Influence of environmental factors on the development of bottom ice protist communities during the winter–spring transition

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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 net observed growth rates of diatoms and nanoflagellates were significantly higher during the pre-bloom (24 February to 25 March) than the bloom (ca. 3 April to 23 May) period under low snow cover but were not different under high snow cover. 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 3 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, likely 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 *N. frigida*, a key species of landfast ice across circumarctic regions, was the most abundant bottom ice algal diatom throughout the entire season. During the post-bloom period, colonial and solitary diatoms declined more rapidly than nanoflagellates, suggesting that nanoflagellates, presumably heterotrophic, were better adapted to melting sea-ice conditions. 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.

KEY WORDS: Diatoms · Flagellates · Sea ice · Light · Nutrients · Ice protists · Taxonomic composition · Arctic

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 1985, Gosselin et al. 1997) and a high diversity of heterotrophic organisms ranging from bacteria (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 (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 during the last 10 yr (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, Nozais et al. 2001), contributing significantly to carbon cycling in Arctic regions (Michel et al. 2006).

The incorporation of protists into sea ice starts during fall at the time of ice formation (Gradinger & Ikävalko 1998, Riedel et al. 2007b, 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 1985, 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). 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. 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 have been studied in many Arctic regions (Chukchi Sea: Clasby et al. 1976; Alaskan Beaufort Sea: Horner & Schrader 1982; Barrow Strait: Smith et al. 1988, Welch & Bergmann 1989; Frobisher Bay: Hsiao 1980; 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 2 contrasting snow covers from mid-winter to late spring. This investigation provides key insights for comparison to previous data collected 3 decades ago in the Canadian (Hsiao 1980) and Alaskan (Horner & Schrader 1982) Beaufort Sea.

MATERIALS AND METHODS

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).

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, 3 to 6 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 m² to account for horizontal patchiness in the sea-ice algal biomass (Gosselin et al. 1986, Rysgaard et al. 2001). The bottom 4 cm section 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
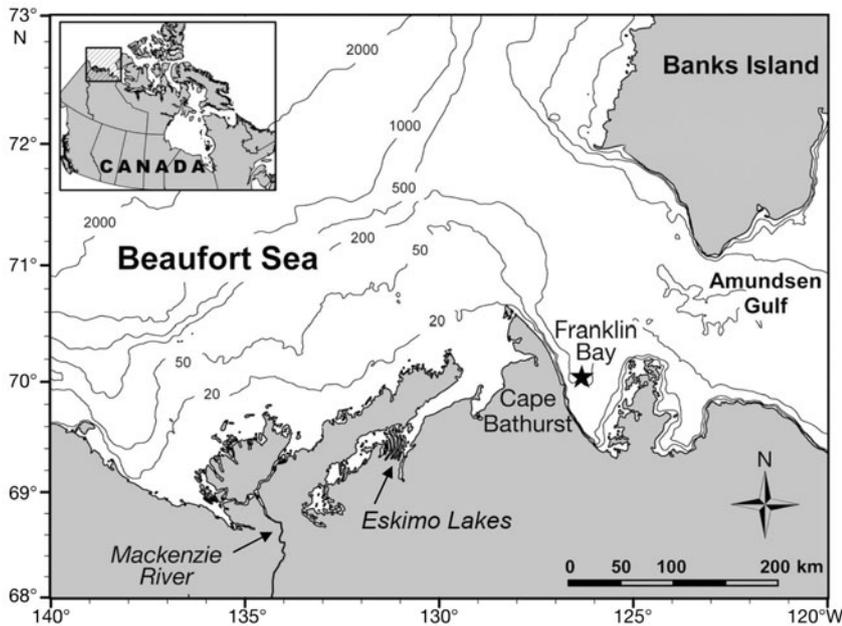
Fig. 1. Canadian Beaufort Sea, showing the location of the overwintering sampling site in Franklin Bay (indicated by star). For comparison, the sampling station area of Hsiao (1980) in Eskimo Lakes is shown. Isobaths: water depth in m

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 to 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 onboard 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 4 samples

in February and early March when cell abundances were low. For these samples, 100 to 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 & Hasle (1990), Medlin & Priddle (1990), Poulin (1990, 1993), Thomsen (1992), Hasle & Syvertsen (1997) and von Quillfeldt (1997). Chl *a* and POC concentrations and protist abundances were corrected for the dilution effect of added seawater as described by 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).

Statistical analyses. Kendall's coefficient of rank correlation (τ) and Wilcoxon signed-ranks tests were computed to infer relationships between 2 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 periods (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 & Rohlf 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 regres-

sion using the Gauss-Newton algorithm. The equation used was:

$$B = B_{max} \times S / (K_m + S) \qquad (1)$$

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.

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). Sea-ice thickness under both snow covers increased from 1.32 m on 24 February to a 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 2 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 2 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
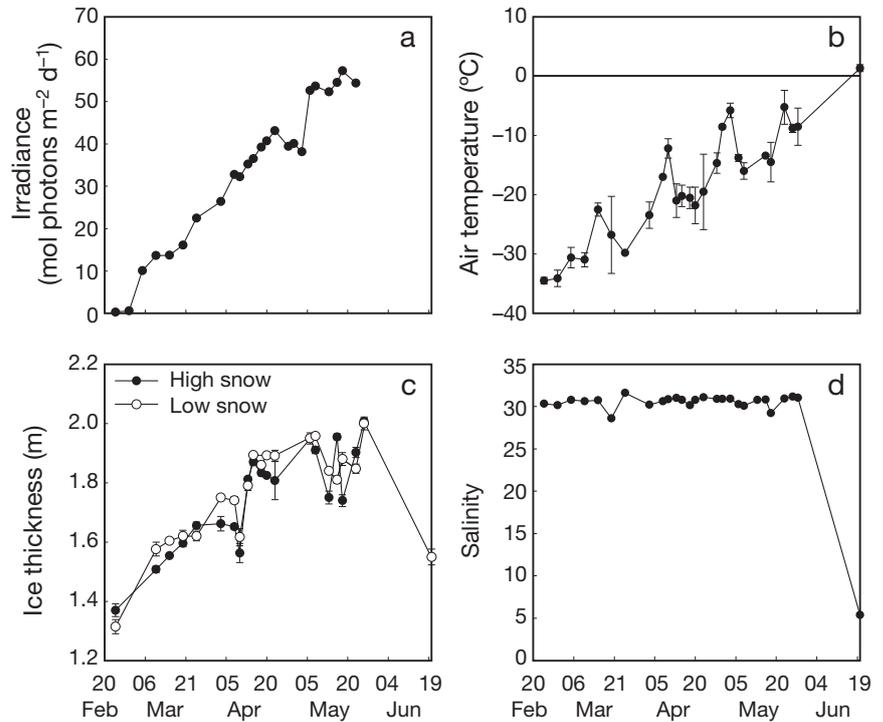

Fig. 2. Temporal variations of (a) incident irradiance, (b) air temperature, (c) ice thickness under high (>10 cm) and low (<10 cm) snow cover, and (d) surface water salinity in Franklin Bay from February to June 2004. In (b) and (c), mean values ± SD are shown
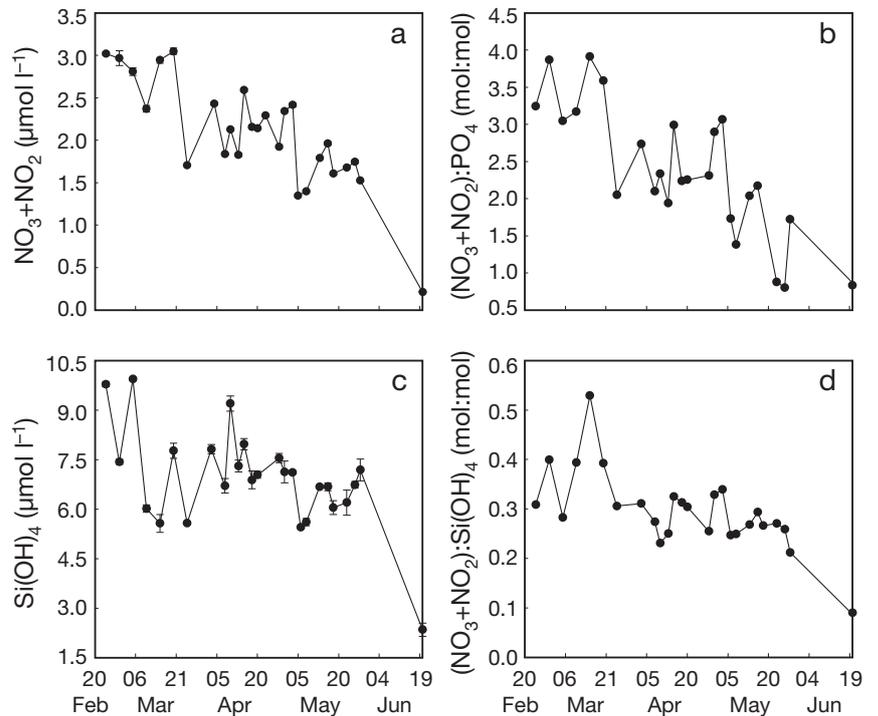

Fig. 3. Temporal variations of (a) nitrate+nitrite (NO_3+NO_2) concentration, (b) ratio of NO_3+NO_2 to phosphate (PO_4), (c) silicic acid (Si[OH]$_4$) concentration, and (d) ratio of NO_3+NO_2 to Si(OH)$_4$ in the surface water in Franklin Bay from February to June 2004. In (a) and (c), mean values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

Table 1. Descriptive statistics of environmental and biological variables measured under high (>10 cm) and low (<10 cm) 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 signed-ranks test. n: number of observations; nd: not detected; ns: not significant

Variable	High snow site					Low snow site					p
	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
Chl 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	22	1.4	13.4	48.5	11.3	25	ns
POC:chl a (g:g)	16	215	2509	532		20	91	1001	194		ns

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 irradiance 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 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.

Chl a concentrations were <1.16 mg m^{-2} in sea ice under both snow covers prior to the bloom period (ca. 3 April to 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 1 wk 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 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 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 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 signed-ranks test, p = 0.76)

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 2 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).

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 signed-ranks test, p < 0.05), while the abundances of colonial and solitary diatoms were not significantly different under low snow cover (Wilcoxon signed-ranks test, p = 0.31). Dur-
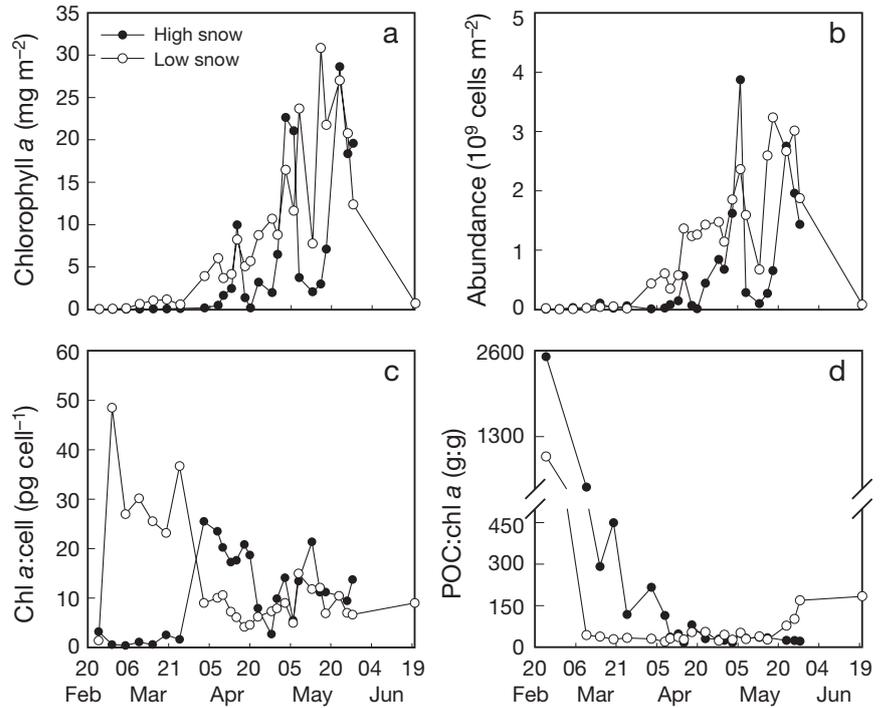

Fig. 4. Temporal variations of (a) chlorophyll *a* (chl *a*) concentration, (b) total cell abundance (i.e. diatoms + flagellates + dinoflagellates), (c) ratio of chl *a* to total protist abundance, and (d) ratio of particulate organic carbon (POC) to chl *a* in the bottom ice under high (>10 cm) and low (<10 cm) snow cover in Franklin Bay from February to June 2004
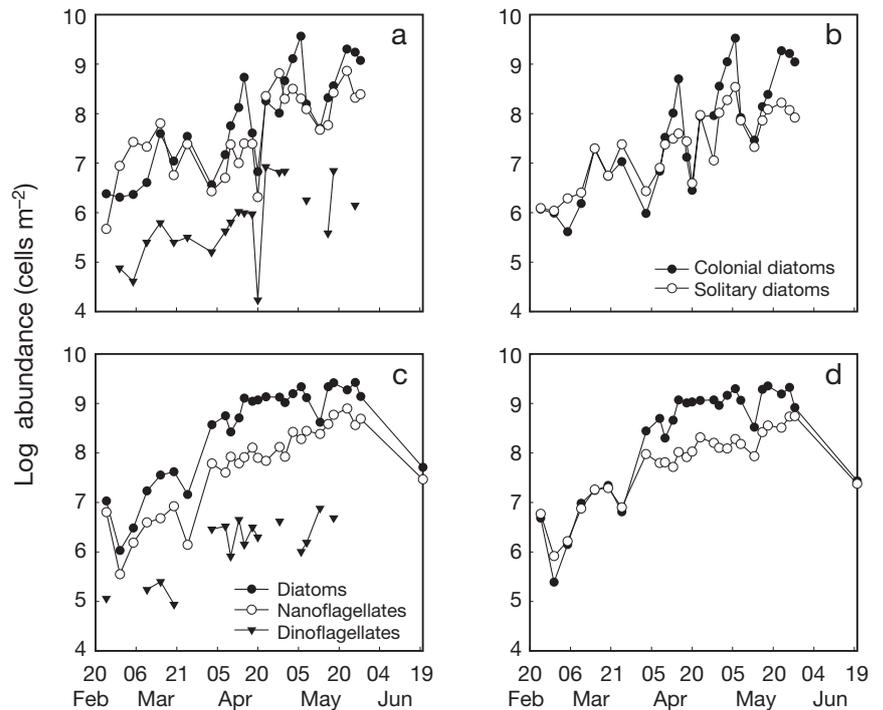

Fig. 5. Temporal variations of the abundances of (a,c) diatoms, nanoflagellates and dinoflagellates, and (b,d) solitary and colonial diatoms in the bottom ice under (a,b) high (>10 cm) and low (<10 cm) snow cover in Franklin Bay from February to June 2004. In (a) and (c), the discontinuous line indicates that dinoflagellates were not detected on these dates

ing 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).

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 (ANCOVA, $p < 0.001$) but not statistically different under high snow cover sites (ANCOVA, $p > 0.05$, 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 significant (ANCOVA, $p > 0.05$). 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 0 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 2 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 12 algal classes were recorded for high and low snow cover, respectively (Appendix 1). 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 sam-

pling period (Appendix 1). Dinoflagellate cysts were observed in only 1 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*, *Nitzschia promare*, *Navicula* sp. 6, and *Navicula 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, *Navicula pelagica*, and *Nitzschia promare*, except in a higher proportion under high snow than low snow cover. In addition, the abundance of unidentified flagellates (<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 either snow cover or with air temperature under low snow cover (Table 3). Chl *a* concentrations and diatom and nanoflagellate abundances were not significantly

Table 2. Average percent numbers of empty diatom cells and estimated (±SE) net observed growth rate (r_n) of diatoms and nanoflagellates under high (>10 cm) and low (<10 cm) snow cover during the bottom ice algal pre-bloom (24 February to 25 March), bloom (ca. 3 April to 23 May), and post-bloom (high snow: 23 to 28 May; low snow: 23 May to 20 June) periods. Negative r_n values indicate a decline in cell abundances. All rates were significantly different from 0 ($p \leq 0.05$), except values in *italics*; na: data not available

| | Empty diatoms (%) | Diatom r_n (d^{-1}) | | | Nanoflagellate r_n (d^{-1}) |
		Total	Colonial	Solitary	
High snow cover					
Pre-bloom	4.9	0.10 ± 0.028	0.10 ± 0.038	0.10 ± 0.025	*0.09 ± 0.054*
Bloom	14.4	0.08 ± 0.025	0.09 ± 0.030	0.06 ± 0.025	0.09 ± 0.022
Post-bloom	29.9	na	na	na	na
Low snow cover					
Pre-bloom	3.5	0.20 ± 0.032	0.23 ± 0.044	0.18 ± 0.027	0.15 ± 0.028
Bloom	18.9	0.03 ± 0.009	0.03 ± 0.009	0.03 ± 0.006	0.05 ± 0.006
Post-bloom	60.1	*−0.15 ± 0.012*	*−0.16 ± 0.022*	*−0.13 ± 0.010*	*−0.11 ± 0.018*

Table 3. Kendall's coefficients of rank correlation (τ) between environmental and biological variables under high (>10 cm) and low snow (<10 cm) cover. Pairwise deletion of missing data; *p $\leq$ 0.05; **p $\leq$ 0.01; ***p $\leq$ 0.001; ns: not significant

	Chl a	Diatoms	Nano-flagellates	Dino-flagellates
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}

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.

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 2 contrasting irradiance conditions. In this section, we 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.

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 was 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 by 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 to 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, 3 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 to 25 March) characterized by low chl a biomass and cell abundance but high net observed growth rates, (2) a bloom period (3 April to 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 1 wk, 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 to 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 the southeastern Beaufort Sea, as has been shown in other Arctic environments by Gosselin et al. (1985, 1986), Welch et al. (1991), and Mundy et al. (2007).

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 (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 2 snow depths (Table 1). In addition, the bottom ice algal bloom, which was mostly composed of pennate diatoms, was delayed by 1 wk 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 2 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 1 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 to 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 to 0.23 d^{-1}) than during (0.03 to 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 2 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 to 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 2 to 3 times more abundant under low snow than high snow cover, whereas the centric diatom *Melosira arctica* was 16 times more abundant (Appendix 1). The only solitary centric diatom showing higher abundances under low snow cover was the epiphytic species *Attheya septentrionalis*, which was mainly attached to *N. 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 2 to 3 times more abundant under low snow than high snow cover, while the heterotrophic species *Telonema subtilis* (Shalchian-Tabrizi et al. 2006) was 2 times more abundant under high snow cover (Appendix 1). 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.

Heterotrophic organisms

There is evidence 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 (Appendix 1). 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.

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, Horner & Schrader 1982, Poulin et al. 1983, Okolodkov 1992, Rat-

kova & Wassmann 2005). 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 2 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. *N. 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 White and Barents Seas (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 (Appendix 1). 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 the 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, Okolodkov 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.

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 2 to 10 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 of 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 results 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.

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 2 variables, with chl *a* concentrations up to 320 mg m^{-2} at NO$_3$ concentrations ≥6 µmol l^{-1} (Fig. 6). 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 µmol 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 1 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
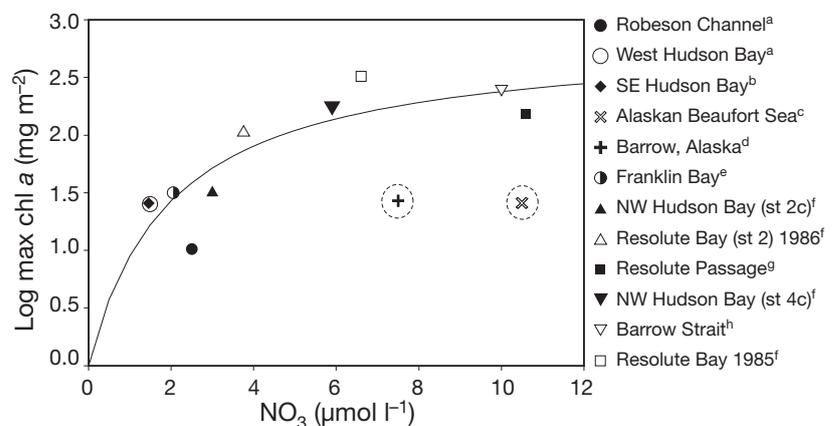
Fig. 6. Relationship between maximum bottom ice chlorophyll *a* (chl *a*) concentrations and NO$_3$ concentrations in the surface water from different studies conducted on Arctic first-year landfast ice: [a]Dunbar & Acreman (1980), [b]Gosselin et al. (1990), [c]Horner & Schrader (1982), [d]Lee et al. (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. Dashed encircled data were excluded from the regression

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 to 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.

CONCLUSIONS

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. *N. 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).

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Appendix 1. 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 (>10 cm) and low (<10 cm) snow depth, respectively); nd: taxon not detected; [a]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[a]	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[a]	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 cf. *paxillifer* var. *tumidula* (Grunow) Witkowski, Lange-Bertalot & Metzeltin	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[a]	4.7	49	0.73	96	8.4	55	0.66	93
E. kjellmanii var. *kariana* (Grunow) Poulin & Cardinal[a]	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
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[a]	8.4	48	3.0	81	11	56	2.7	78
F. oceanica (Cleve) Hasle[a]	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
Manguinea 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[a]	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[a]	20.5	178	1.6	62	40	316	2.0	63

Appendix 1 (continued)

Ice protist	High snow				Low snow			
	A	A_{max}	A (%)	Occ. (%)	A	A_{max}	A (%)	Occ. (%)
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
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[a]	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[a]	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[a]	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[a]	0.08	1.3	0.23	23	0.05	0.42	0.10	19
N. frigida Grunow[a]	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[a]	5.8	50	0.38	54	13	43	0.97	67
N. promare Medlin[a]	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[a]	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
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[a]	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[a]	0.01	0.25	0.03	12	0.13	3.0	0.01	7
P. cf. *pseudodelicatissima* (Hasle) Hasle[a]	7.2	45	1.2	85	21	105	1.5	85
P. pungens (Grunow ex Cleve) Hasle[a]	0.11	2.8	<0.01	4	0.11	2.1	<0.01	7
P. seriata (Cleve) H. Peragallo[a]	0.56	5.8	0.17	38	0.21	2.5	0.03	15
P. turgidula (Hustedt) Hasle[a]	0.10	1.0	0.02	12	0.23	6.2	0.01	4
Pseudo-nitzschia spp. [a]	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[a]	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
Unidentified pennate cells	14.3	93	4.2	100	71	448	7.1	100
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

Appendix 1 (continued)

Ice protist	High snow				Low snow			
	A	A_{max}	A (%)	Occ. (%)	A	A_{max}	A (%)	Occ. (%)
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
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. *rubra* (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