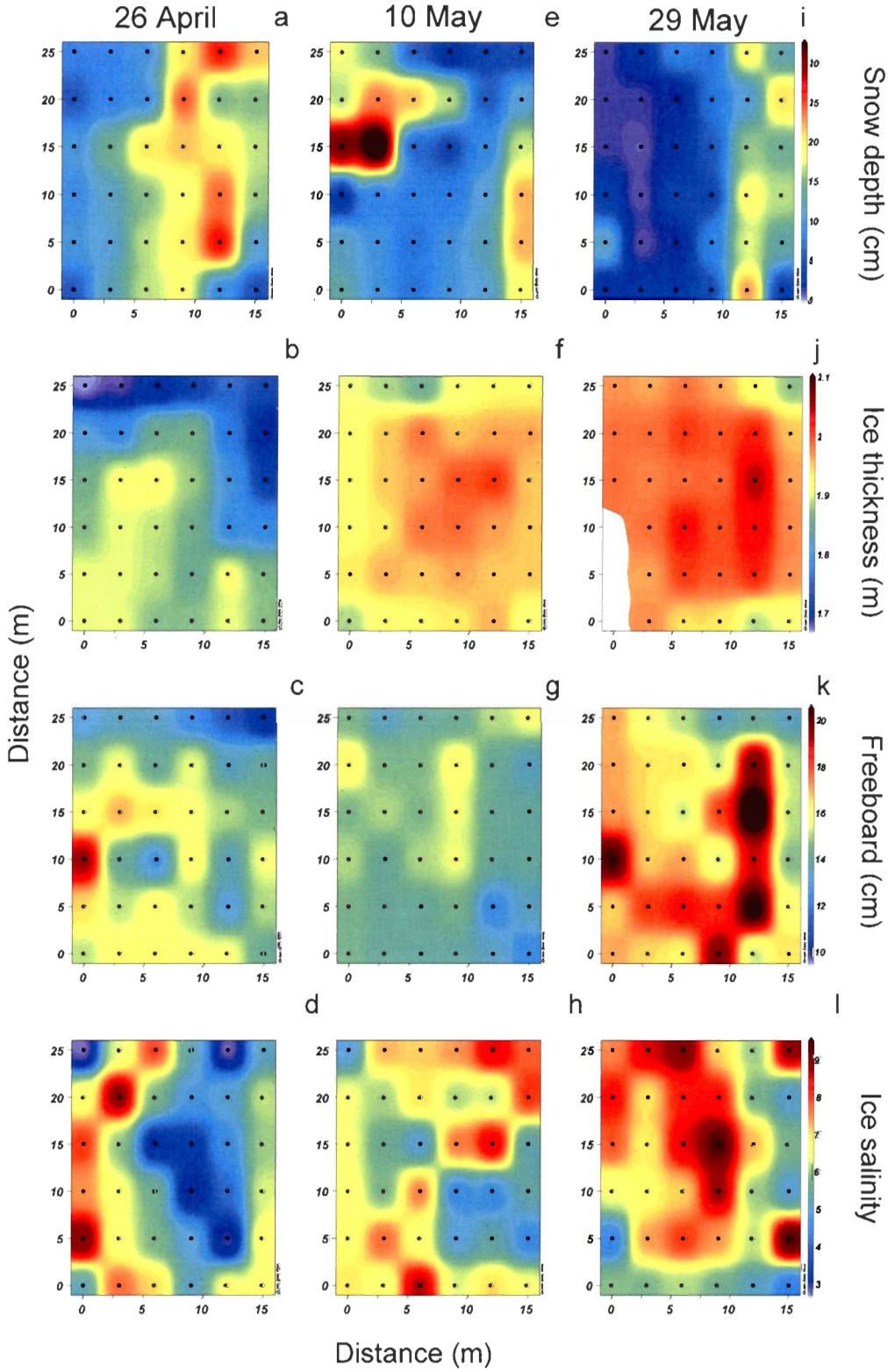

Fig. 2. Horizontal variations in (a, e, i) snow depth, (b, f, j) ice thickness, (c, g, k) ice freeboard height, and (d, h, l) bottom ice salinity in Franklin Bay on (a–d) 26 April, (e–h) 10 May and (i–l) 29 May 2004

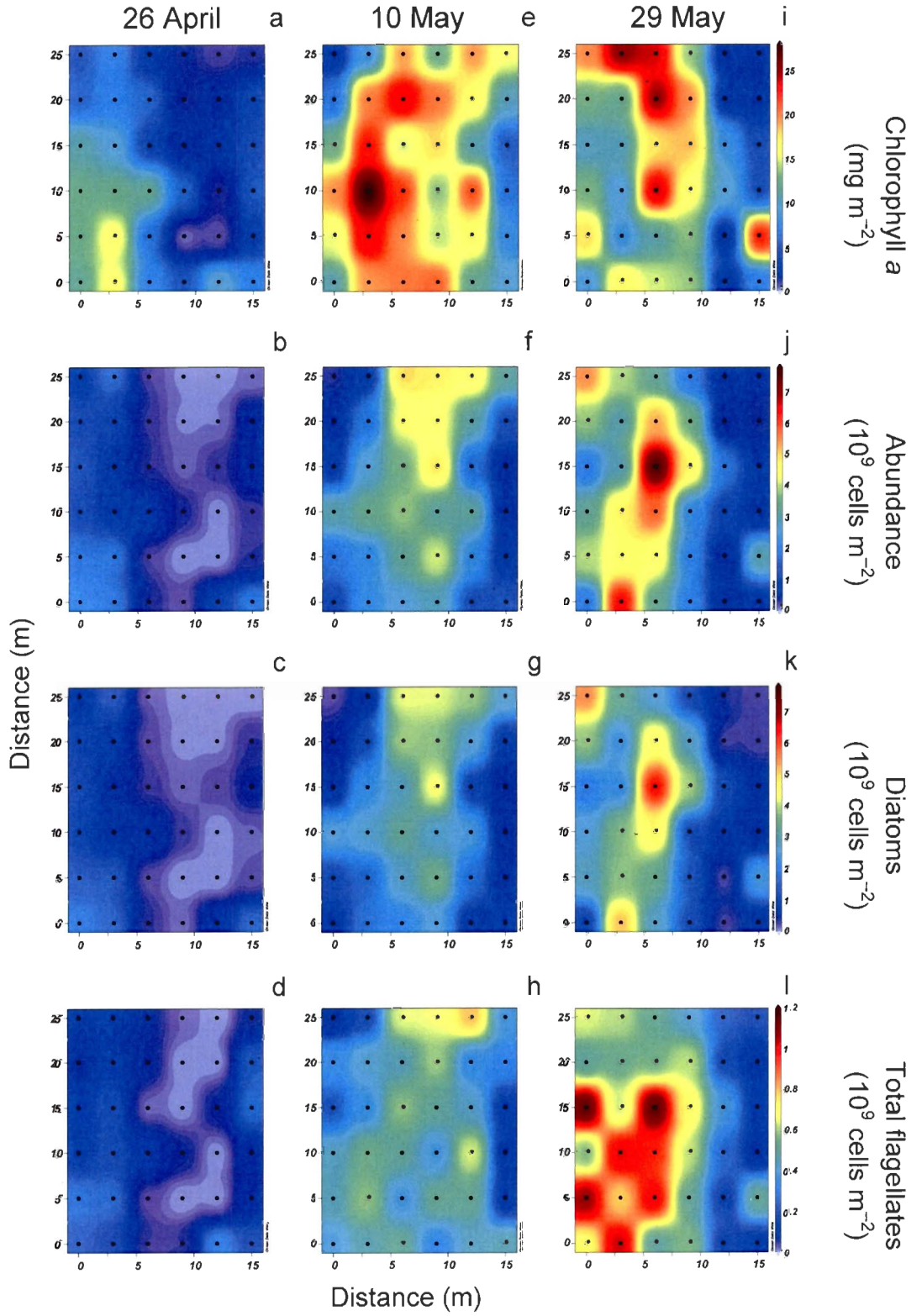

Fig. 3. Horizontal variations in (a, e, i) chlorophyll *a* concentration, and (b, f, j) total protist, (c, g, k) diatom and (d, h, l) total flagellate (dinoflagellates + flagellates) abundances in the bottom ice of Franklin Bay on (a–d) 26 April, (e–h) 10 May and (i–l) 29 May 2004

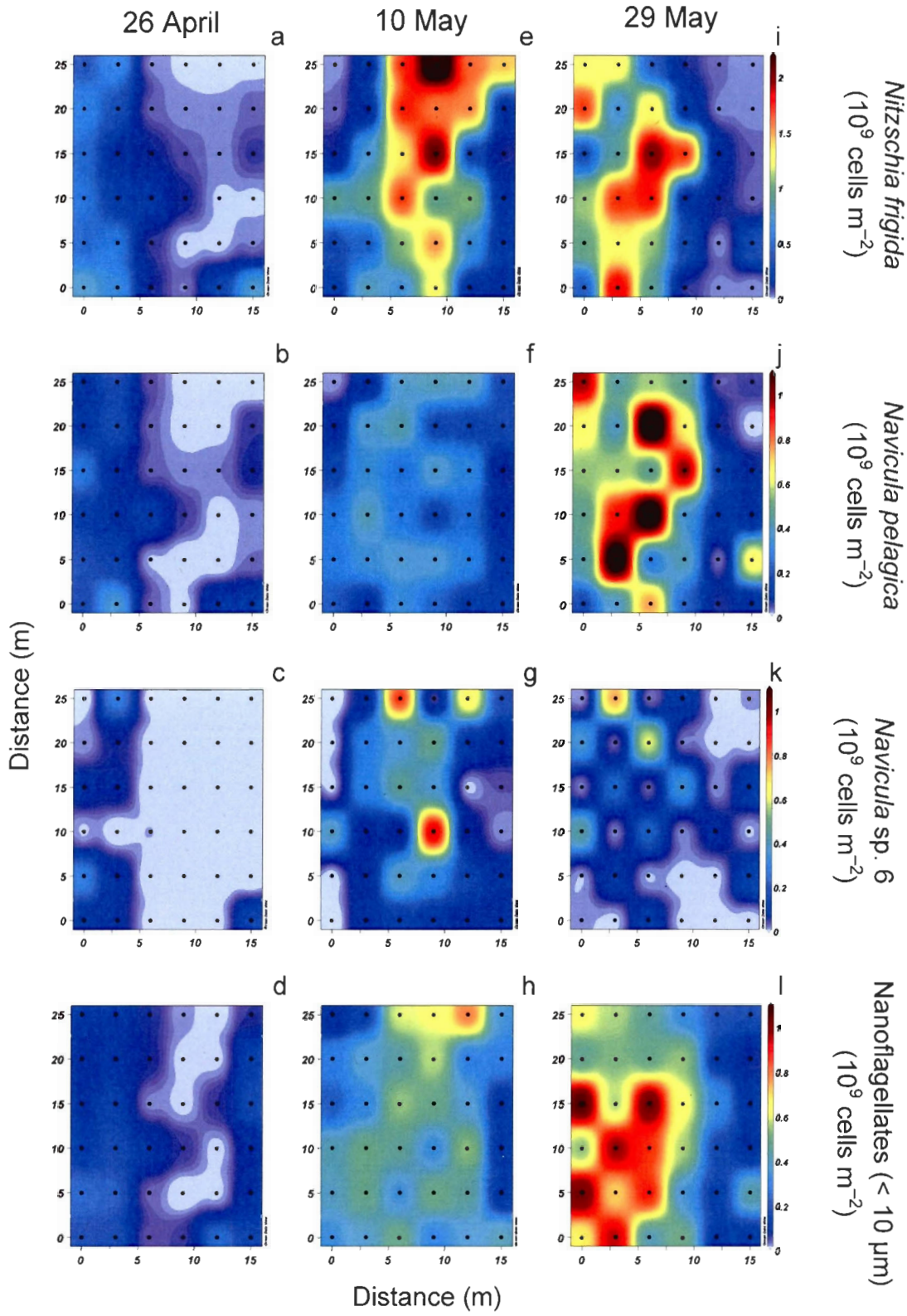

Fig. 4. Horizontal variations in (a, e, i) *Nitzschia frigida*, (b, f, j) *Navicula pelagica*, (c, g, k) *Navicula* sp. 6, and (d, h, l) nanoflagellate < 10 µm cell abundances in the bottom ice of Franklin Bay on (a–d) 26 April, (e–h) 10 May and (i–l) 29 May 2004

Table 2. List of protists recorded in bottom first-year landfast ice in Franklin Bay on 26 April, 10 May and 29 May 2004. A: mean abundance (10^6 cells m^{-2}); A (%): mean relative abundance (%); Occ (%): number of samples in which the taxon occurred (%); nd: taxon not detected

Ice protist	26 April			10 May			29 May		
	A	A (%)	Occ. (%)	A	A (%)	Occ(%)	A	A (%)	Occ (%)
COSCINODISCOPHYCEAE									
Actinoptychus senarius (Ehrenberg) Ehrenberg	0.02	0.01	8	0.16	0.01	6	nd	nd	nd
Attheya longicornis Crawford & Gardner	0.21	0.02	19	1.16	0.04	28	1.37	0.06	19
A. septentrionalis (Østrup) Crawford	7.48	0.58	69	65	1.86	97	85.91	2.81	100
Melosira arctica Dickie	nd	nd	nd	0.57	0.03	3	1.22	0.09	6
Porosira glacialis (Grunow) Jørgensen	< 0.01	< 0.01	3	nd	nd	nd	0.12	0.01	3
Thalassiosira spp.	0.24	0.11	39	0.23	0.01	8	0.17	0.03	14
Unidentified centric cells	0.22	0.05	28	0.36	0.01	11	0.31	0.02	8
FRAGILARIOPHYCEAE									
Fossula arctica Hasle, Syvertsen & von Quillfeldt	nd	nd	nd	nd	nd	nd	0.44	0.02	3
Synedropsis hyperborea (Grunow) Hasle, Medlin & Syvertsen	4.71	0.58	86	19.9	0.79	94	43.3	1.8	100
BACILLARIOPHYCEAE									
Amphora laevis var. *laevissima* (Gregory) Cleve	0.57	0.15	56	1.55	0.11	39	2.85	0.31	47
Bacillaria paxillifer var. *tumidula* Hustedt	0.63	0.14	47	0.09	0.01	8	0.62	0.10	22
Craspedopleura kryophila (Cleve) Poulin	nd	nd	nd	0.01	< 0.01	3	0.16	0.01	8
Cylindrotheca closterium (Ehrenberg) Reimann & Lewin	3.14	1.22	92	9.92	0.63	89	18.2	1.19	100
Diploneis litoralis var. *clathrata* (Østrup) Cleve	0.87	0.26	67	1.92	0.20	39	4.61	0.53	56
Entomoneis gigantea var. *septentrionalis* (Grunow) Poulin & Cardinal	0.53	0.07	36	1.80	0.08	42	1.35	0.07	25
E. kjellmanii (Cleve) Poulin & Cardinal	0.79	0.18	64	7.74	0.33	83	7.89	0.30	81

Table 2 – Continued

E. kjellmanii var. *kariana* (Grunow) Poulin & Cardinal	6.89	0.84	92	28.7	1.04	94	16.3	0.55	81
E. kjellmanii var. *subtilis* (Grunow) Poulin & Cardinal	1.88	0.32	83	5.1	0.23	75	5.25	0.28	69
E. paludosa var. *hyperborea* (Grunow) Poulin & Cardinal	0.21	0.03	22	1.44	0.06	36	2.17	0.09	44
Fragilariopsis cylindrus (Grunow) Krieger	12.4	3.23	100	36.5	1.63	100	15	1.13	81
F. oceanica (Cleve) Hasle	nd	nd	nd	nd	nd	nd	7.7	0.61	11
Fragilariopsis spp.	0.24	0.03	8	nd	nd	nd	5.66	0.23	19
Gyrosigma concilians (Cleve) Okolodkov	0.82	0.29	61	0.81	0.08	28	1.36	0.14	36
G. hudsonii Poulin & Cardinal	0.32	0.13	44	0.50	0.05	17	1.13	0.09	31
G. tenuissimum var. *hyperborea* (Grunow) Cleve	0.56	0.17	53	0.43	0.06	25	1.07	0.07	28
Gyrosigma / Pleurosigma complex	0.15	0.04	25	0.12	0.02	8	0.17	0.02	11
Haslea crucigeroides (Hustedt) Simonsen	1.07	0.29	72	1.24	0.10	31	1.10	0.09	25
H. kjellmanii (Cleve) Simonsen	0.08	0.01	6	0.17	0.01	6	nd	nd	nd
H. spicula (Hickie) Lange-Bertalot	1.0	0.37	64	1.47	0.13	33	2.16	0.32	42
H. vitrea (Cleve) Simonsen	0.12	0.02	14	0.16	0.01	8	1.03	0.09	19
Kurpiszia kryokonites (Cleve) Witkowski, Lange-Bertalot & Metzeltin	< 0.01	< 0.01	3	0.09	0.01	6	0.16	0.01	8
K. subprotracta (Cleve) Witkowski, Lange-Bertalot & Metzeltin	0.06	0.02	11	nd	nd	nd	nd	nd	nd
Manguinia rigida (M. Peragallo) Paddock	nd	nd	nd	nd	nd	nd	0.09	0.03	3
Meuniera membranacea (Cleve) Silva	0.38	0.08	39	0.90	0.08	28	1.16	0.09	31
Navicula algida Grunow	0.03	< 0.01	3	nd	nd	nd	nd	nd	nd
N. directa (W. Smith) Ralfs	1.61	0.42	69	1.88	0.13	44	3.38	0.30	58
N. gelida var. *radissonii* Poulin & Cardinal	0.98	0.21	58	1.22	0.11	28	0.65	0.11	17
N. cf. *granii* (Jørgensen) Gran	0.16	0.01	3	nd	nd	nd	nd	nd	nd
N. cf. *impexa* Hustedt *sensu* Poulin & Cardinal	0.42	0.14	42	0.29	0.03	17	0.28	0.05	14
N. kariana Grunow	nd	nd	nd	0.20	0.01	8	0.48	0.03	11
N. kariana var. *detersa* Grunow	0.14	0.03	14	0.09	0.02	8	0.26	0.01	8
N. kariana var. *frigida* (Grunow)	0.04	0.02	8	nd	nd	nd	nd	nd	nd

Cleve

Table 2 – Continued

N. lineola var. *perlepida* (Grunow) Cleve	nd	nd	nd	nd	nd	nd	0.66	0.02	3
Navicula pagophila var. *manitounukensis* Poulin & Cardinal	0.08	0.06	14	nd	nd	nd	nd	nd	nd
N. pelagica Cleve	92.4	11.9	100	260	11.4	100	454	16.6	100
N. pellucidula Hustedt	1.13	0.24	44	3.76	0.20	44	0.25	0.03	14
N. recurvata Gran	0.09	0.02	11	0.12	< 0.01	3	0.11	< 0.01	3
N. septentrionalis (Grunow) Gran	3.18	0.51	42	36.3	1.55	83	76.9	2.76	89
N. superba Cleve	nd	nd	nd	nd	nd	nd	0.09	0.01	6
N. superba var. *subacuta* Gran	0.06	0.01	6	0.06	< 0.01	3	nd	nd	nd
N. transitans Cleve	0.28	0.07	31	0.50	0.05	22	0.96	0.17	28
N. transitans var. *derasa* (Grunow) Cleve	0.30	0.08	33	0.83	0.07	25	0.84	0.10	28
N. transitans var. *derasa* f. *delicatula* Heimdal	0.01	< 0.01	3	0.06	0.01	3	nd	nd	nd
N. transitans / kariana complex	0.12	0.05	28	0.12	< 0.01	3	nd	nd	nd
N. trigonocephala Cleve	< 0.01	< 0.01	3	0.36	0.02	11	0.74	0.06	25
N. trigonocephala var. *depressa* Østrup	0.06	0.03	14	0.43	0.04	22	0.15	0.04	11
N. valida Cleve & Grunow	0.04	0.01	6	0.17	0.02	8	0.14	0.02	11
N. valida var. *minuta* Cleve	0.16	0.06	28	0.41	0.03	11	0.50	0.06	17
N. vanhoeffenii Gran	< 0.01	0.01	3	1.55	0.08	22	65.6	2.50	53
Navicula sp. 1	0.35	0.10	8	1.87	0.10	11	nd	nd	nd
Navicula sp. 6	40	3.38	81	219	7.45	92	111	3.87	47
Navicula spp.	0.54	0.16	50	1.53	0.12	42	4.54	0.39	67
Nitzschia angularis W. Smith	nd	nd	nd	nd	nd	nd	0.02	< 0.01	3
N. arctica Cleve	6.56	0.91	69	15.8	0.70	89	15.4	0.63	69
N. brebissonii var. *borealis* Grunow ex Cleve	0.14	0.03	17	0.34	0.02	11	0.07	0.01	6
N. frigida Grunow	232	25.3	100	864	28.8	100	692	20.4	100
N. laevissima Grunow	0.13	0.03	19	1.43	0.05	25	1.06	0.04	28
N. lanceolata var. *pygmaea* Cleve	0.08	0.02	8	0.04	< 0.01	3	nd	nd	nd
N. longissima (Brébisson) Ralfs	8.26	0.86	58	2.22	0.15	44	3.36	0.37	50
N. neofrigida Medlin	48.4	5.26	100	135	4.35	100	132	3.97	92
N. promare Medlin	57.4	5.81	92	97.8	4.04	92	101	3.49	81
N. scabra Cleve	0.05	0.01	8	1.87	0.08	17	17.50	0.66	78
Nitzschia spp.	0.26	0.06	33	0.73	0.06	28	6.24	0.40	53
Pauliella taeniata (Grunow) Round & Basson	2.64	0.25	17	7.33	0.24	6	5.66	0.24	11
Petroneis glacialis (Cleve) Witkowski, Lange-Bertalot & Metzeltin	0.16	0.03	17	0.28	0.02	11	0.27	0.02	11

Table 2 – Continued

P. quadratarea var. *bicontracta* (Østrup) Heiden	0.01	0.01	3	0.09	0.01	6	0.14	0.01	6
P. quadratarea var. *constricta* (Østrup) Heiden	0.17	0.02	11	0.23	0.01	11	0.74	0.06	28
P. quadratarea var. *densestriata* Cleve	0.14	0.07	31	0.25	0.07	8	0.15	0.03	11
P. quadratarea var. *minor* (Østrup) Heiden	nd	nd	nd	0.07	0.01	6	0.16	0.01	6
P. semiinflata (Østrup) Gran	0.06	0.01	8	0.60	0.03	19	2.01	0.14	47
Plagiotropis spp.	0.04	< 0.01	3	nd	nd	nd	nd	nd	nd
Pleurosigma clevei Grunow	0.09	0.02	14	0.09	0.01	6	nd	nd	nd
P. stuxbergii Cleve & Grunow	0.20	0.05	36	0.15	0.01	8	nd	nd	nd
P. stuxbergii var. *rhomboides* (Cleve) Cleve	0.23	0.05	22	0.51	0.03	17	0.21	0.01	8
Pseudogomphonema arcticum (Grunow) Medlin	2.16	0.23	75	8.36	0.34	78	12.7	0.52	83
P. groenlandicum (Østrup) Medlin	0.05	0.01	6	0.12	< 0.01	3	0.52	0.05	17
Pseudo-nitzschia delicatissima (Cleve) Heiden	0.45	0.06	28	3.99	0.14	61	9.98	0.42	67
P. cf. *pseudodelicatissima* (Hasle) Hasle	4.49	0.51	83	28.2	0.95	94	8.4	0.53	72
P. pungens (Grunow ex Cleve) Hasle	nd	nd	nd	nd	nd	nd	0.35	0.04	6
P. seriata (Cleve) H. Peragallo	1.14	0.17	39	7.19	0.19	36	1.86	0.08	31
P. turgidula (Hustedt) Hasle	0.10	0.01	3	0.24	0.01	3	1.02	0.09	19
Pseudo-nitzschia spp.	0.62	0.08	36	2.43	0.07	25	4.38	0.24	53
Stauroneis radissonii Poulin & Cardinal	5.21	0.84	97	10.2	0.53	89	10.2	0.49	83
Stenoneis inconspicua var. *baculus* (Cleve) Cleve	0.16	0.05	3	0.80	0.03	22	0.42	0.03	19
S. obtuserostrata (Hustedt) Poulin	1.26	0.33	67	1.4	0.15	42	1.37	0.13	44
Pennate sp. 1	0.78	0.21	56	4.97	0.34	61	13.26	1.08	78
Pennate sp. 2	0.68	0.17	28	4.51	0.25	61	5.54	0.36	39
Pennate sp. 3	1.94	0.32	75	0.46	0.06	8	nd	nd	nd
Pennate sp. 4	0.16	0.05	14	0.53	0.04	14	1.70	0.17	22
Pennate sp. 5	1.56	0.20	53	5.93	0.30	61	2.75	0.20	31
Pennate sp. 6	2.20	0.24	64	4.27	0.21	61	2.66	0.13	36
Pennate sp. 7	0.34	0.03	17	0.82	0.07	14	nd	nd	nd
Pennate sp. 8	0.28	0.13	39	0.86	0.06	28	nd	nd	nd
Pennate sp. 9	0.86	0.10	31	0.26	0.02	11	nd	nd	nd
Pennate sp. 10	0.29	0.03	14	nd	nd	nd	nd	nd	nd
Pennate sp. 11	0.17	0.03	14	nd	nd	nd	nd	nd	nd

Unidentified pennate cells	39.7	7.06	100	179	7.72	100	296	10.9	100

Table 2 – Continued

DINOPHYCEAE									
Amphidinium sphenoides Wülff	0.14	0.01	8	nd	nd	nd	nd	nd	nd
Alexandrium tamarense (Lebour) Balech	nd	nd	nd	nd	nd	nd	0.02	< 0.01	3
Gymnodinium wulffii Schiller	0.10	0.02	14	0.29	0.03	14	0.66	0.08	25
Gymnodinium sp. 1 *sensu* Bérard-Therriault et al.	nd	nd	nd	nd	nd	nd	0.11	0.01	3
Gymnodinium / Gyrodinium complex	0.30	0.04	19	0.48	0.03	14	1.55	0.11	39
Heterocapsa arctica Horiguchi	0.12	0.01	11	0.27	0.01	11	1.24	0.08	31
Oxytoxum sp. 1	0.04	< 0.01	3	nd	nd	nd	0.17	0.01	6
Peridiniella catenata (Levander) Balech	0.02	< 0.01	3	0.26	0.01	8	0.17	0.04	6
Protoperidinium spp.	nd	nd	nd	nd	nd	nd	0.17	< 0.01	6
Dinophyceae spp.	0.81	0.13	44	4.14	0.27	67	6.5	0.43	89
Thecate dinophyceae sp. 1	0.16	0.03	19	nd	nd	nd	nd	nd	nd
Thecate dinophyceae	1.81	0.27	86	12.1	0.55	100	9.3	0.47	92
CHRYSOPHYCEAE									
Dinobryon faculiferum (Willén) Willén	1.73	0.17	47	3.76	0.15	64	0.50	0.04	17
Dinobryon sp. 1	nd	nd	nd	0.33	0.01	3	nd	nd	nd
Chrysophyceae sp. 1 *sensu* Bérard-Therriault et al.	nd	nd	nd	nd	nd	nd	0.06	< 0.01	3
Chrysophyceae spp.	0.27	0.05	28	1.23	0.04	19	0.35	0.03	11
CHOANOFLAGELLIDEA									
Calliacantha spp.	1.83	0.25	72	6.61	0.35	86	1.33	0.07	19
Choanoflagellidea spp.	1	0.13	56	5.46	0.24	81	18.6	0.67	92
CRYPTOPHYCEAE									
Hemiselmis virescens Droop	0.18	0.03	17	0.23	0.01	6	1.59	0.21	31
Plagioselmis prolonga Butcher ex Novarino, Lucas & Morrall	0.02	< 0.01	3	nd	nd	nd	0.16	0.02	6
Rhodomonas maculata Butcher ex Hill & Wetherbee	0.24	0.04	22	1.04	0.08	31	1.8	0.23	36
Teleaulax spp.	0.02	0.01	6	nd	nd	nd	nd	nd	nd
Cryptophyceae spp.	2.97	0.52	86	6.74	0.47	89	8.50	0.80	81
EUGLENOPHYCEAE									
Eutreptiella spp.	0.22	0.04	31	0.59	0.03	19	1.57	0.09	44
Euglenophyceae spp.	0.04	0.02	14	0.66	0.04	19	2.1	0.12	47
PEDINOPHYCEAE									
Resultor mikron (Throndsen) Moestrup	0.39	0.06	22	0.57	0.04	19	2.21	0.15	47
PRASINOPHYCEAE									

Pseudoscourfieldia marina (Throndsen) Manton	0.03	0.01	8	0.15	0.01	8	1.04	0.11	22
Table 2 – Continued									
Pterosperma cf. *undulatum* Ostenfeld	0.16	0.01	11	nd	nd	nd	nd	nd	nd
Pyramimonas cf. *nansenii* Braarud	0.64	0.10	47	0.87	0.07	28	0.55	0.08	28
P. orientalis Butcher ex McFadden, Hill & Wetherbee	0.31	0.04	25	0.84	0.03	22	2.44	0.13	56
P. virginica Pennick	0.06	< 0.01	3	0.11	< 0.01	3	nd	nd	nd
Pyramimonas spp.	0.35	0.04	22	0.93	0.05	31	1.43	0.12	44
Prasinophyceae spp. (2–5 µm)	0.03	0.01	6	0.29	0.01	8	1.05	0.06	19
PRYMNESIOPHYCEAE									
Imantonia rotunda Reynolds	0.01	< 0.01	3	0.63	0.04	11	0.51	0.03	11
Prymnesiophyceae spp.	0.01	0.00	3	nd	nd	nd	0.22	0.04	8
CHLOROPHYCEAE									
Chlainomonas cf. *rubra* (Stein & Brooke) Hoham	1.14	0.27	69	2.18	0.15	47	2.01	0.18	44
Chlorophyceae sp. 1	1.21	0.28	58	1.19	0.10	25	2.97	0.13	28
Chlorophyceae spp.	1.83	0.35	75	1.78	0.10	44	1.87	0.08	31
HETEROTROPHIC FLAGELLATES									
Telonema subtilis Griessmann	0.94	0.15	53	2.79	0.13	64	8.83	0.36	78
UNIDENTIFIED FLAGELLATES									
Flagellate sp. 1	nd	nd	nd	nd	nd	nd	0.03	< 0.01	3
Flagellate sp. 2	0.02	0.01	6	0.79	0.04	28	0.47	0.04	14
Flagellate sp. 3	nd	nd	nd	nd	nd	nd	0.82	0.17	11
Flagellate sp. 4	0.01	0.01	6	0.68	0.03	3	nd	nd	nd
Flagellates ≤ 5 µm	76.4	14.6	100	269	12.2	100	65.7	3.31	100
Flagellates 6–10 µm	23.1	4.65	100	98	4.47	100	115	6.26	100
Flagellates 11–20 µm	6.19	1.03	97	18.5	0.93	97	11	0.79	86
Flagellates > 20 µm	1.02	0.22	72	1.72	0.08	44	0.90	0.08	33
Number of species			**107**			**100**			**100**
Number of taxa			**135**			**124**			**126**

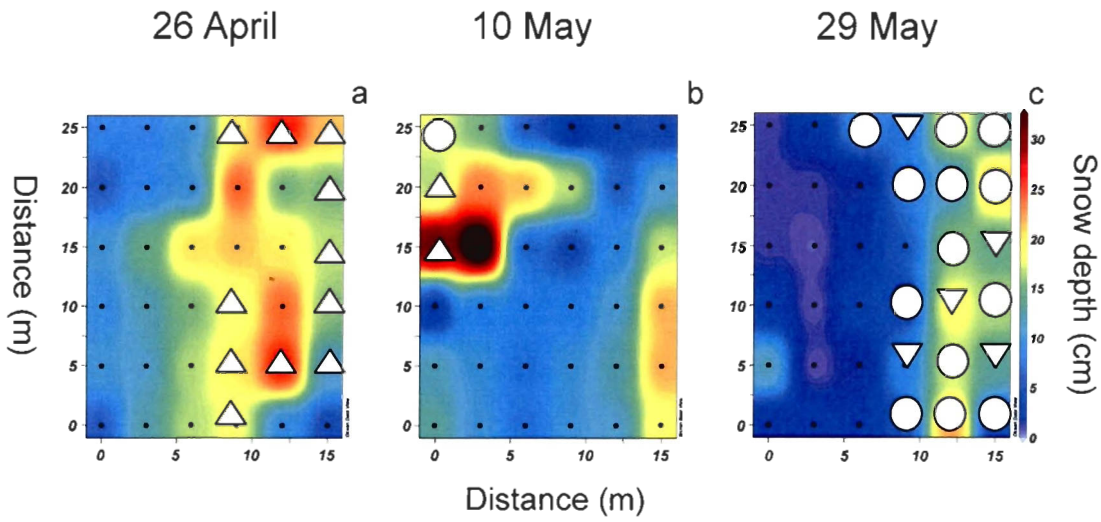

Fig. 5. Distribution of four groups of taxonomically similar bottom ice protist community obtained from a cluster analysis plotted on the snow depth graph at three sampling dates. Group I is represented by inverted triangles, Group II by small black dots, Group III by triangles and Group IV by circles

3.3.3. Distribution of bottom ice protists and spatial processes

On 26 April, one-third (34%) of the total variation in the abundance of diatom taxa was explained by shared environmental and spatial data, while non-spatial environmental and purely spatial processes explained 17% and 13% of the variation, respectively (Table 3). In contrast, the variability in the flagellated taxa was mainly explained by the non-spatial environmental pattern (28%) and spatial structuring shared by the environmental data (19%), while purely spatial processes appeared to have no significant effect on the taxonomic composition. Roughly one-third (36%) of the variation in the diatom taxa and more than half (55%) in the flagellated taxa remained unexplained during that period (Table 3).

On 10 May, approximately one-quarter (25% and 29%) of the variation in the diatom and flagellated taxa, respectively, were explained by the non-spatial environmental pattern, while the spatial structuring shared by the environmental data and purely spatial processes showed no significant relationship in the distribution of both diatom and flagellated taxa (Table 3). Approximately three-quarters of the variation in the diatom (77%) and flagellated (75%) taxa remained unexplained during that period (Table 3).

On 29 May, one-quarter (26%) of the total variation in the diatom taxa was explained by the spatial structuring shared by the environmental data, while non-spatial environmental patterns and purely spatial processes did not show any significant effect on their distribution (Table 3). In contrast, the variation in the distribution of flagellated taxa was mainly explained by the spatial structuring shared by environmental data (41%) and purely spatial processes (16%). Similar to the diatom taxa, the non-spatial environmental pattern showed no significant relationship in the distribution of flagellated taxa. Three-quarters (76%) of the variation in the diatom taxa and less than half (40%) in the flagellated taxa remained unexplained on this last sampling date (Table 3).

3.3.4. Environmental variables and taxonomic composition

The relations between the snow depth, ice thickness, ice freeboard height and bottom ice salinity, and the taxonomic composition of bottom ice diatoms and flagellated cells (i.e., flagellates + dinoflagellates) during the three sampling days were quantified using PCCA, which included PCNM variables (Dray et al. 2006), as covariate matrix to remove the effect of space (Fig. 6). On 26 April, the diatom taxa were positioned in a bidimensional space

defined mainly by snow depth and ice freeboard height ($r = -0.99$ and -0.98, respectively) along the first axis and by bottom ice salinity and ice thickness ($r = 0.87$ and -0.66, respectively) along the second axis (Fig. 6a). Diatom taxa were mostly dispersed along the first axis and the only significant vector was snow depth (global $r^2 = 0.26$, $p \leq 0.05$). In contrast to diatoms, flagellated taxa were almost equally dispersed along both axes (Fig. 6d). The first axis was mainly correlated with ice freeboard height and ice thickness ($r = 0.85$ and 0.74, respectively), and the second axis with snow depth and bottom ice salinity ($r = 0.72$ and -0.71, respectively). The significant vectors were the bottom ice salinity, snow depth and ice freeboard height (global $r^2 = 0.40$, 0.23 and 0.22, respectively; $p \leq 0.05$).

On 10 May for the diatom taxa, the first axis was correlated with snow depth ($r = 0.80$) and the second axis with bottom ice salinity and ice freeboard height ($r = -0.99$ and 0.76, respectively). The diatom taxa were mainly positioned along the first axis (Fig. 6b). The significant vectors were snow depth, bottom ice salinity and ice freeboard height (global $r^2 = 0.34$, 0.19 and 0.17, respectively; $p \leq 0.05$). For the flagellated taxa, the first axis was correlated with ice thickness and ice freeboard height ($r = -0.76$ and -0.74, respectively), and the second axis with snow depth and bottom ice salinity ($r = 0.88$ and 0.77, respectively). The flagellated taxa were mainly dispersed along the second axis. The significant vectors were bottom ice salinity and snow depth (global $r^2 = 0.26$ and 0.16, respectively; $p \leq 0.05$).

On 29 May, diatoms were spread equally along the first and second axes. The first axis was correlated with ice freeboard height and bottom ice salinity ($r = -0.99$ and 0.92,

respectively), while the second axis was correlated with snow depth ($r = 0.90$) and ice thickness ($r = 0.86$). The only significant vector was bottom ice salinity (global $r^2 = 0.21$, $p \leq 0.05$). For the flagellated taxa, the first axis was correlated with snow depth and ice thickness ($r = -0.99$ and 0.86, respectively), and the second axis was correlated with ice freeboard height and bottom ice salinity ($r = -0.99$ and -0.92, respectively). The flagellated taxa were mainly positioned along the second axis. The significant vector was bottom ice salinity and snow depth (global $r^2 = 0.26$ and 0.16, respectively; $p \leq 0.05$).

Table 3. Percentages of variation of taxonomic data matrix of diatoms and flagellated (i.e., flagellates and dinoflagellates) cells explained by environment and by space (Borcard et al. 1992)

Source of variation	26 April		10 May		29 May	
	Diatoms	Flag. cells	Diatoms	Flag. cells	Diatoms	Flag. cells
Non-spatial environmental variation	17	28	25	29	–1	3
Spatially structured environmental variation	34	19	–1	–6	26	41
Purely spatial variation	13	–2	–1	2	–1	16
Unexplained variation	36	55	77	75	76	40

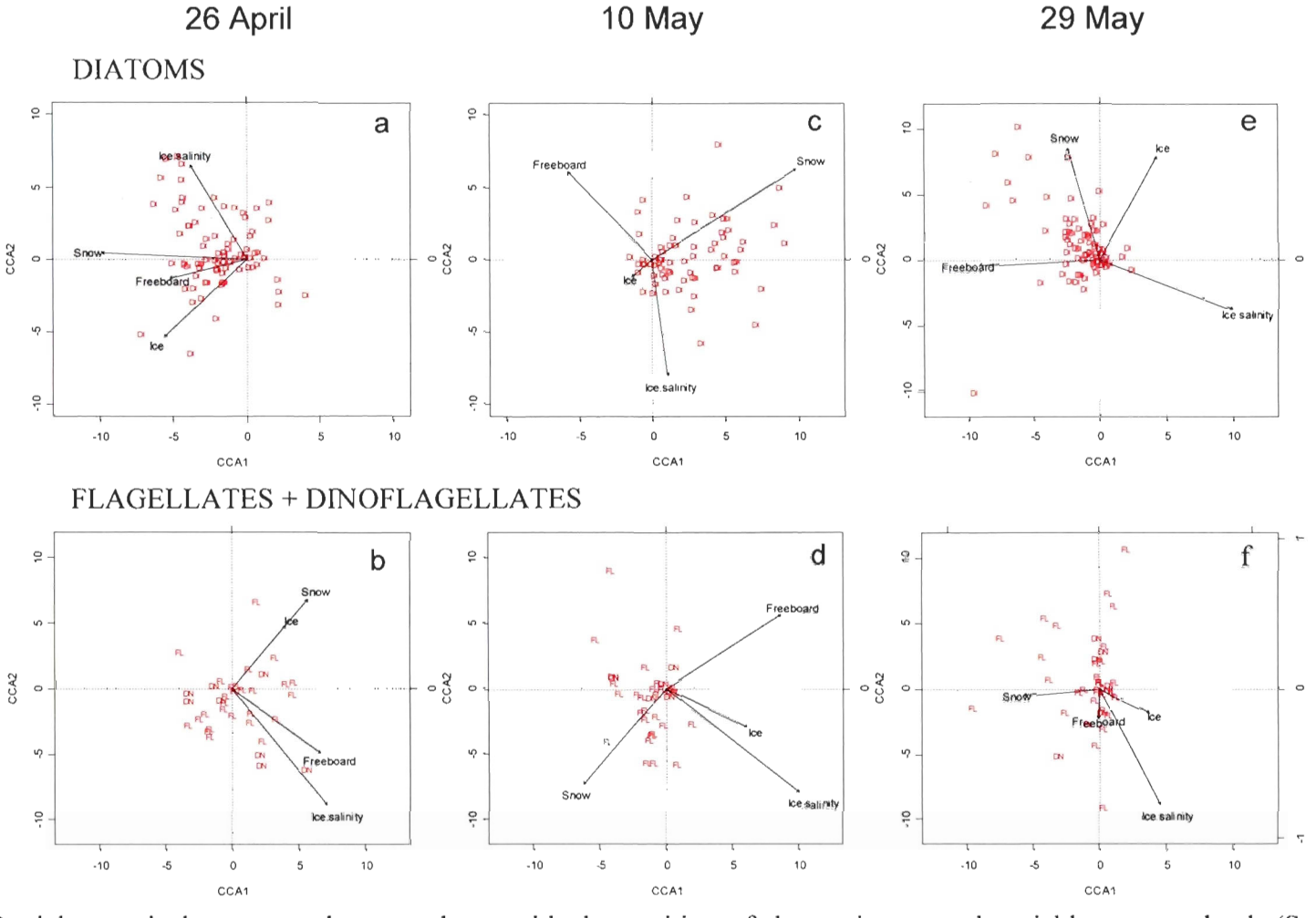

Fig. 6. Partial canonical correspondence analyses with the position of the environmental variables: snow depth (Snow), ice thickness (Ice), ice salinity (Ice salinity), ice freeboard height (Freeboard) as vectors, and abundance of (a, c, e) diatoms (DI) and (b, d, f) flagellates (FL) and dinoflagellates (DN) distributed in the space of the 2 canonical axes in (a, b) 26 April, (c, d) 10 May and (e, f) 29 May 2004

3.4. Discussion

3.4.1. Seasonal variation

This study was conducted between the second half of the ice algal bloom and the beginning of the bloom decline in the landfast ice of Franklin Bay (Chapitre II). Indeed, chl *a* biomass and protist abundance in the bottom ice increased from late April to mid-May and remained relatively constant until the end of May (Table 1). This trend followed the seasonal increases in incident and sub-ice irradiance, and seasonal decreases in snow depth and nitrate concentrations in the surface water (Chapitre II, Table 1). This seasonal pattern is consistent with the pattern observed in first-year landfast ice in other Arctic regions (Welch & Bergmann 1989, Gosselin et al. 1990, Welch et al. 1991). In contrast to cell abundance, the number of protist taxa slightly decreased from 135 taxa on 26 April to 124–126 taxa on the two last sampling dates in May, respectively (Table 2). Similar numbers of protist taxa were recorded elsewhere in the Arctic (Hsiao 1980, Poulin et al. 1983, Okolodkov 1992, von Quillfeldt 1997, Ratkova & Wassmann 2005).

In this study throughout the bloom period, the bottom ice community was dominated by pennate colonial diatoms (*Nitzschia frigida*, *Navicula* sp. 6, *Navicula pelagica*, *Nitzschia promare*) and nanoflagellates ≤ 5 µm, with the arborescent colony-forming *N. frigida* being the most abundant diatom as previously reported from the Chukchi Sea (Okolodkov 1992, von Quillfeldt et al. 2003), the Canadian Arctic (Hsiao 1980, Sime-Ngando et al. 1997), the Greenland Sea (von Quillfeldt 1997), the Barents Sea (Syvertsen 1991), the White Sea (Ratkova & Wassmann 2005), the Russian shelf

(Okolodkov 1992) and the central Arctic Ocean (Booth & Horner 1997, Gosselin et al. 1997).

The taxonomic composition of the bottom ice community varied throughout the period (Table 2). The most abundant diatoms (e.g., *Nitzschia frigida*, *Navicula* sp. 6, *Nitzschia promare*) showed the highest cell numbers on 10 May and decreased afterwards, while *Navicula pelagica*, *N. septentrionalis*, *N. vanhoeffenii*, *Attheya septentrionalis*, *Synedropsis hyperborea* and the flagellates ≤ 10 µm steadily increased in numbers from late April to late May (Table 2). Moreover, the cluster analysis indicated that the community characterized by flagellates ≤ 5 µm and unidentified pennates (Group III) declined from late April to mid-May and had disappeared in late May (Fig 5). In contrast, two new communities characterized by *Navicula pelagica*, *Nitzschia frigida* and flagellates 6–10 µm (Group I), and by unidentified pennates, *N. pelagica* and flagellates ≤ 10 µm (Group IV) were well-established in the bottom ice horizon in late May. The communities of Groups I, III and IV were all associated with thick snow cover sites. These results clearly indicate a succession pattern within the ice protist community.

This species succession over a month period is probably due to changing environmental conditions, such as an increasing irradiance but decreasing nutrient availability, and more specifically nitrates, in the bottom ice (Margalef 1978). Some species such as *Attheya septentrionalis* and *Nitzschia frigida* can acclimate well to increasing bottom ice irradiance (Hegseth 1992), while other species have difficulties to adjust their photosynthetic apparatus to changing irradiances. The colonial diatoms *Nitzschia promare* and *Navicula* sp. 6 probably fall in this latter group with decreasing cell abundance by the

end of May (Table 2). It is also possible that the increasing air temperature may have caused some warming within the ice sheet, which may have resulted in some flushing events of bottom ice protists to the underlying water column (Mundy et al. 2005).

Similar results were recorded by Barlow et al. (1988) in Hudson Bay, where *Nitzschia* and *Navicula* species dominated the bottom ice protist community during the bloom period, while a decrease of *Nitzschia frigida* and an increase of *Navicula* species were observed during the melting period. They suggested that *N. frigida* was probably more susceptible to the detrimental effect of low salinity as suggested by Poulin et al. (1983), while *Navicula* species could be more tolerant to these changing conditions.

Moreover, the high number of nanoflagellates ≤ 10 µm under high snow cover sites at the end of May suggests that these taxa are better adapted to changing light and nutrient regime. Bottom ice flagellated cells may move upward to enhance their exposure to light or move downward to access the nutrient pool (Eicken 1992, Melnikov 1997). Furthermore, some flagellates may switch their trophic status from autotrophy to heterotrophy under light limiting conditions.

The increase in the cell numbers of *Navicula pelagica*, *N. vanhoeffenii*, *N. septentrionalis*, *Attheya septentrionalis* and *Synedropsis hyperborea* on the last sampling date can be linked to their capacity to grow for a certain time in the water column after being released from the sea ice. As seeding cells, these species are thought to play a role on the onset of the phytoplankton bloom (Michel et al. 1993).

3.4.2. Horizontal variation

During this study, the chl *a* biomass and the abundance of diatoms and other protists in the bottom ice horizon showed significant horizontal patchiness (Figs. 3 & 4). Throughout the study period, the ice protists were distributed in patches with diameter ranging from 5.8 to 11.7 m. These patch diameters are similar to those previously observed for bottom ice chl *a* biomass in a High Arctic fjord in northeast Greenland (Rysgaard et al. 2001) but smaller than the values of ca. 20–90 m estimated in the southeastern Hudson Bay (Gosselin et al. 1986). Our results clearly demonstrate that the snow cover distribution was the most important variable controlling the horizontal distribution of bottom ice algae, as observed in a few previous studies (Gosselin et al. 1986, Rysgaard et al. 2001). These studies showed that the snow distribution, through its influence on the transmitted irradiance reaching the bottom ice, most likely controls the patchiness of the bottom ice algal biomass at small scale. In contrast, Robineau et al. (1997) did not find any difference in the chl *a* distribution at small scale (< 20 m) in the landfast ice in the Saroma-ko Lagoon (Japan), but they reported patch size for the chl *a* biomass of 70, 100 and 500 m. Therefore, snow depth appeared to be the most important variable controlling the small-scale horizontal distribution of the bottom ice chl *a* biomass and protist abundance during the vernal growth season.

In this study, PCCA analyses allowed us to assess the direct relationships between some environmental variables and diatom and flagellated taxa independent of purely spatial processes. At the first sampling day on 26 April, mainly environmental processes ($\leq 51\%$) explained the distribution of both diatoms and flagellates (Table 3, while purely spatial

processes did not account for a very high fraction of the variation ($\leq$ 13%) in both groups of taxa. Snow depth was the most important environmental factor influencing the distribution of diatom taxa, while snow depth, bottom ice salinity and ice freeboard height were responsible for the distribution of flagellated taxa (Fig. 6). The unexplained variation ranged between 36 and 55%, which was comparable to the variation reported by Borcard et al. (1992) for oribatid mite assemblages.

During the second sampling date on 10 May, the environmental variation explained one-quarter of the distribution of diatom and flagellated taxa, while three-quarters of the variation remained unexplained ($\geq$ 77%) for both groups. These results are comparable to the 63% unexplained variation reported by Borcard et al. (1992) on a forest community, but almost two times higher than in the study of Monti et al. (1996) on bottom and ice–water interface microalgal community. Snow depth appeared to be the most important environmental factor influencing the distribution of both diatom and flagellated taxa in the bottom ice community (Fig. 6).

At the last sampling date on 29 May, the unexplained variation still remained very high for diatoms while decreasing to 40% for flagellates. Contrasting the two previous sampling dates, space explained 26% and 57% of the distribution of the diatom and flagellated taxa, respectively. Bottom ice salinity and snow depth were the two main environmental factors influencing the distribution of both diatom and flagellated taxa (Fig. 6). We suspect that the spatial distribution of the bottom ice salinity and snow depth was influencing the distribution of both diatom and flagellated taxa with, however, still an important fraction of the variation remaining unexplained.

On the last sampling day, we observed an increasing importance of the bottom ice salinity on the distribution of protist taxa in Franklin Bay. During the study, the bottom ice salinity showed a patchy distribution on the first two sampling dates, while a significant gradient was observed on 29 May. Similarly, microalgal patchiness related to the spatial distribution of the bottom ice salinity was observed by Gosselin et al. (1986) in landfast ice in southeastern Hudson Bay. These authors suggested that during the melting period and associated decay of the bottom ice interface, the horizontal variability of the microalgal distribution was governed by the thermal properties of the snow–ice cover. Thus, these results suggest that the bottom ice salinity was an important factor influencing the small-scale distribution of protist taxa at the end of the season in Franklin Bay.

Ice thickness showed a gradient on the first sampling date in late April and patchy distribution in May. However, in a small scale of our study we did not observe any pronounced influence of this variable on the taxonomic composition of protist taxa. Legendre et al. (1991) reported that the ice growth rate was the main environmental factor controlling the horizontal mesoscale distribution of the algal biomass and taxonomic composition in sea ice along a salinity gradient in southeastern Hudson Bay. Similarly, Steffens et al. (2006) demonstrated that the ice thickness was structuring the habitat at a large scale in the Gulf of Bothnia in the Baltic Sea, which was also corroborated by Granskog et al. (2005) in the same area.

Our results indicate that snow depth and bottom ice salinity appeared to be the two most important environmental variables explaining the patchiness of both diatom and flagellated taxa. However, the variability in the snow cover alone seemed to govern the

patchiness of the bottom ice chl *a* biomass and protist abundance in first-year landfast ice in Franklin Bay.

3.5. Conclusion

During the spring bloom, the bottom ice protist community was dominated by pennate colonial diatoms, e.g., *Fragilariopsis cylindrus*, *Nitzschia frigida*, *Navicula pelagica*, *N. septentrionalis*, *N. vanhoeffenii*, *Navicula* sp. 6, *Synedropsis hyperborea*, and flagellates (6–10 μm), with the arborescent colony-forming *N. frigida* being the most abundant diatom. The bottom ice community, in terms of chl *a* biomass and cell abundance, was distributed in patches varying from 6 to 12 m in diameter throughout the sampling season. In general, the relative abundance of flagellates < 10 μm were higher under high snow sites, while diatoms were more abundant under low snow sites.

Snow depth and bottom ice salinity were the two environmental variables best responsible for the horizontal heterogeneity of both diatom and flagellated taxa. The horizontal distribution of diatom taxa was controlled by snow depth in late April and by snow depth and bottom ice salinity in late May. For flagellated taxa, the distribution was controlled by a combination of environmental factors in late April and by snow depth and bottom ice salinity in May.

The most abundant diatoms, *Nitzschia frigida*, *Navicula* sp. 6 and *Fragilariopsis cylindrus*, showed an increase in cell numbers from late April to mid-May, but they decreased afterwards. In contrast, *Navicula pelagica*, *N. septentrionalis*, *N. vanhoeffenii*, *Attheya septentrionalis*, *Synedropsis hyperborea* and the flagellates (6–10 μm) steadily

increased in numbers from late April to the end of May. This species succession was most likely related to the surface water nutrient depletion and the seasonal increase in bottom ice irradiance.

CONCLUSION GÉNÉRALE

This thesis provides extensive information about the seasonal development of bottom landfast ice protists in the western Canadian High Arctic from the time of cell entrapment in autumn through the spring bloom period to its decline and decay in late June. In this research, we described for the first time the changes in the taxonomic composition of protists during the early stages of sea-ice formation in autumn. This research also provided unique information on the development of bottom ice protist community under two contrasting snow covers in relation to environmental variables driving the algal biomass, cell abundance and taxonomic composition during the winter–spring transition. This thesis provided key insights for comparison with previous reports collected almost three decades ago in the Canadian (Hsiao 1980) and Alaskan (Horner & Schrader 1982) Beaufort Sea, and set excellent baseline information for future bottom ice ecosystem investigations, where global warming may influence their dynamics (ACIA 2005).

Information on the incorporation of protists in sea ice during the autumn is still very scarce (Gradinger & Ikävalko 1998, Tuschling et al. 2000, Riedel et al. 2007b). In Chapitre I, the results showed that protists are incorporated within the sea ice as soon as the ice begins to form in early autumn. The taxonomic composition of protists in sea ice and surface water changed as the autumn progressed. In new ice, the taxonomic composition was very similar to that observed in the underlying water column, while as the sea ice developed to nilas, young ice and first-year ice, the taxonomic composition in the sea ice became markedly different from that in the underlying surface water. This study showed a

decrease in the number of protist taxa in sea ice as the season progressed, which can be explained by restricted space availability in the brine channels, mechanical damage of cells or different survival strategies.

In this research, small photosynthetic eukaryotic cells ($< 4\ \mu m$) dominated the protist community in both newly formed sea ice and underlying surface water, but they were less abundant in sea ice than in surface waters. In contrast, large algae ($\geq 4\ \mu m$) were more abundant in sea ice than in surface waters. Therefore, this study clearly showed a selective incorporation of large cells ($\geq 4\ \mu m$) in newly formed sea ice.

During the present study, photosynthetic prokaryotes were observed in the sea ice of the Mackenzie River plume. However, picocyanobacteria are probably not a permanent resident of sea ice, since the picocyanobacteria population observed in the coastal zone is largely derived from allochthonous inputs of microbiota from the Mackenzie River and other nearby inflows (Waleron et al. 2007).

Another interesting finding is the presence in newly formed sea ice of the potentially toxic diatom *Pseudo-nitzschia* cf. *pseudodelicatissima*, belonging to genus *Pseudo-nitzschia* known to produce a neurotoxic amino acid responsible for Amnesic Shellfish Poisoning (ASP) in humans (Bates et al. 1998) and causing extensive death of seabird and marine mammal in temperate coastal waters (Work et al. 1993, Scholin et al. 2000. It will become important in future work to determine the fate and dynamics of these potentially harmful algae in the context of global warming affecting the Arctic environment.

Futhermore, this research showed that some algal species can overwinter in sea ice without being structurally or physiologically damaged during ice growth. This study

concluded that the formation of diatom resting spores and dinoflagellate cysts is a minor survival strategy in Arctic sea ice. However, the great difficulty in recognizing some of these resting stages should foster interest in such studies aiming at determining these overwintering survival strategies of diatoms and dinoflagellates in Arctic sea ice.

In Chapitre II, it was demonstrated that accumulation of protists in the bottom horizon of first-year landfast ice started as early as the end of February, while the high net observed growth rates indicated an active growth of bottom ice protists. Incident irradiance was the main environmental factor controlling the chlorophyll *a* (chl *a*) biomass and taxonomic composition of protists during the pre-bloom period and differentiated the community between high and low snow covers. The higher net observed growth rates under low snow suggested that a higher transmission of incident irradiance to the bottom ice layer favored the growth of autotrophic protists (mainly diatoms) at the beginning of the season, while flagellated cells, which were presumably heterotrophic, dominated under the high snow cover. However during the bloom period, colonial diatoms (*Nitzschia frigida*, *N. promare*, *Navicula* sp. 6, *N. pelagica* and *Fragilariopsis cylindrus*) dominated the bottom ice community irrespective of the snow cover.

In addition, the results of this research suggested that the maximum bottom ice algal biomass attained during the vernal growth season depended mainly on the nitrate supply from the upper water column. Thus, the amount of nutrients available in surface waters at the end of the winter is an important factor determining the magnitude of the ice algal spring bloom as recently demonstrated by Lavoie et al. (2005, 2009).

Moreover, the arborescent colonial diatom *Nitzschia frigida* was the predominant bottom ice alga throughout the entire season and I suggested that this diatom can be regarded as a key endemic species of landfast ice across pan-Arctic regions. Finally, considering the importance of flagellated cells in Arctic sea ice, it is becoming increasingly important to improve our knowledge of the taxonomy of these cells and of their role in sea ice.

Large-scale horizontal distributions of bottom ice algal biomass, abundance and taxonomic composition have been studied previously (Poulin et al. 1983, Legendre et al. 1991, Monti et al. 1996). However, the research presented in Chapitre III is the first to consider the horizontal distribution of bottom ice protist abundance and taxonomic composition at a small scale (< 25 m) throughout the spring bloom period. The results showed that the bottom ice diatoms, flagellates and dinoflagellates displayed small-scale patchiness that was mainly controlled by the distribution of the snow cover.

The taxonomic composition of the bottom ice community changed from the time I conducted the first spatial study at the end of April to the last one at the end of May. The most abundant diatoms (i.e., *Nitzschia frigida*, *Navicula* sp. 6 and *Fragilariopsis cylindrus*) showed an increase in cell numbers from late April to mid-May, but they decreased afterwards. In contrast, *Navicula pelagica*, *N. septentrionalis*, *N. vanhoeffenii*, *Attheya septentrionalis*, *Synedropsis hyperborea* and the flagellates $\leq 10\,\mu m$ steadily increased in numbers from late April to the end of May. This species succession was most likely related to the surface water nutrient depletion and the seasonal increase in irradiance reaching the bottom ice horizon.

Interactions between living organisms and their physical environment occur at definite spatial and temporal scales, which give rise to spatial patterns. These need to be assessed to untangle the environmental processes responsible for structuring those communities (Borcard et al. 2004). In late April and mid-May, most of the variation in the horizontal distribution of protist taxa was explained by environmental processes, such as snow depth, while spatial processes were increasingly more important by the end of May, when snow depth and bottom ice salinity were the two most important factors. The results of Chapitre III demonstrated that the distribution of diatom taxa is more influenced by the snow depth condition than the flagellated taxa, where the latter can shift from autotrophy to heterotrophy under unfavourable light conditions.

The impact of global warming presently affecting the Arctic has an unprecedented effect on the bottom ice protist communities (Arrigo et al. 2008). Thick, multi-year sea ice has been increasingly replaced by thinner annual sea-ice cover, which may result in enhanced productivity in the bottom horizon of annual landfast ice. Delayed freeze-up of the ice in autumn, decreased ice thickness and accelerated sea-ice melt in spring (ACIA 2005, Serreze et al. 2007, Comiso et al. 2008) are presently contributing to an increase of the pan-Arctic primary production in surface waters, potentially modifying the marine ecosystem structure and pelagic–benthic coupling (Arrigo et al. 2008).

It is, therefore, becoming very important to increase our knowledge and understanding of the processes regulating the development of the bottom ice protist communities in response to global warming. It will become imperative in the future to get a better knowledge of the taxonomic composition of flagellated cells and the role they play in

sea-ice communities. However, we need to improve our methodological approach by adequate preparation of the samples in the field (Garrison & Buck 1986) or collecting the brine samples (Stoecker et al. 1997) in order to identify live protists in light and electron microscopy as well as maintaining cultures and using current molecular tools (Lovejoy et al. 2006).

It will also be important to better understand how the Arctic global warming will affect the timing, bloom duration and release of sea-ice algae to the water column. Changes in the dynamics of the ice algal bloom will affect the transfer of energy and matter within the sympagic (ice-associated), pelagic and benthic food webs (Michel et al. 2006, Seuthe et al. 2007). Another concern of interest is the production of dimethylsulfoniopropionate (DMSP) and dimethylsulfide (DMS) by sea-ice algae and its impact in cloud formation and climate regulation (Levasseur et al. 1994, Thomas & Dieckmann 2002). Another issue concerns the production of exopolymeric substances by ice diatoms, which was recently recognized as a potential source of organic carbon for heterotrophic bacteria and protists (Krembs et al. 2002, Riedel et al. 2007b). Thus still much remains to be done in this field of study.

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