Microalgal composition and primary production in Arctic sea ice: a seasonal study from Kobbefjord (Kangerluarsunnguaq), West Greenland

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ABSTRACT: We investigated the microalgal community in sea ice and in the water column of Kobbefjord, West Greenland, through an entire sea ice season. Temporal variation in physical (photosynthetically active radiation [PAR], temperature, brine volume) and chemical (salinity, nutrient concentration) properties confirmed that sea ice is a very dynamic habitat. Nevertheless, a viable sea ice algal community was present throughout the year, with a species succession from flagellate dominance (dinoflagellates and cryptophytes) in December to February, followed by *Chaetoceros simplex* (a centric diatom) in March and pennate diatoms in May. Sea ice algal composition, biomass and productivity were influenced by PAR and brine volume, with colonization (enhanced by large brine volume) apparent during sea ice melt. Sea ice chlorophyll levels were generally low (< 0.5 µg chl l^{-1}), with 2 distinct blooms (maxima of 1.8 and 2.6 µg chl l^{-1} in March and May, respectively). Primary production mirrored biomass dynamic, which had 2 seasonal peaks of ca. 21 and 15 mg C m^{-2} d^{-1}. Integrated primary production over 7 mo was 0.8 g C m^{-2} in sea ice and 94.4 g C m^{-2} in the water column, with the vast majority of the pelagic production occurring just after sea ice melt (when primary production peaked at 4.2 g C m^{-2} d^{-1}). There was no conclusive evidence of algal seeding. Sea ice algae contributed 30 % of total (sympagic plus pelagic) primary production during the sea ice season, but less than 1 % annually.

KEY WORDS: Sea ice · Algae · Arctic · Primary production · Sympagic · Temporal · Flagellates · Diatoms

INTRODUCTION

Sea ice environments are highly dynamic and have large variations in temperature, salinity and nutrient availability (Gradinger et al. 1999). Organisms are incorporated during sea ice formation (Gradinger & Ikävalko 1998) and some are able to survive and even flourish within the 3-dimensional network of brine channels and inclusions. The primary producers of this habitat are diverse; most algal phyla have been reported from sea ice, but pennate diatoms are considered the dominant group (Horner 1985). Most measurements of Arctic sea ice algal primary production range from 5–15 g C m^{-2} yr^{-1} (Arrigo 2003), but values below 1 g C m^{-2} yr^{-1} have been reported from coastal fast ice environments (e.g. Rysgaard et al. 2001). The sea ice algal contribution to total annual primary production ranges from <1 % (Rysgaard et al. 2001) to 66 % (Horner & Schrader 1982), with marked spatial variation resulting, in part, from differences in the length of the sea ice cover season (Haecky & Andersson 1999).

In addition to primary production within the ice matrix, sea ice can affect the pelagic spring bloom. Sea ice algae may act as inocula with possible influence on both the species composition and magnitude of the pelagic spring bloom (e.g. Syvertsen 1991). This influence is still subject to debate; for sea ice algae to have

these effects on the pelagic community, the inocula must be viable, competitive and remain suspended when released into the water column.

Comprehensive long-term studies are needed in order to understand the ecological dynamics of this vast ecosystem, including its contribution to total primary production. Much of the taxonomic research has focused on the lowermost sea ice layer (e.g. Cota et al. 1991), and the complicated and expensive logistical demands of Arctic sea ice research have restricted the number of seasonal studies. This study aims to (1) describe the dynamics of the sea ice microalgal community throughout a season, (2) identify relations between microalgal communities in sea ice and seawater and (3) quantify the contribution of sea ice algae to total (sympagic + pelagic) primary production.

MATERIALS AND METHODS

Kobbefjord (Danish name), or Kangerluarsunnguaq (Greenlandic Inuktitut name), is a sill fjord near Nuuk, West Greenland (Fig. 1). The fjord is ca. 17 km long, and 0.8 to 2.0 km wide. The innermost part of the fjord (depth ~100 m) is usually sea ice covered, with extensive interannual variation. This study spans 7 mo from November 27, 2005, prior to sea ice formation, to June 27, 2006, when all sea ice had vanished. Two positions in the fjord were visited approximately every 3 wk, 1 on the sea ice (64° 09.69′ N 51° 27.17′ W) and 1 on the seaward-growing or receding floe edge.

At the sea ice station, light intensity (Li-Cor 190SA quantum Q, Li-Cor), air temperature (Testo 110 thermometer) and snow thickness were determined, and sea ice cores were taken using an ice auger (Mark III, Kovacs Enterprises). Sea ice thickness was measured and sea ice temperature profiles were immediately ob-

tained by drilling a hole (diam. 3 mm) and measuring the core temperature (Testo 110 thermometer). Two cores were cut into 10 cm slices for determination of salinity, algal composition, chlorophyll, and nutrient concentrations (nitrate + nitrite, silicate, phosphate). The lower 10 cm of 5 cores were obtained for measurement of primary production. Sea ice samples were transported to the laboratory in polyethylene containers, and melted at 10 µmol photons $m^{-2}\,s^{-1}$ at 4°C, a process that took 2 to 3 d. The photon irradiance levels at which the sea ice was melted were chosen as representative of expected low/minimum irradiance in the sea ice, based on the assumption that the sea ice algae would remain viable but not grow excessively during thawing. An additional ice core was kept frozen for dissolved inorganic carbon (DIC) analysis. Seawater samples for algal composition, primary production, DIC, nutrient and chlorophyll analysis were collected with a Niskin water sampler (KC Denmark) at depths of 1, 5, 10, 15, 25 and 50 m at the floe edge. CTD-profiles (CTD plus SIS-1000, Sensoren Instrumente Systemen) were obtained on all sampling dates at 1 or both stations.

The conductivity of melted sea ice was measured (Thermo Orion 3-star with Orion 013610MD conductivity cell) and converted to salinity (Grasshoff et al. 1983). Sea ice brine salinity was calculated as a function of temperature (Cox & Weeks 1983) and brine volume as a function of bulk salinity, density and temperature (Cox & Weeks 1983, Leppäranta & Manninen 1988). Seawater and melted sea ice samples were GF/C filtered, and kept frozen (–18°C) until nutrient analysis. Phosphate (PO_4^{3-}) concentrations were determined using a standard spectrophotometric approach (Koroleff 1983). Nitrate + nitrite $(NO_3^- + NO_2^-)$ concentrations were measured by vanadium chloride reduction (Braman & Hendrix 1989). Silicate (SiO_2) concentrations were determined by a standard spectrophotometric method (Strickland & Parsons 1972, Grasshoff et al. 1983). Triplicate measurements were performed on each sample with standard deviations <0.05 µM (PO_4^{3-}), 0.5 µM (NO_x) and 0.2 µM (SiO_2).

Melted sea ice and seawater samples were preserved in Lugol's solution (to a final concentration of 1 %) for taxonomic analysis. The samples were allowed to settle for minimum 16 h in 10 or 50 ml chambers before counting algae and protozoa at 200× magnification. Analyses were performed using an inverted microscope (Leica DM IL) and photo documentation was obtained with a digital microscope camera (Leica DFC280). The identification of species and morphological groups was primarily based on the
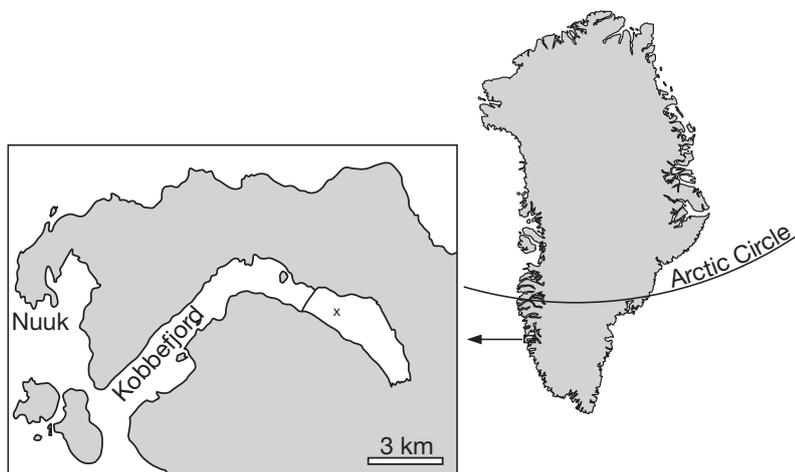

Fig. 1. Kobbefjord/Kangerluarssunguaq, West Greenland. Line marks maximum sea ice extent. x: sea ice station (64° 09.69′ N, 51° 27.17′ W)

work of Tomas (1997). Melting sea ice directly induces osmotic stress which may cause cell lysis, and different approaches have been taken to mitigate this (e.g. melting the sea ice in ample pre-filtered water (Quillfeldt 1996, Ikävalko 1998)). As the algal sea ice environment undergoes large natural variations in salinity and microhabitat configuration (i.e. brine inclusions), it is likely that sea ice algae have high halotolerance. Melting sea ice directly and slowly at a low temperature, as in this study, also exposes the algae to osmotic stress, but provides an advantage in that all measurements are performed on the same core. Sea ice algae are more tolerant to decreasing salinites than to increasing salinities (Kirst & Wiencke 1995), and the presence of flagellate cells such as prasinophytes indicates that the sea ice algae in Kobbefjord were capable of coping with the osmotic stress. Sea ice algae were measured (with a Leica IM500), and carbon content was calculated according to equations derived from Menden-Deuer & Lessard (2000).

Seawater and melted sea ice samples were GF/C filtered ($<$0.1 bar) for chlorophyll determination. Chlorophyll was extracted in 96% ethanol for 18 h (Jespersen & Christoffersen 1987). Fluorescence was measured (TD-700 fluorometer, Turner Designs) before and after addition of 200 µl 1 M hydrochloric acid. Addition of hydrochloric acid degrades chlorophyll-like pigments (Aminot & Rey 2000), and the difference between the two measurements is thus total chlorophyll. The fluorometer measurements were calibrated against spectrophotometrically determined chlorophyll content in water samples (Dansk Standardiseringsråd 1986) using a linear regression ($r^2 = 0.99$, p $\ll$ 0.01, n = 13).

Primary production was measured in melted bottom sea ice and seawater from a depth of 10 m at the floe edge using the ^{14}C incubation technique (Steeman-Nielsen 1952). The samples were incubated in Winkler bottles for 2 h under constant conditions of 40 µmol photons m^{-2} s^{-1} and 4°C. Though incubation should ideally be performed under *in situ* conditions of photosynthetically available radiation (PAR), temperature and spectral composition, microalgae are able to quickly adapt to changes in light conditions (Glud et al. 2007), and incubation under known conditions can be extrapolated. However, melting sea ice is likely to have affected the physiological condition of the sea ice algae, and primary production of sea ice is possibly underestimated. Using PerkinElmer Ultima Gold scintillation liquid, the samples were counted with a PerkinElmer TriCarb 2800 TR liquid scintillation analyzer. Dissolved inorganic carbon (DIC) was measured in sea ice (melted in an airtight plastic bag (Hansen et al. 2000) with a CM5012 CO_2 coulometer as described by Rysgaard & Glud (2004). Asiaq (Greenland Survey) supplied hourly irradiance (W m^{-2}), which was con-

verted to PAR after calibration ($r^2 = 0.99$, p $\ll$ 0.001, n = 133) with a LiCor 1400 quantum meter. Available PAR on each sampling date was calculated at several depths (5, 15, 30 and 45 cm in sea ice and 5, 15, 25 and 50 m in seawater) using attenuation coefficients of 0.09 m^{-1} (seawater), 0.9 m^{-1} (sea ice) (Roberts et al. 2002) and 4.8 m^{-1} (snow) (Glud et al. 2007). Primary production was calculated using the measured concentration of DIC. Primary production was corrected for available PAR and chlorophyll concentration assuming linear relations, and integrated for the entire sea ice core/water column. The values were then integrated for the season.

To assess whether temporal variation exceeded horizontal heterogeneity, a sea ice spatial study was conducted in mid-March. Ten sea ice cores were obtained at a distance of 0, 10 cm, 50 cm, 1 m, 5 m, 10 m, 50 m, 100 m, 500 m and 1000 m from the sea ice station towards the northern shore of the fjord. Sea ice thickness and temperature profiles (Testo 110 thermometer) were measured and the cores were cut into 15 cm slices for determination of salinity, algal composition, chlorophyll and nutrient concentrations (as above).

To compare species compositions of the sea ice and pelagic algal communities, we used the PRIMER software package (Clarke 1993) to analyze species abundance data. Total abundance was 4th root-transformed before a similarity matrix based on the Bray-Curtis similarity measure was constructed. The resemblance in species composition between samples was then ordinated using non-metric multidimensional scaling (MDS). In addition, the Shannon-Wiener, Pielou's evenness and ES200 diversity indices were calculated for the sea ice algae.

RESULTS

Abiotic parameters

Sea ice (Fig. 2a) grew at ca. 7 mm d^{-1} throughout December and January. The growth rate then slowed, and ice cover remained relatively constant around 55 cm until the beginning of April. At maximum extent, the sea ice covered ca. 8 km^2. The sea ice did not break, but melted in May at a rate of 30 mm d^{-1}. The amount of snow (Fig. 2a) covering the sea ice varied during the season, with approximately 15 cm during winter. In March, the snow was blown away by a storm, followed by a heavy snowfall of 40 cm in April, which remained until May. Surface PAR over the year fitted a bell-shaped curve, with a mean daily surface value (Fig. 2b) of 60 µmol m^{-2} s^{-1} in January and 600 µmol photons m^{-2} s^{-1} mid-June. Dry snow has a high reflection index and attenuation coefficient, and
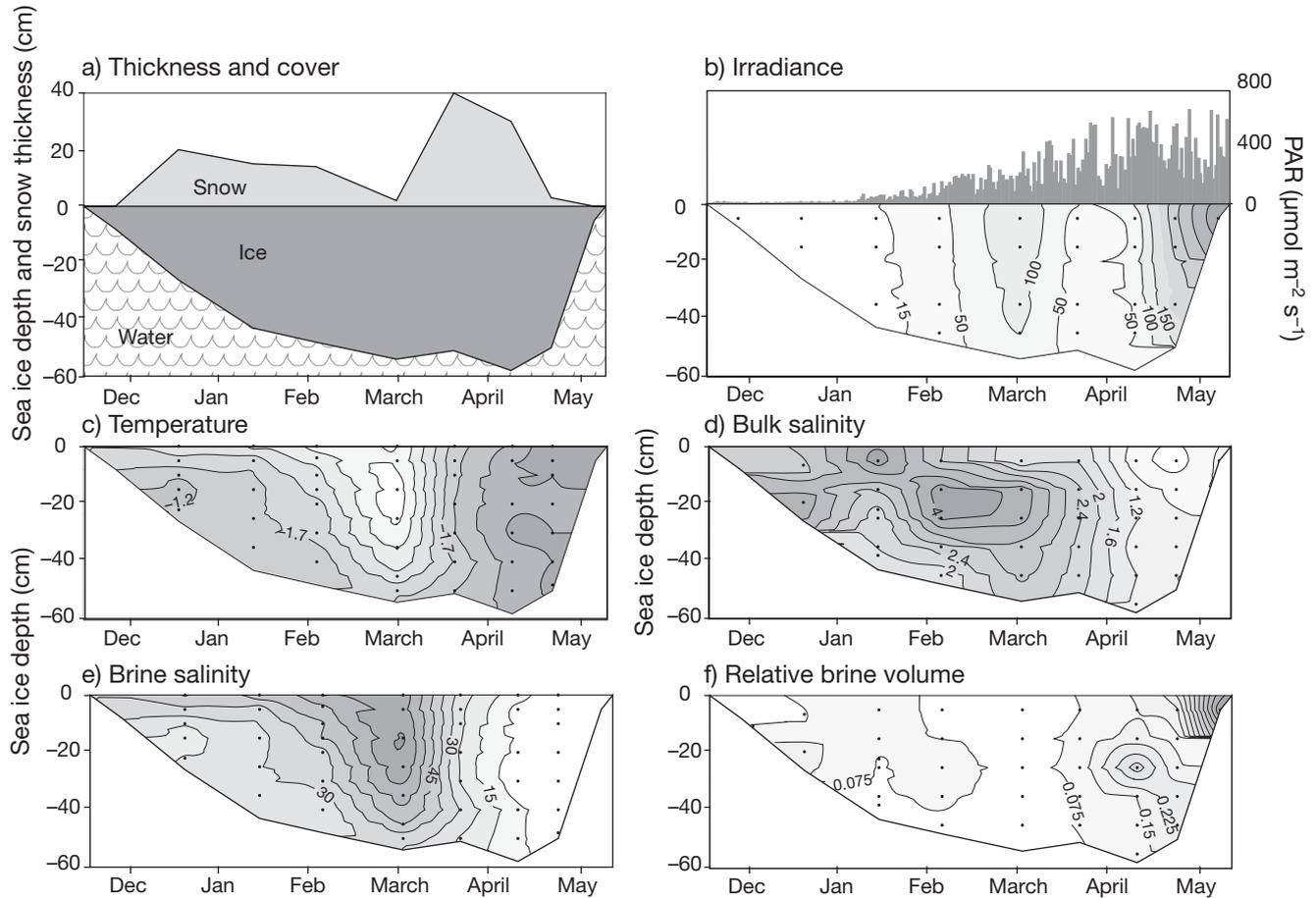
Fig. 2. Sea ice development in Kobbefjord over the season 2005–2006. (a) Sea ice thickness and snow cover (cm), (b) average daily photon irradiance (PAR, µmol m⁻² s⁻¹) in sea ice and at surface, (c) temperature (°C), (d) bulk salinity, (e) brine salinity, (f) relative brine volume fraction. The black dots represent duplicate measurements

the snow cover greatly influenced the estimated irradiance within sea ice (Fig. 2b). Photon irradiance throughout the sea ice was very low (<15 µmol m⁻² s⁻¹) in winter, increasing to 100 µmol m⁻² s⁻¹ in March. The snow cover in April attenuated PAR, and when the snow disappeared in May, sea ice photon irradiance increased to 200 µmol m⁻² s⁻¹. Sea ice reached a minimum temperature of –4°C in March, and then gradually warmed to 0°C in late May (Fig 2c). Sea ice bulk salinity (Fig. 2d) varied vertically throughout winter, with lower values in the bottom sea ice. Overall, bulk salinity decreased with sea ice age, resulting in nearly fresh (salinity <1) conditions in May. Brine salinity (Fig. 2e) was calculated from the sea ice temperature and followed an inverse pattern, with a maximum salinity of 70 in March. The relative brine volume (v/v, Fig. 2f) decreased to a minimum of 0.05 in March. The volume increased towards sea ice melt, with a pocket of high brine volume at a depth of 10 to 25 cm in early May.

During the sea ice season, we observed a weak halocline (salinity change of 0.5) and a weak thermocline (temperature change of 0.2°C) ca. 1 m below sea ice, while the rest of the water column was well mixed. At the onset of sea ice melt, the water column became stratified, with a halocline (salinity change from 32 to 33.2 at 5 m) and a gradual thermocline (from 3.2°C at 1 m to 0.5°C at 15 m).

Overall, seawater salinity varied from 32 to 33.5, while temperature varied from –0.4°C to 2°C (across all depths).

Nutrient (phosphate, silicate and nitrate+nitrite) concentrations in the sea ice varied temporally and differently by ionic species. The concentration of nitrate+ nitrite (Fig 3a) initially decreased from 2.5 µM in December to <0.5 µM in the middle sea ice in March. There was an increase in concentration throughout the sea ice, reaching 4 µM in the top sea ice in late April, followed by a decrease to <1 µM during ice melt in May. Phosphate concentration (Fig. 3b) decreased from 0.3 µM in December to ~0.15 µM throughout the sea ice in February. In March, there was a slight increase to 0.2 µM in the upper sea ice, while the

a) Nitrate + nitrite

b) Phosphate

c) Silicate
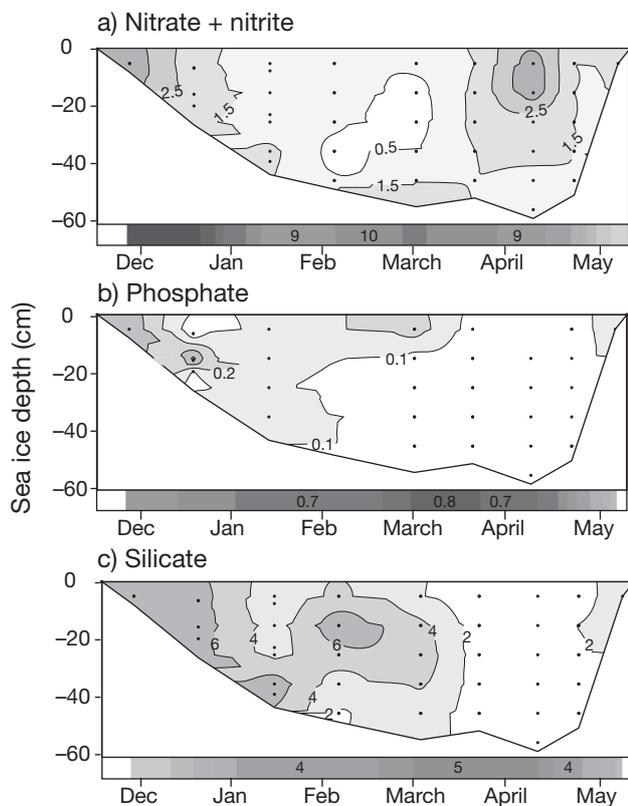

Fig. 3. Nutrient concentrations (µM) in bulk sea ice (contour lines) and seawater (bar). (a) NO$_x$ (nitrate + nitrite), (b) phosphate, (c) silicate. The black dots represent duplicate measurements

remainder of the sea ice had concentrations <0.1 µM. The phosphate concentration in the upper sea ice decreased in April, and the entire sea ice contained <0.1 µM until sea ice melt, when there was an increase to 0.14 µM. Silicate concentrations (Fig. 3c) varied from 4 to 6.5 µM in winter. In March, the concentration decreased, reaching minimum concentrations (<1 µM) in April. In May, the concentration increased to 2 µM. Silicate concentrations were correlated with salinity ($r^2 = 0.66$, $p < 0.001$, $n = 28$) until March ($r^2 = 0.00$, $p < 0.1$, $n = 26$), suggesting little biological influence in winter. Nitrate + nitrite and phosphate concentrations showed no consistent correlation pattern.

Throughout the sea ice cover season, there was little vertical variation in seawater nutrient concentrations in the upper 50 m of the water column. Initial seawater concentrations (at the time of sea ice formation) of nitrate + nitrite, phosphate and silicate were 13, 0.5 and 3 µM, respectively (Fig. 3, bars). During the sea ice season, the concentration of nitrate + nitrite remained varied from 9 to 11 µM, while the concentration of phosphate and silicate varied from 0.7 to 0.9 µM and 4 to 6 µM, respectively. All nutrient concentrations decreased during sea ice thaw in May.

Biotic parameters

Algae were present in the sea ice throughout the season. Small (~5 µm) unidentified flagellates (Fig. 4a), Prasinophyceae (Fig. 4b), Dinophyceae (Fig. 4c), Cryptophyceae (Fig. 4d) and Bacillariophyceae (both centric, particularly *Chaetoceros simplex* [Fig. 4e], and pennate [Fig. 4f]) were regular components of the sea ice algal community. In addition, Dictyochophyceae (*Dictyocha speculum*), Haptophyta (*Chrysochromulina* spp.), Chrysophyceae, Euglenophyceae (e.g. *Eutreptiella* spp.), Raphidophyceae and Chlorophyceae occurred in low numbers. Initially, most taxa were represented in the sea ice, resulting in high ES200 and Shannon-Wiener diversity indices (Fig. 5a). Index values decreased (due to lysis, grazing, release to water column, etc.) to a minimum in March, followed by an increase towards sea ice melt in May. Pielou's evenness index was less pronounced, but also showed a drop in March. Based on dominance (the relative numerical contribution of one group), 3 assemblages are recognized: flagellates in January/February, the centric diatom *Chaetoceros simplex* mid-March and pennate diatoms in May. The flagellates in winter were gymnodinoid dinoflagellates (e.g. *Gymnodinium* spp.), cryptophytes (particularly *Rhodomonas*), prasinophytes (*Pyramimonas* spp.) and small (~5 µm) unidentified flagellates. All flagellate groups remained in the sea ice throughout the season, but became of less numerical importance. Only 2 diatom species were observed in winter, both rarely and in low abundance (<1%). In March, one of these species (*Chaetoceros simplex*) bloomed and became dominant, contributing up to 75% of the total sea ice algal abundance. During April, *C. simplex* was of reduced numerical importance (~15%) as several new genera of pennate diatoms (*Navicula*, *Nitzschia*) appeared, and cryptophyte and small (~5 µm) flagellate abundance increased. Dinoflagellate cysts occurred concurrently with a decrease in dinoflagellates, particularly in the lower parts of the sea ice. During sea ice melt in May, the pennate diatoms became numerically dominant (>70%).

Converting cell numbers into biomass by applying the equations of Menden-Deuer & Lessard (2000) did not change the overall succession pattern, but shifted the relative contributions of the respective taxonomic groups as well as the integrated annual importance. This was particularly true for small cells that were present in high numbers, but had small cell volumes and low carbon contents. When calculations were based on algal cell carbon instead of algal cell density, the integrated annual contribution of the small (~5 µm) unidentified flagellates decreased (14 to 1%), as did the contribution of *Chaetoceros simplex* (27 to 20%). Concurrently, the integrated annual contribution for other
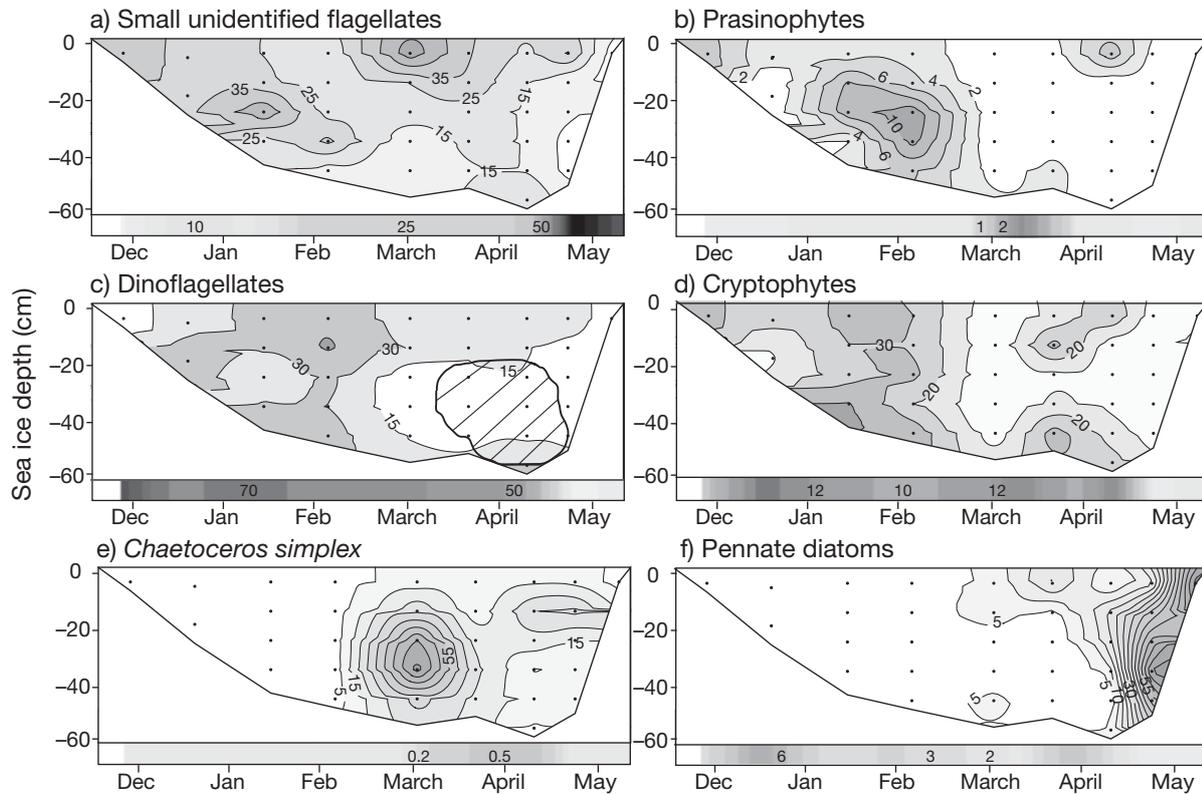
Fig. 4. Contribution of algal phyla (%, based on cells l^{-1}) to sea ice (contour lines) and pelagic (bar) microalgal community. (a) Small (~5 µm) unidentified flagellates; (b) prasinophytes; (c) dinoflagellates, the hatched area indicates presence (>10%) of dinoflagellate cysts; (d) Cryptophytes; (e) *Chaetoceros simplex*, a small centric diatom; (f) pennate diatoms. The black dots represent duplicate measurements
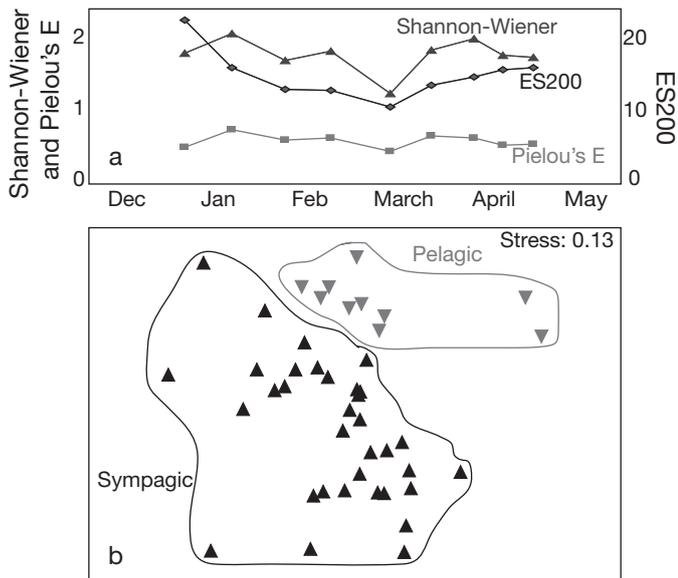

Fig. 5. (a) Diversity indices in sea ice (Pielou's E: Pielou's evenness index), and (b) MDS ordination of all algal samples showing separation of pelagic and sympagic groups

groups increased, particularly for pennate diatoms (25 to 42%).

The MDS ordination (Fig. 5b) showed that the sea ice and pelagic algal assemblages fell into separate groupings. Sixteen percent of the dissimilarity between these groups was due to *Chaetoceros simplex*, small flagellates and *Rhodomonas* sp. The pelagic algal community in the upper 50 m of the water column (Fig. 4, bars) consisted primarily of dinoflagellates (*Gymnodinium* spp.) during the sea ice season (>60%), with dinoflagellates cysts observed in small numbers in late April. Pennate diatoms were present in the seawater throughout the season (1 to 7%). An increase in prasinophytes (0 to 2%) occurred in February. Centric diatoms were virtually absent in seawater during sea ice cover, with the exception of a small increase in the abundance of *Chaetoceros simplex* in March. Initially, small (~5 µm) unidentified flagellates contributed merely 1.5%. During the sea ice season, they became abundant, contributing 10 to 35% until sea ice melt (late May) when they dominated numerically (99%). At this time, several species of *Chaetoceros* (including, but not restricted to *C. simplex*) and *Thalassiosira* appeared.
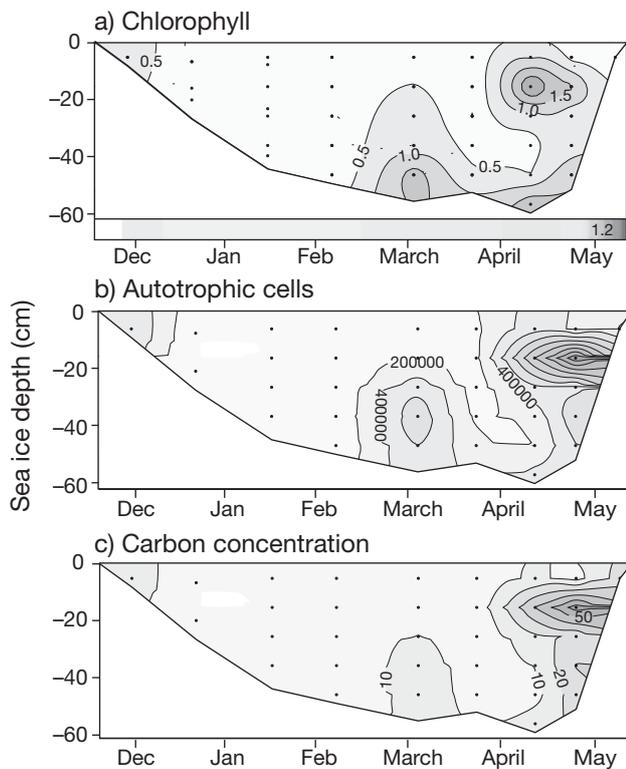
Fig. 6. (a) Chlorophyll concentrations (µg chl l^{-1}) in sea ice (contour lines) and in the water column (bar). (b) Densities of autotrophic cells (cells l^{-1}) in sea ice. (c) Carbon concentration (µg C l^{-1}) in sea ice. The black dots represent duplicate measurements
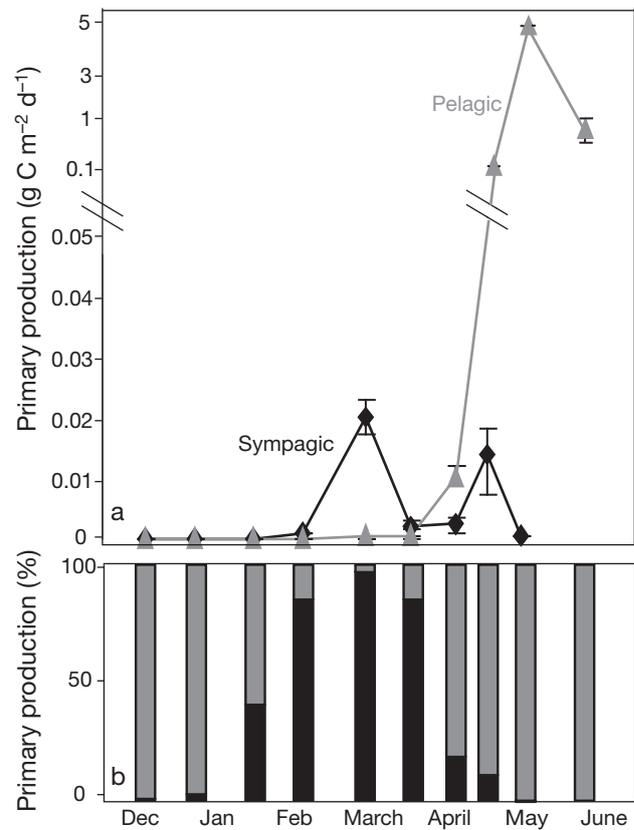

Fig. 7. (a) Primary production (g C m^{-2} d^{-1}) in sea ice (sympagic) and seawater (pelagic); bars are ranges (minimum and maximum). (b) Relative contributions (%) of sympagic and pelagic algae to primary production

Sea ice chlorophyll levels (Fig. 6a) were low (<0.5 µg chl l^{-1}) throughout winter. In March, a bottom sea ice bloom (1.8 µg chl l^{-1}) was observed. During April and May, a widespread bloom was present, reaching a maximum of 2.6 µg chl l^{-1}. Algal cell densities in sea ice (Fig. 6b) were positively related to chlorophyll (r^2 = 0.5, p < 0.01, n = 33), and tracked a similar pattern, with a bottom sea ice bloom in March (0.6 × 10^6 cells l^{-1}) and a widespread bloom in May (1.0 × 10^6 cells l^{-1}). Sea ice algal carbon content in the bottom sea ice (Fig. 6c) also peaked in March (~10 µg C l^{-1}) and in May (~60 µg C l^{-1}). In the seawater, chlorophyll concentrations were negligible (<0.05 µg chl l^{-1}) until late May when a bloom occurred. The bloom reached a maximum of 1.8 µg chl l^{-1} at 10 to 15 m, after which chlorophyll decreased to 1.2 µg chl l^{-1} mid-June.

Sea ice primary production (integrated by sea ice core, Fig. 7a, and as relative contribution, Fig. 7b) showed two distinct peaks of similar magnitude in March (21 mg C m^{-2} d^{-1}) and May (15 mg C m^{-2} d^{-1}). Before and between the peaks, production was low. Annual sea ice primary production was 0.78 g C m^{-2}.

Primary production in seawater was negligible until sea ice melt (late May), when a large peak (4.2 g C m^{-2} d^{-1}) occurred. By mid-June, pelagic primary production had decreased to 0.7 g C m^{-2} d^{-1}. Total pelagic production during the stable sea ice cover period was low (ca. 1.8 g C m^{-2}). If only the season with stable sea ice cover is considered, the contribution of sea ice algae was 30%. However, including the large bloom at sea ice melt time and the ensuing pelagic primary production (i.e. the entire 7 mo), total pelagic primary production in the upper 50 m of the water column was 94.4 g C m^{-2}. The contribution of sea ice algae to total (pelagic + sympagic) primary production was thus a mere 0.8% over 7 mo.

Heterogeneity

Sea ice thicknesses ranged from 52 to 67 cm along the 1000 m transect. Parameters varied, with average sea ice core values of 1.8 to 3.6 (bulk salinity), 0.4 to 1.2 µg l^{-1} chlorophyll, 0.05 to 0.2 µM phosphate, 3.2 to 6.1 µM silicate and temperatures of −3.3 to −2.4°C.

Taxonomic composition was not investigated in detail, but all sea ice cores were dominated by *Chaetoceros simplex*. To assess sea ice variability, data from the temporal (7 mo) and horizontal (March) study were combined for a 3-way ANOVA with the independent variables of depth, time and distance. Data were not transformed, and ANOVA assumptions were met. The assumption for this analysis is that the measured horizontal variation mid-March is not significantly different from variation at other times during the season. The analysis showed that there was a significant effect ($p < 0.01$) of time on chlorophyll ($F_{7,49} = 9.0$), temperature ($F_{6,24} = 66.4$), salinity ($F_{6,27} = 11.4$), phosphate ($F_{6,39} = 6.5$) and silicate ($F_{7,49} = 33.0$). There was also a significant effect ($p < 0.01$) of depth on chlorophyll ($F_{13,49} = 7.8$), temperature ($F_{40,24} = 6.8$), salinity ($F_{13,27} = 2.8$), phosphate ($F_{12,39} = 4.2$) and silicate ($F_{11,49} = 6.5$). The interaction between depth and time was significant for chlorophyll, temperature and silicate ($F < 4$, $p < 0.01$), but not salinity and phosphate ($F < 2$, $p > 0.3$). For distance, there was a significant effect on phosphate and silicate ($p < 0.05$), but not on chlorophyll, temperature and salinity ($p > 0.05$).

DISCUSSION

Algae were present in sea ice throughout the season, and the community followed a distinct succession with dominance of different taxonomic groups at different times. Pennate diatoms were observed only late in the season, while flagellates and the centric diatom *Chaetoceros simplex* were dominant in winter and spring, respectively. Though great spatial variation can be found within sea ice (e.g. Rysgaard et al. 2001), the temporal variation in Kobbefjord was, except for phosphate and silicate, not due to sea ice heterogeneity; most of the temporal variation was within the algal assemblage.

The changes in sea ice algal composition in Kobbefjord were related to PAR and brine volume. The influences of brine volume are manifold, with both direct physical constraints (e.g. available habitat) and indirect changes in abiotic conditions (e.g. nutrient concentrations). Previous studies have shown that colonisation of sea ice largely depends on brine volume (Krembs et al. 2000), and the seasonal changes in brine volume likely influence both the succession within the sympagic algal community and colonization by pelagic algae. In April and May in Kobbefjord, the thaw-induced increased brine volume allowed percolation processes and direct exchange of organisms between sea ice and seawater. No new species of pennate diatoms had been observed previously in the sea ice, and their appearance documents an outside influence

on the sea ice algal community. The appearance of cytoplasts indicated that pennate diatoms were not thriving, and whether they actively colonize the sea ice is not known.

The importance of PAR on species composition is indicated by flagellate dominance under low light (winter, and the period with heavy snow cover), while diatoms dominated during periods of increased PAR (March and May). It is likely that the sea ice flagellates supplemented or substituted photosynthesis with mixotrophy or heterotrophy. A species of *Rhodomonas* (the dominant sea ice cryptophyte genus) has been identified as a likely mixotroph (Hammer et al. 2002), and hetero- and mixotrophy is common among dinoflagellates (Arrigo 2003). However, pennate diatoms are also nutritionally diverse (e.g. Horner 1985), and their absence during winter and spring is a subject for further studies.

A further factor known to influence the development of sea ice algal communities is grazing (Gradinger et al. 1999), but we have no means to evaluate this aspect. Ciliates (e.g. *Philasterine* sp., *Holophrya simplex*) were present throughout the season, and decreased in abundance at sea ice melt (data not shown).

Dinoflagellate cysts were observed in sea ice in April, but were only found scattered in the seawater. The absence of an increase in pelagic and sympagic dinoflagellates coupled with the spiny structure of the cysts (they were observed to cluster) indicates that the cysts were exported to deeper waters. Cysts are resistant stages that survive temporally harsh environmental conditions, and subsequently excyst (Stoecker et al. 1997); it is likely that the cysts bloomed later in the season or 'over-summered' to excyst when incorporated into sea ice the following season.

Sea ice algal biomass (max. 2.6 µg chl l^{-1}, Fig. 6a) was low, but similar to previously reported values (e.g. Horner & Schrader 1982). The presence of a chlorophyll maximum within the sea ice in April/May emphasizes the need for studies of the entire sea ice core, not only the bottom sea ice.

There is usually a spring peak in sea ice primary productivity as light levels increase, followed by a decrease due to e.g. nutrient limitation (Haecky & Andersson 1999). Sympagic primary production (integrated through the sea ice cores) in Kobbefjord was correlated to irradiance ($r^2 = 0.66$, $p < 0.05$, $n = 8$), and followed a different pattern with 2 distinct peaks of similar magnitude in March and May, concurrent with the irradiance maxima.

Algae are generally assumed to require nutrients in a ratio of 106C:16N:15Si:1P, the so-called Redfield ratio amended to include a diatom requirement for silicate (Parsons et al. 1961). Based on this assumption, nitrogen was limiting sea ice algal growth in March

(N:P of 4) and late May (N:P of 10), while silicate was a limiting factor in late April (Si:P of 7), a time when pennate diatoms began to appear. The observed increases in nitrogen and silicate concentrations in April and May, respectively, may be due to remineralisation within the sea ice and/or exchange with the seawater. Another possibility is that heavy snow cover depressed the sea ice, causing surface flooding and subsequent inflow of nutrients to the sea ice.

The annual sympagic primary production of 0.78 g C m^{-2} in Kobbefjord is comparable to measurements in Young Sound fjord on the northeastern Greenland coast (Rysgaard et al. 2001), and to measurements further offshore in the Greenland Sea (Gradinger et al. 1999, Mock & Gradinger 1999). Gradinger (1999) suggested that biomass in pack ice is much lower than in fast-ice areas due to the lower nutrient supply, different physical constraints (ice temperature, brine salinity, radiation) or biological interactions (grazing and growth rates). However, the sea ice algal biomasses in Young Sound and Kobbefjord are lower than in other coastal fast-ice areas with similar latitudes, sea ice and snow thicknesses, irradiances and nutrient concentrations (Cota et al. 1991). A possible explanation for the relatively low sea ice primary production and biomass in Greenlandic fjords is greater homogeneity of snow and ice cover (which attenuate light) than in offshore regions where snow cover is much more variable and where cracks in the sea ice or floe edges allow enhanced light penetration and, consequently, elevated primary production (Glud et al. 2007). Another explanation may be related to differences in the initial algal colonization of sea ice in Greenlandic fjords and other Arctic regions. However, more work is needed to resolve this issue.

Pelagic algal biomass and primary production were negligible during the sea ice season, presumably due to PAR limitation. When PAR increased at sea ice melt, a bloom occurred. Short-lived pelagic blooms near the sea ice edge are common, and are attributed to a combination of light availability, water stratification (Heide-Jørgensen et al. 2007) and possibly seeding by sea ice algae (Syvertsen 1991). The peak in pelagic primary production and biomass was followed by a decrease that was concurrent with a tripling in zooplankton cell density (data not shown), indicating that grazing is likely of importance in controlling the pelagic microalgal biomass in Kobbefjord, as is the case in other Greenlandic fjords (Rysgaard et al. 1999). The pelagic bloom in Kobbefjord consisted mainly of small flagellates, which were already present in both sea ice and seawater. Several species that had not previously been observed (*Thalassiosira spp.* and *Chaetoceros spp.*) also contributed to the bloom. Though there were indications that some sea ice algae (prasino-

phytes, *C. simplex*) remained suspended and viable when released from the sea ice (Fig. 4b,e), multivariate analysis (Fig. 5) showed that the sympagic and pelagic community were 2 separate entities. The fact that the last two pelagic sampling dates (post sea ice melt) were outliers indicates that the pelagic winter and the sympagic community were connected and that the pelagic summer community was influenced by pelagic species, rather than being seeded from the sea ice.

In Kobbefjord, sympagic primary production of 0.78 g C m^{-2} contributed 0.8% to the total (sympagic + pelagic) primary production. Though the sympagic primary production may be an underestimate, sea ice primary production is not a major contributor on an annual basis. However, sea ice algae are important primary producers during the season of stable sea ice cover, when pelagic primary production is low.

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