



New measurements of phytoplankton and ice algal production in the Arctic Ocean

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Abstract—During the Canada/U.S. 1994 Arctic Ocean Section, algal biomass (Chlorophyll *a*) and primary production were measured in the water column, at the ice–water interface and in the bottom 2–4 cm of the sea ice along a transect from the Chukchi Sea to the Nansen Basin via the North Pole. Algal biomass and primary production were determined for 0.7–5 μm and $> 5 \mu\text{m}$ size fractions. The algal release rate of DO^{14}C during incubation was also measured. In the Chukchi Sea and in leads of the Makarov and Nansen Basins, total maximum particulate phytoplankton production rates were 2570, 73 and 521 $\text{mg C m}^{-2} \text{ day}^{-1}$, respectively. At these stations, where ice cover varied from 55 to 90%, large phytoplankton ($> 5 \mu\text{m}$) represented 61–98% of the total algal biomass. At stations with higher ice coverage ($> 90\%$), the total phytoplankton production decreased to 9–57 $\text{mg C m}^{-2} \text{ day}^{-1}$. At these stations, small phytoplankton (0.7–5 μm) accounted for 59–88% of the total biomass and more than 64% of the total production. Along the transect, the percentage of the total phytoplankton production released as extracellular carbon was generally less than 20%, except in the Canadian Basin where it ranged from 31 to 65%. Total particulate ice algal production ranged from 0.5 to 310 $\text{mg C m}^{-2} \text{ day}^{-1}$ and showed maximum rates in the central Arctic Ocean. Large cells ($> 5 \mu\text{m}$) generally dominated the ice algal community, representing 50–100% of the total biomass and more than 50% of the total production. Ice algae released on average 34% of total carbon fixed during the 4–12 h incubation. Ice algae contributed on average 57% of the entire primary production (water column + sea ice) in the central Arctic and 3% in the surrounding regions. Total primary productivity in the central Arctic Ocean is estimated at 15 $\text{g C m}^{-2} \text{ year}^{-1}$, a value at least 10 times higher than previously reported. The difference between estimates is due in part to the previously unmeasured contribution of the particulate production by ice algae and the release of DOC by both ice and pelagic algae. © 1998 Elsevier Science Ltd. All rights reserved

INTRODUCTION

The central Arctic Ocean has been characterized as a region of extremely low primary production resulting from the year round presence of ice and a short photosynthetic season. Apollonio (1959) and English (1961) estimated on the basis of limited discrete stations that the annual phytoplankton production in the central Arctic Ocean was less than 1 g C m^{-2} . Since then, models of the Arctic carbon budget have generally assumed that most organic material is imported from the extensive surrounding shelves that are ice-free in summer, and that negligible primary production takes place in the central basins (e.g. Walsh, 1995). In

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summer, the minimum ice extent in the Arctic Ocean is approximately $5.5 \times 10^6 \text{ km}^2$ (Parkinson and Cavalieri, 1989), which represents 79% of the total area of this ocean. The earlier estimates of production in the central Arctic did not take into consideration the potential production of ice algae or of the production of dissolved organic carbon (DOC) by pelagic and ice algae.

Based on very limited data and assumptions derived from non-polar oceans, Subba Rao and Platt (1984) and Legendre *et al.* (1992) estimated a mean annual phytoplankton production for the arctic waters north of 65°N at 27 g C m^{-2} in shelf regions ($< 200 \text{ m}$) and at 9 g C m^{-2} in offshore regions ($> 200 \text{ m}$). Within the first-year sea ice, they estimated an average annual production of 10 g C m^{-2} . Within multi-year ice, Legendre *et al.* (1992) used an annual value of 0.6 g C m^{-2} , while Subba Rao and Platt (1984) assumed no ice algal production. From these values, Subba Rao and Platt (1984) estimated that arctic ice algae contribute to less than 3% of the total annual primary production, while Legendre *et al.* (1992) estimated the ice algal contribution as 3 to 25%.

From 26 July to 26 August 1994, the United States and Canada conducted a joint interdisciplinary expedition to increase the observational base necessary for understanding the role of the Arctic in global change. The general goal of the present study was to provide new measurements of primary productivity in the Arctic Ocean. The specific objectives were (1) to determine the contribution of phytoplankton and sea ice algae to the particulate and dissolved primary production, and (2) to determine the environmental factors influencing the photosynthesis within the different regions of the Arctic Ocean. Some preliminary results concerning the first objective were presented in Wheeler *et al.* (1996). In this report, latitudinal changes in algal production and biomass are discussed in more detail.

METHODS

Sampling and laboratory analyses

Sampling was conducted on both first- and multi-year ice of the Arctic Ocean from 26 July to 26 August 1994, onboard the icebreaker USCGC *Polar Sea*. The transect began on the continental shelf of the Chukchi Sea on the western side of the Arctic, crossed the North Pole and terminated in the deep Nansen Basin on the eastern side of the Arctic (Fig. 1). Ice algal and phytoplankton sampling was carried out at 15 and 21 stations, respectively.

At each water column station, the vertical profile of irradiance (PAR: photosynthetically active radiation, 400–700 nm) was first measured with a PNF-300 radiometer (Biospherical Instruments). Water samples were then collected at 7 optical depths (100, 50, 30, 15, 5, 1 and 0.1% surface PAR) with a rosette sampler equipped with 10 l Niskin bottles and a high precision CTD probe (Sea-Bird Electronics). The optical depths were chosen to correspond to irradiances available in a simulated *in situ* incubator (described below). PAR was also measured at 10 min intervals from July to August on the deck of the ship near the incubator, with a LI-COR 190 SA quantum meter.

At each ice station, ice cores were taken with a SIPRE ice corer (7.5 or 10.5 cm internal diameter). The lowest 2–4 cm of ice was cut and melted in surface water filtered through $0.2 \mu\text{m}$ polycarbonate membranes in order to minimize osmotic stress (Bates and Cota, 1986). Concentrations and rates determined on ice samples were corrected for the dilution effect of added seawater as described in Cota and Sullivan (1990). Samples from the ice–water interface were collected by SCUBA divers, using a 2.2 l syringe sampler (“slurp gun”)

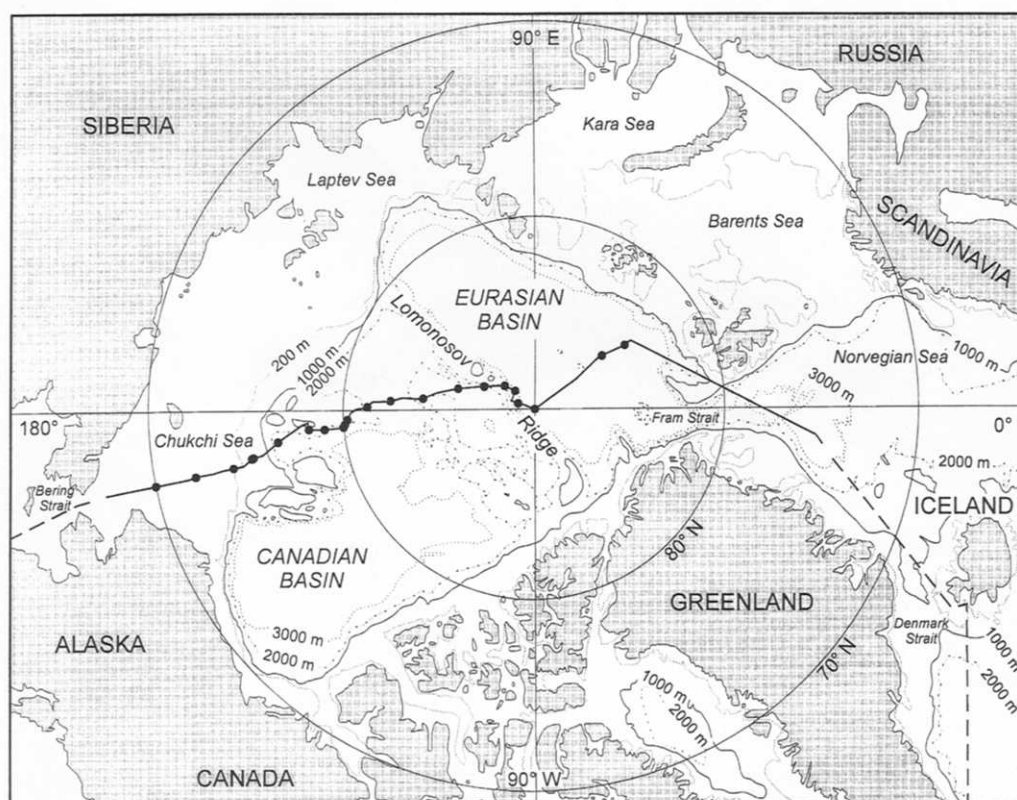


Fig. 1. Map of the stations in the Arctic Ocean.

(Gosselin *et al.*, 1990); these samples were free of ice. Ice cores and interfacial water samples were taken at a minimum of 3 sites at each station to obtain a representative mean (Gosselin *et al.*, 1986). At each ice station, snow depth, ice thickness and percent ice cover and irradiance above and under the ice (LI-COR 185 B underwater PAR meter) were recorded.

Samples for dissolved inorganic nutrients (phosphate, silicic acid, nitrate, nitrite, ammonium) were processed immediately after collection, using a Technicon Autoanalyzer (Atlas *et al.*, 1971). Subsamples for the determination of chlorophyll *a* (chl *a*) were filtered onto Whatman GF/F glass fiber filters (total algal biomass: B_T) and onto Poretics polycarbonate 5 μm membranes (biomass of large algae: B_L). Concentrations of chlorophyll *a* were determined on a R010 Turner Designs fluorometer, after 24 h extraction in 90% acetone at 5 °C without grinding (Parsons *et al.*, 1984). Samples taken from the ice bottom, the ice–water interface, in water surface, and at the depth of the Chl *a* maximum were preserved with formaldehyde buffered with sodium acetate (final concentration of ca. 1%). Cells were identified and enumerated using the standard inverted-microscope method (phase contrast illumination: Utermöhl, 1931; Hasle, 1978). Cell numbers were transformed into C biomass using formulas given in Booth (1993); see Booth and Horner, 1997, for more details). The carbon biomass of dinoflagellates and flagellates reported here is lower than in Booth and Horner (1997) who used chlorophyll autofluorescence to determine the abundance of these two groups.

Primary production rate was estimated from seven photic depths (100, 50, 30, 15, 5, 1 and 0.1% surface PAR) using the ^{14}C uptake method (Parsons *et al.*, 1984). Two light and one dark 500 ml Nalgene polycarbonate bottles were filled with water from each optical depth (pre-filtered on Nitex 202 μm), inoculated with 5 or 20 μCi (0.19 or 0.76 MBq) of $\text{NaH}^{14}\text{CO}_3$ and placed for 12 h in Plexiglas deck incubators at the appropriate irradiance level. Ice algal samples from the ice–water interface and the bottom surface of the ice were incubated for 4–12 h in 250 ml Corning culture tissue flasks at the irradiance measured *in situ*. The incubator was cooled with running seawater continuously pumped by the ship from a depth of about 8 m. The total amount of radioisotope in each bottle was determined by immediately pipetting 50 μl subsamples into 15 ml of ScintiSafe Plus 50% (Fisher) scintillation cocktail containing 50 μl of 6 N NaOH. At the end of the incubations, a volume of 3 or 5 ml of the water was transferred to scintillation vials, acidified with 6 N HCl and left open on a shaken table, in a fume hood for at least 4 h in order to measure the total production of organic carbon (dissolved + particulate) (Lewis and Smith, 1983). The sample was then neutralized with 6 N NaOH before adding the scintillation cocktail. Half of each bottle was filtered onto Whatman GF/F glass fiber filters (total particulate algal production: P_T); the other half was filtered onto Poretics polycarbonate 5 μm membranes (production of large algae: P_L). The filters were rinsed with non-radioactive filtered seawater before being removed from the filtration apparatus, after which they were dropped into borosilicate scintillation vials. Under the hood, 200 μl 0.5 N HCl was added to each vial in order to remove the non-incorporated ^{14}C (Lean and Burnison, 1979). Following the evaporation of the acid, scintillation cocktail was added. The activity was measured on a Beckman LS 5801 liquid scintillation counter. Total (dissolved + particulate) and particulate primary production was calculated according to Parsons *et al.* (1984), using a value of 25 000 mg C m^{-3} for the concentration of dissolved inorganic carbon. In all primary productivity calculations, dark values were subtracted from corresponding light values assuming that the measured dark fixation of ^{14}C is due solely to bacterial processes occurring similarly in clear and opaque bottles (Li *et al.*, 1993). The release rate of DO^{14}C by

microalgae (P_E) was calculated as the difference between total (dissolved + particulate) production and particulate primary production (P_T).

During the phytoplankton incubations, the simulated *in situ* irradiance was not corrected for the attenuation of PAR by snow, ice and ice algae. To correct *a posteriori* for this effect, all values of integrated phytoplankton production (100 to 0.1% surface PAR) reported in this paper were transformed in order to take into account changes in percent ice cover (see arguments in Smith, 1995):

$$P_{\text{corrected}} = [P_{\text{uncorrected}} * ((100 - \phi)/100)] + [P_{\text{uncorrected}} * \phi/100 * E_s/E_0]$$

where ϕ is the percentage of ice cover, E_s is the sub-ice irradiance and E_0 is the incident irradiance. The ratio $E_s:E_0$ varied between 0.03 and 0.27. The integrated values of ice algal production and biomass were multiplied by the percentage of ice cover (ϕ). Production and biomass by small algae (0.7–5 μm) were calculated as the difference between P_T and P_L and B_T and B_L , respectively.

Numerical analysis

Spearman's rank correlation was used to determine the correlation between physical, chemical and biological variables (Siegel and Castellan, 1988). The Kruskal–Wallis one-way analysis of variance was used to test differences between two phytoplankton production regimes (i.e. $P_L:P_T$ and $B_L:B_T < 50\%$ and $P_L:P_T$ and $B_L:B_T > 50\%$). In order to test the null hypothesis that the algal community is not structured along the transect in the Arctic Ocean, the carbon biomass of the various algal taxonomic groups was analyzed using a statistical method described as "chronological clustering" by Legendre *et al.* (1985). This method partitions data series into homogeneous segments (under the constraint of spatial contiguity), following hierarchical agglomeration (Galzin and Legendre, 1987).

RESULTS

Physical and chemical environment

Physical and chemical variables showed large spatial variability across the Arctic Ocean. Figure 2 presents the latitudinal changes in water depth, percent ice cover, ice thickness and snow depth from the Chukchi Sea to the Nansen Basin. The water depth ranged from a minimum of 40 m in the Chukchi Sea to a maximum of 4200 m at the North Pole (Fig. 2a). We crossed the Lomonosov Ridge, which separates the Canadian and Eurasian basins, at 88°48' N (Figs 1 and 2a). First-year ice was present in the Chukchi Sea (70–75° N) and at the Lomonosov Ridge station, while multiyear ice was present at all other stations. The percent ice cover ranged from about 55 to 100% (Fig. 2b), and was lower in the Chukchi Sea (55–80%), reached a maximum in the Canadian Basin (90–100%), and decreased somewhat toward the end of the transect (100–80%). The ice thickness and the snow depth did not show any definite pattern (Fig. 2c and d). The ice thickness varied between 1.1 and 3.2 m along the transect. The snow depth varied from 2 to 30 cm.

Figure 3 shows the latitudinal changes in the physical properties of the upper water column. In the euphotic layer, the mean integrated water temperature decreased from -1.5 to -1.8 °C while the mean integrated salinity increased from 29 to 34 along the transect (Fig. 3a and b). The depth of the surface mixed layer, defined as the depth where the vertical

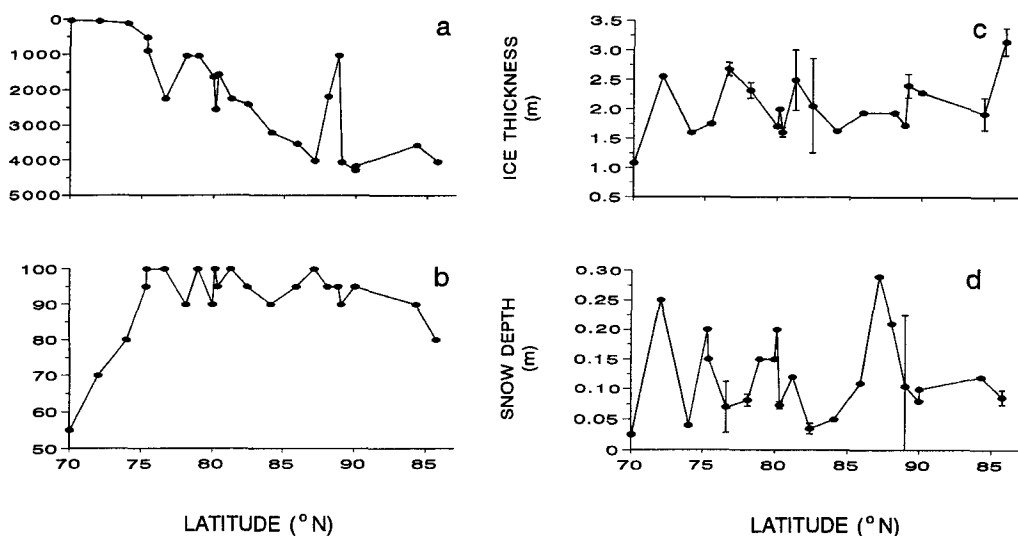


Fig. 2. Latitudinal changes in water depth (a), ice cover (b), ice thickness (c) and snow depth (d) in the Arctic Ocean in July–August 1994. Means and standard deviations are indicated for some stations in panels c and d.

gradient in σ_t (σ_t) is higher than 0.02 per meter, was very shallow (<12 m) in the Chukchi Sea, between 24 and 63 m in the Canadian Basin, and between 11 and 18 m in the Eurasian Basin (Fig. 3c). The incident irradiance during the sampling period was higher in the western part of the transect than in the eastern part (Fig. 3d), with the sky being almost completely cloud-covered east of 80° N. Between 3 and 27% of the incident irradiance passed through the snow-ice cover (Fig. 3e). The ratio between the depth of the euphotic layer (0.1% isolume) and the depth of the surface mixed layer was also variable along the transect, but at most stations this ratio was higher than 1 (Fig. 3f), indicating that the euphotic zone was generally deeper than the surface mixed layer. The ratio was very high (up to eight) in the Chukchi Sea and the Nansen Basin where ice cover was lower than 85%, and near one in the Canadian Basin where ice coverage was greater than 90%. Hence, despite the ice cover, light reached the bottom of the surface mixed layer at most stations along the transect. These physical conditions favor algal production in the upper layer of the Arctic Ocean (see below).

The latitudinal changes in the average integrated concentrations of phosphate, silicic acid, nitrate + nitrite, ammonium and nutrient ratios in the euphotic layer are presented in Fig. 4. Phosphate and silicic acid concentrations decreased along the transect from about 1.7 to 0.5 μM and from about 50 to 2 μM , respectively (Fig. 4a and b). However, nitrate + nitrite and ammonium show a different horizontal pattern (Fig. 4c and d), decreasing from 14 to 1 μM from 72°N to 80°N and then gradually increasing up to 7 μM in the Nansen Basin. Ammonium, representing between 5 and 15% of the total dissolved inorganic nitrogen (i.e. nitrate + nitrite + ammonium), showed a horizontal pattern similar to nitrate + nitrite (Fig. 4d). The total dissolved inorganic nitrogen to phosphate ratio was always lower than the ratio of 15:1 of Redfield *et al.* (1963) (Fig. 4e). Furthermore, the dissolved inorganic nitrogen to silicic acid ratio was also lower than the value of 1.1 of Redfield *et al.* (1963) at all stations except in the Nansen Basin where it reached a maximum

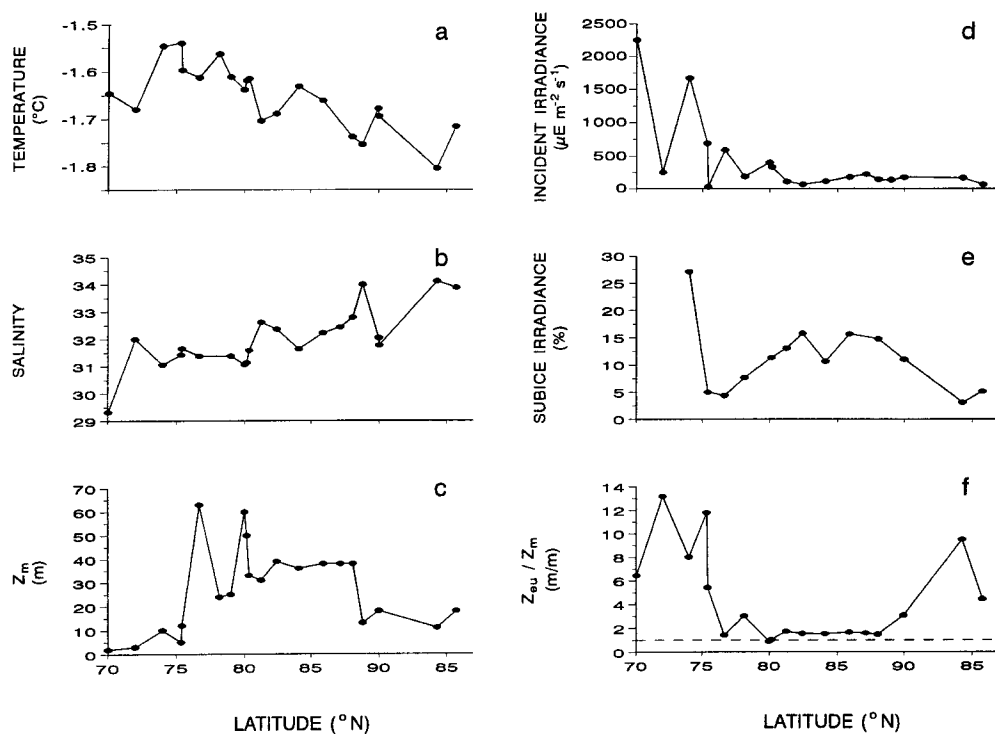


Fig. 3. Latitudinal changes in mean integrated water temperature (a) and mean integrated salinity (b) in the euphotic layer, surface mixed layer depth (Z_m) (c), incident irradiance (d), sub-ice irradiance as a percentage of incident irradiance (e) and the ratio between the depth of the euphotic layer and the depth of the surface mixed layer ($Z_{eu}:Z_m$) (f) in the Arctic Ocean in July–August 1994. Water temperature and salinity are integrated over the euphotic zone from surface to 0.1% light level and divided by the depth of the euphotic layer to obtain the mean integrated values.

value of 3 (Fig. 4f). This suggests possible deficiency in dissolved inorganic nitrogen relative to dissolved phosphate and silicon in the Chukchi Sea and the Canadian Basin, while silicon is in low concentration relative to phosphorus and nitrogen in the Nansen Basin.

Phytoplankton and ice algal production

The latitudinal changes in the daily rate of primary production (particulate and dissolved) and the concentration of chlorophyll *a*, an index of algal biomass, in the water column and in the bottom layer of sea-ice are presented in Fig. 5. In the water column, the values were integrated over the euphotic zone, while the value for sea ice includes the algae growing in the bottom 2–4 cm of the ice and at the ice–water interface. The total phytoplankton biomass ranged from 1.2 to 445 mg Chl *a* m⁻², whereas the ice algal biomass ranged from 0.1 to 14 mg Chl *a* m⁻² (Fig. 5b and d). In the sea ice, the centric diatom *Melosira arctica*, which grows suspended at the ice–water interface, was the dominant species at the two most productive stations (75° 25' N and 88° N). At the other stations, the high production rates were observed in the bottom 2–4 cm of the ice. The distribution of *Melosira arctica* was very patchy, even at the same sampling location. In a sample collected at 88° N, the biomass of *Melosira arctica* reached a maximum value of 200 mg Chl *a* m⁻².

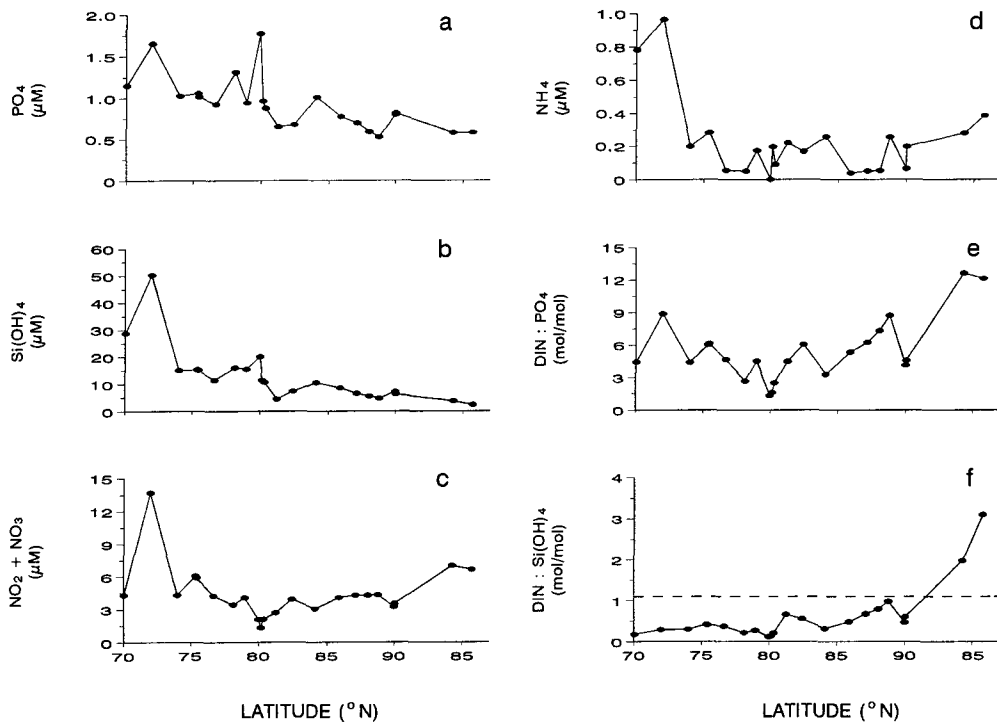


Fig. 4. Latitudinal changes in mean integrated concentrations of phosphate (a), silicic acid (b), nitrate + nitrite (c), ammonium (d), and ratio of the mean integrated concentration of dissolved inorganic nitrogen ($\text{DIN} = \text{NO}_3 + \text{NO}_2 + \text{NH}_4$) to the mean integrated concentration of phosphate (e), and ratio of the mean integrated concentration of DIN to the mean integrated concentration of silicic acid in the euphotic layer in the Arctic Ocean in July–August 1994. Nutrient concentrations are integrated over the euphotic zone from surface to 0.1% light level and divided by the depth of the euphotic layer to obtain the mean integrated values. In f, horizontal dashed line: critical values of 1.1 of Redfield *et al.* (1963).

The horizontal distributions of phytoplankton and ice algal particulate production rates were similar to their respective biomass concentrations (Fig. 5a and c). Particulate phytoplankton production was maximum in the Chukchi Sea ($2570 \text{ mg C m}^{-2} \text{ day}^{-1}$; Fig. 5a). In the Canadian and Eurasian basins, phytoplankton production was much lower, ranging from 9 to $73 \text{ mg C m}^{-2} \text{ day}^{-1}$, except at the end of the transect where the rate increased to $521 \text{ mg C m}^{-2} \text{ day}^{-1}$. In the water column, the release rates of dissolved organic carbon ranged from undetectable to $356 \text{ mg C m}^{-2} \text{ day}^{-1}$ and were generally lower than the particulate production rates (Fig. 5a). The horizontal variation in ice algal production was very different from that of the phytoplankton (Fig. 5c). Ice algal production was high at $75^\circ 25' \text{ N}$ and in the central Arctic between 83° N and 90° N . Elsewhere, the values were low. The ice algal particulate and dissolved production varied from 0.5 to $310 \text{ mg C m}^{-2} \text{ day}^{-1}$ and from undetectable to $45 \text{ mg C m}^{-2} \text{ day}^{-1}$, respectively. Production and biomass of ice algae were greatest in the central Arctic Ocean.

In the Chukchi Sea and in leads of the Makarov and Nansen basins, maximum total particulate phytoplankton production rates were 2570, 73 and $521 \text{ mg C m}^{-2} \text{ day}^{-1}$, respectively (Fig. 5a). At these stations, large phytoplankton ($> 5 \mu\text{m}$) represented 61–98%

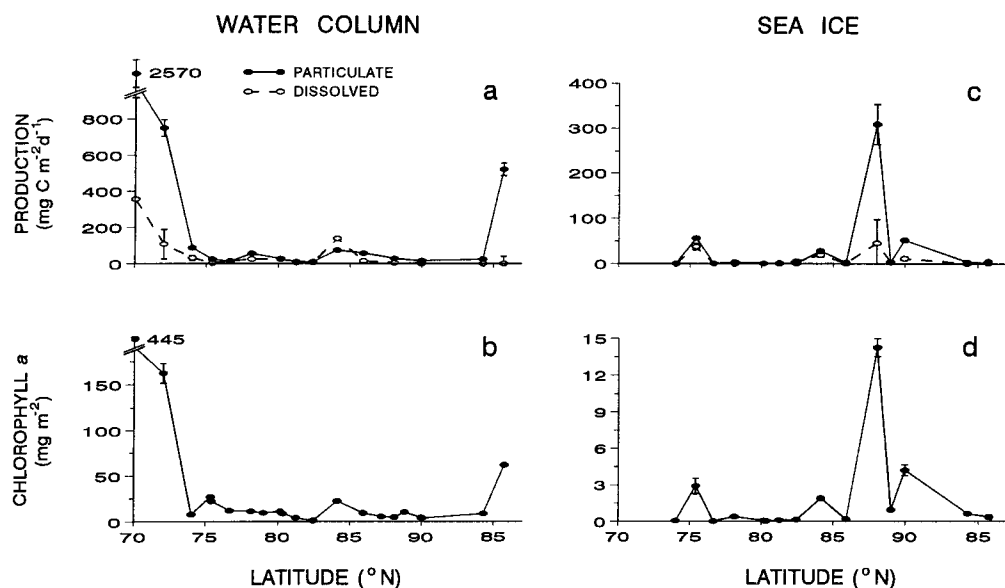


Fig. 5. Latitudinal changes in areal rates of dissolved (P_E) and total particulate (P_T) primary production (a, c) and concentration of total chlorophyll a (B_T) (b, d) in the water column and in sea ice in the Arctic Ocean in July–August 1994 (mean \pm standard deviation).

of the total algal biomass (Fig. 6b). At the other stations, the total particulate phytoplankton production decreased to 9–57 $\text{mg C m}^{-2} \text{ day}^{-1}$ (Fig. 5a), and large phytoplankton ($> 5 \mu\text{m}$) accounted for only 11–41% of the total biomass and generally less than 20% of the total particulate production (Fig. 6a and b). Large cells ($> 5 \mu\text{m}$) generally dominated the ice algal community, representing 50–100% of the total biomass and more than 50% of the total particulate production, except at a few stations at the beginning of the transect (Fig. 6c and d).

The percentage of total phytoplankton production released as extracellular carbon (Fig. 7a) was less than 20% at either end of the transect, but ranged from 31–65% in the Canada and Makarov basins (76° – 84°N). Ice algae released on average 34% of the total carbon fixed (Fig. 7c). The production:biomass ($P_T:B_T$) ratios of phytoplankton and ice algae did not show any definite pattern (Fig. 7b and d). In the water column, the $P_T:B_T$ ratio ranged from 1 to 10 $\text{mg C mg Chl } a^{-1} \text{ day}^{-1}$ while the ratios were generally higher in the sea ice, with values ranging from 4 to 23 $\text{mg C mg Chl } a^{-1} \text{ day}^{-1}$. For phytoplankton and ice algae, the mean values were 4.6 and 11.7 $\text{mg C mg Chl } a^{-1} \text{ day}^{-1}$, respectively.

Correlation analysis was used to test the relationships between phytoplankton production and biomass and the variables of ice cover, surface mixed layer depth, DIN concentration and total mesozooplankton biomass (Table 1). Changes in total mesozooplankton biomass along the transect are presented in Wheeler *et al.* (1996) and Thibault *et al.* (1997). Most of the phytoplankton areal production rates and all areal biomass concentrations were inversely correlated with percent ice cover, surface mixed layer depth or total mesozooplankton (Table 1). P_S , P_T and P_L were directly correlated with DIN concentration. P_E was positively correlated with incident irradiance ($r_s = 0.631$, $p < 0.05$). In contrast to algal production and biomass, none of the ratios were significantly correlated

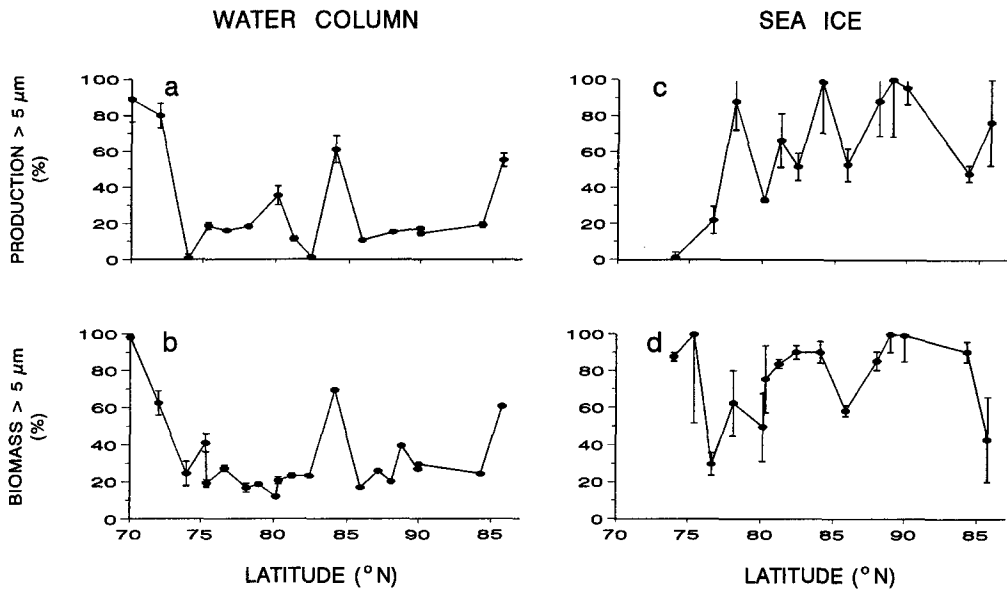


Fig. 6. Latitudinal changes in the relative contribution of microalgal cells larger than $5\text{ }\mu\text{m}$ to total particulate primary production ($P_L:P_T$) (a, c) and to total chlorophyll a ($B_L:B_T$) (b, d) in the water column and in sea-ice in the Arctic Ocean in July–August 1994 (mean \pm standard deviation). Standard deviations are computed according to Kendall and Stuart (1977).

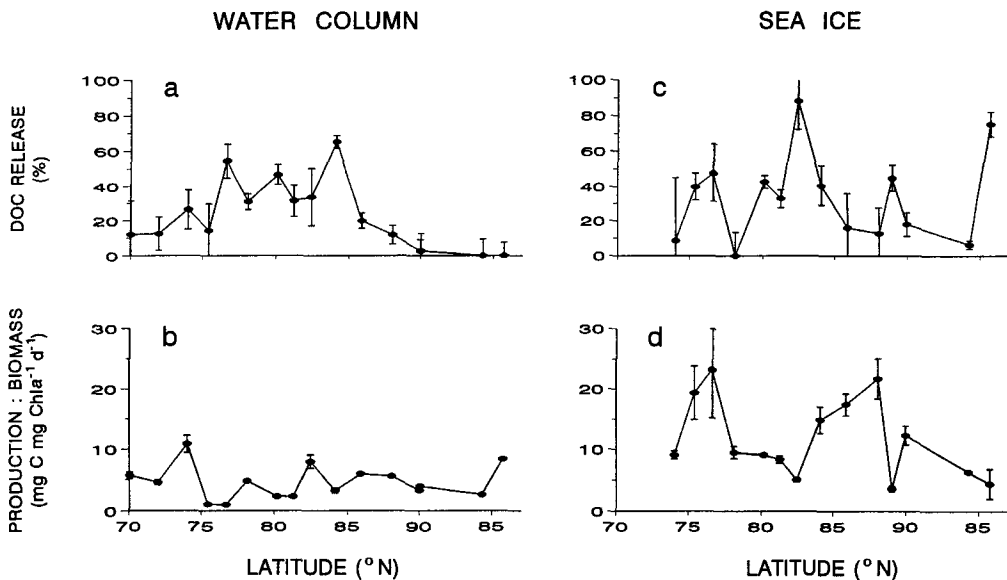


Fig. 7. Latitudinal changes in percentage of total primary production (dissolved + particulate) released as dissolved organic carbon (DOC) (a, c) and ratio of total particulate production to total algal biomass ($P_T:B_T$) (b, d) in the water column and in sea-ice in the Arctic Ocean in July–August 1994 (mean \pm standard deviation). Standard deviations are computed according to Kendall and Stuart (1977).

Table 1. Spearman's rank correlation coefficients between the percentage of ice cover, surface mixed layer depth (Z_m), dissolved inorganic nitrogen concentration (DIN), total carbon biomass of mesozooplankton and areal production (P), areal chlorophyll *a* biomass (B) and biological ratios in the euphotic layer of the water column in the Arctic Ocean in July–August 1994. Pairwise deletion of missing data

	Ice cover	Z_m	DIN	Mesozooplankton
Surface mixed layer depth (Z_m)	0.496*			
Dissolved inorganic nitrogen (DIN)	−0.338	−0.669 [†]		
Mesozooplankton biomass	0.414	0.533*	−0.472	
Total production ($P_T + P_E$)	−0.716 [†]	−0.413	0.424	−0.552*
Total particulate production (P_T)	−0.778 [†]	−0.523*	0.471	−0.538*
Particulate production of large algae (P_L)	−0.527*	−0.341	0.297	−0.393
Particulate production of small algae (P_S)	−0.800 [‡]	−0.559*	0.571*	−0.560*
Dissolved production (P_E)	−0.324	−0.066	−0.087	−0.308
Total biomass (B_T)	−0.348	−0.397	0.483*	−0.585*
Biomass of large algae (B_L)	−0.527*	−0.603 [†]	0.627 [†]	−0.606*
Biomass of small algae (B_S)	−0.127	−0.238	0.399	−0.618*
% DOC release	0.380	0.595*	−0.519*	0.150
$P_T:B_T$	−0.654 [†]	−0.236	0.274	−0.116
$P_L:P_T$	−0.418	−0.365	0.294	−0.429
$B_L:B_T$	−0.522*	−0.478*	0.451*	−0.121

* $0.01 < p \leq 0.05$, [†] $0.001 < p \leq 0.01$, [‡] $p \leq 0.001$.

with total mesozooplankton. The percentage of the total production released as DOC was directly correlated with the depth of the surface mixed layer and inversely correlated with DIN concentration and DIN:PO₄ ratio ($r_s = -0.538$, $p < 0.05$), while the $P_T:B_T$ ratio was inversely correlated with percent ice cover and directly correlated with the percent incident irradiance at the ice–water interface ($r_s = 0.576$, $p < 0.05$). The $B_L:B_T$ ratio was correlated with percent ice cover, surface mixed layer depth and DIN concentration, while the $P_L:P_T$ ratio did not show any significant correlation. Total mesozooplankton biomass and DIN concentration were correlated with surface mixed layer depth, while surface mixed layer depth was directly correlated with percent ice cover (Table 1).

In contrast to phytoplankton, ice algal production and biomass were not correlated ($p > 0.05$) with percent ice cover, Z_m , DIN concentration or total mesozooplankton biomass. For ice algae, $P_T + P_E$, P_T , P_L , P_E , B_T and B_L were inversely correlated ($p < 0.05$) with surface water temperature. $P_T + P_E$ and P_E were negatively correlated ($p < 0.05$) with incident irradiance. $P_T + P_E$, B_T and B_L were also positively correlated ($p < 0.05$) with surface nitrate + nitrite concentration. Along the transect, surface temperature and nitrate + nitrite concentration ranged from -1.73 to -1.27 °C and from <0.05 to 5.8 µM, respectively. These variables were inversely correlated ($r_s = -0.848$, $p < 0.001$). The two highest values in algal production and biomass at the ice–water interface were observed at stations (75°25' N and 88° N) covered with first-year ice and a thick snow cover (≥ 0.2 m; Fig. 2d). The ice algal ratios were not significantly correlated ($p > 0.05$) with physical and chemical variables or with mesozooplankton biomass.

Taxonomic composition

The algal carbon biomass and the relative contribution of various algal groups to total algal carbon biomass were determined in the upper layer of the water column, at the ice–

Table 2. Average carbon biomass of the various algal groups at the depth of the maximum chlorophyll *a* concentration in the upper layer of the water column, at the ice–water interface and in the ice bottom in July–August in the Arctic Ocean. The percent carbon algal biomass is in parenthesis. The total algal carbon biomass is also presented. Stations were grouped according to the results of chronological clustering (under the constraint of spatial contiguity)

Latitude	Centric diatoms	Pennate diatoms	Flagellates (< 10 µm)	Flagellates (> 10 µm)	Heterotrophic dinoflagellates	Autotrophic dinoflagellates	Silicoflagellates	Total C biomass
Phytoplankton (mg C m ⁻³)								
70–72° N	590 (90.8)	15.5 (2.4)	8.5 (1.3)	7.8 (1.2)	27.1 (4.2)	0.57 (0.0)	0.00 (0.0)	650
74–86° N	4.1 (33.9)	0.75 (6.1)	0.61 (5.0)	0.38 (3.1)	4.7 (38.4)	0.61 (5.0)	1.03 (8.4)	12.2
87° N	0.0 (1.7)	0.06 (2.9)	0.29 (15.1)	0.58 (30.2)	0.9 (47.2)	0.06 (2.9)	0.00 (0.0)	1.9
88–90–85° N	0.7 (13.4)	0.45 (8.1)	0.52 (9.4)	0.20 (3.6)	2.8 (51.1)	0.24 (4.3)	0.55 (10.1)	5.5
84° N	48.7 (93.8)	0.50 (1.0)	0.23 (0.5)	0.00 (0.0)	2.3 (4.4)	0.13 (0.2)	0.07 (0.1)	52.0
Sub-ice algae (mg C m ⁻²)								
74–82° N	2.9 (48.6)	1.48 (24.9)	0.044 (0.7)	0.014 (0.2)	0.57 (9.6)	0.14 (2.4)	0.80 (13.5)	5.9
84–90–84° N	77.7 (98.0)	1.17 (1.5)	0.027 (0.0)	0.029 (0.0)	0.29 (0.4)	0.03 (0.0)	0.04 (0.0)	79.3
Ice-bottom algae (mg C m ⁻²)								
74–78° N	0.288 (3.2)	8.4 (92.6)	0.034 (0.4)	0.14 (1.5)	0.19 (2.1)	0.024 (0.3)	0.000 (0.0)	9.1
80–90–85° N	0.385 (1.4)	24.3 (89.2)	0.080 (0.3)	1.05 (3.8)	1.10 (4.0)	0.349 (1.3)	0.000 (0.0)	27.3
84° N	0.609 (21.1)	1.3 (46.0)	0.096 (3.3)	0.44 (15.3)	0.36 (12.4)	0.053 (1.8)	0.000 (0.0)	2.9

water interface and in the bottom surface of the ice (Table 2). Chronological clusterings performed on the carbon biomass of the various algal groups estimated at different stations along the transect (see Methods) allowed the distinction of five homogenous regions at the depth of maximum Chl *a* in the upper layer of the water column, 2 regions at the ice–water interface and 3 regions at the ice bottom (Table 2). In surface water, no homogeneous group of stations was distinguished.

At the depth of maximum Chl *a* concentration in the euphotic layer, there were five groups of stations (Table 2). On the continental shelf of the Chukchi Sea (70°–72° N), the algal biomass was maximum (647 mg C m⁻³) and the algal community was largely dominated by centric diatoms (mostly *Thalassiosira gravida/rotula*). The second group of stations (74°–86° N), located between the slope of the Chukchi Sea and the Makarov Basin, was mainly composed of heterotrophic dinoflagellates (mostly unidentified spp. and *Gymnodinium* spp.) and centric diatoms (mostly *Porosira glacialis*). The third group (87° N) is located at the deepest station of the Canadian Basin (4020 m) and showed the lowest algal C biomass along the transect. The algal community was mainly composed of unidentified heterotrophic dinoflagellates and unidentified flagellates. The fourth group (88° N, 147° E–85° N, 37° E), located between the eastern part of Makarov Basin and the Eurasian Basin, was dominated by unidentified heterotrophic dinoflagellates. As on the continental shelf of the Chukchi Sea (70°–72° N), the last station of the Nansen Basin (84° N, 34° E) was largely dominated by *Thalassiosira gravida/rotula*.

At the ice–water interface, there were two groups of stations along the transect (Table 2). The front between the two groups was over the Mendeleyev Ridge (around 83° N) in the Canadian Basin. The phytoplankton community of the western group of stations had low biomass (5.9 mg C m⁻²) and was mainly composed of centric diatoms (mainly *Melosira arctica*), pennate diatoms (mostly *Nitzschia* spp. and *Pseudogomphonema groenlandica*) and silicoflagellates (*Dictyocha speculum*), while the eastern group had higher biomass (79.3 mg C m⁻²), and was largely dominated by centric diatoms (mostly *Melosira arctica*, *Thalassiosira anguste-lineata* and *Chaetoceros* spp.).

In the ice bottom, stations located on the continental shelf of the Chukchi Sea and in the

western part of the Canadian Basin (74°–78° N; depth < 1000 m) were similar in terms of ice algal composition. At these stations, pennate diatoms (mostly *Nitzschia neofrigida*, unidentified pennates 20–50 µm long and *Nitzschia frigida*) represented 93% of the total algal C biomass. The second group of homogenous stations (80° N, 178° W–85° N, 37° E) was located between the eastern part of the Canadian Basin and the western part of the Eurasian Basin. This region was dominated by pennate diatoms (mostly *Nitzschia* spp., unidentified pennates 20–50 µm long and *Navicula kariana*), but flagellates > 10 µm and dinoflagellates represented ca. 10% of the total algal C biomass, twice the value observed in the first group. This group of stations in the middle of the transect had the highest algal C concentration. The last station in the Nansen Basin formed the third bottom ice algal group, and was composed of a mixed population of pennate diatoms (mostly *Nitzschia frigida*), centric diatoms (*Atthya septentrionalis*, formerly *Chaetoceros septentrionalis*), flagellates and heterotrophic dinoflagellates. This region had the lowest algal C concentration in bottom ice.

The percentage of centric diatoms at the depth of the maximum Chl *a* concentration in the euphotic layer decreased gradually from the Chukchi Sea to 87°N and then increased up to the Nansen Basin (Table 2). In the central Arctic, dinoflagellates and flagellates dominated in the under-ice water column, centric diatoms dominated at the ice–water interface, and pennate diatoms dominated in the bottom of the ice. In the three habitats, regions of maximum algal C biomass were always associated with a dominance of diatoms.

DISCUSSION

Structure of the algal assemblages

The bottom surface of the ice, the ice–water interface and the water column formed distinct habitats, which were colonized by different taxonomic assemblages. Pennate diatoms dominated in the bottom ice, centric diatoms at the ice–water interface and flagellates in the ice-covered water column (Table 2). The size structure of the algal assemblages in the bottom layer of the ice and in the water column was also different: the biomass and production in the sea ice were generally dominated by large algal cells (> 5 µm) while the under-ice water column was dominated by small algal cells (0.7–5 µm). The assimilation number ($P_T:B_T$) of the ice algae was higher than those of the under-ice phytoplankton. This may reflect differences in the taxonomic composition and/or in the physiological state of the algal communities. These characteristics of the algae living in the different habitats of the permanent pack ice of the Arctic Ocean were comparable to those measured in other ice-covered environments at lower latitude. For example, in southeastern Hudson Bay during April–May, Robineau *et al.* (1994) reported that large algae contributed 54–64%, 77–91% and 17–66% of the total pigment biomass in the bottom ice, at the ice–water interface and in the under-ice water column, respectively. In heavily ice-covered areas (50–100%) of the Northeast Water Polynya (77°–81° N), large phytoplankton cells contributed 17–66% (mean = 33) and 6–37% (mean = 23) of the total biomass and total particulate production from mid-May to the end of July (Pesant *et al.*, 1996).

Areas of the Arctic Ocean with ca. 20–45% ice-free water as in the Chukchi Sea, in the Makarov Basin at 83° N and in the Nansen Basin were characterized by high productivity and by biomass and production dominated by large phytoplankton (Table 3). Similarly, the

Table 3. Mean (standard error) for physical, chemical and biological variables in the upper water column in two production regimes ($P_L:P_T$ and $B_L:B_T < 50\%$ and $P_L:P_T$ and $B_L:B_T > 50\%$) in the Arctic Ocean. The biomass of diatoms was determined at the depth of the chlorophyll a maximum. Significant differences ($p < 0.05$) among regimes were tested by Kruskal–Wallis one-way analyses of variance

Variable	$P_L:P_T$ and/or $B_L:B_T$			
	< 50%		> 50%	
Ice cover (%)	95.3	(1.8)	73.8	(3.8)
Mean ammonium (μM)	0.16	(0.04)	0.60	(0.08)
Total production ($P_T + P_E$: $\text{mg C m}^{-2} \text{ day}^{-1}$)	40.8	(164)	1128	(284)
Total particulate production (P_T : $\text{mg C m}^{-2} \text{ day}^{-1}$)	30.3	(147)	978	(254)
Particulate production of large algae (P_L : $\text{mg C m}^{-2} \text{ day}^{-1}$)	4.0	(135)	804	(234)
Particulate production of small algae (P_S : $\text{mg C m}^{-2} \text{ day}^{-1}$)	26.3	(16)	175	(28)
Total biomass (B_T : $\text{mg Chl } a \text{ m}^{-2}$)	9.7	(18.4)	173	(38.0)
Biomass of large algae (B_L : $\text{mg Chl } a \text{ m}^{-2}$)	2.4	(18.9)	148	(39.0)
Centric diatoms (mg C m^{-3})	2.3	(43.6)	310	(87.2)
Pennate diatoms (mg C m^{-3})	0.7	(1.1)	7.9	(2.2)

highest productivity of the Northeast Water Polynya was measured in areas with an average ice cover of 50% and characterized by large phytoplankton contributing 61–100% and 80–100% of the total biomass and production (Pesant *et al.*, 1996).

Phytoplankton and ice algal production

This is the first paper to describe the horizontal variability of phytoplankton and ice algal production across the Arctic Ocean. The areal concentrations of Chl *a* in the euphotic layer of the water column (from 22 to 85 m) were maximum in the Chukchi Sea ($162\text{--}445 \text{ mg m}^{-2}$), decreased to low values ($1\text{--}27 \text{ mg m}^{-2}$) in Canada and Makarov Basins, then increased (62 mg m^{-2}) at the last station of the transect in the Nansen Basin. The algal biomass in the ice-covered Chukchi Sea was similar to values of $50\text{--}500 \text{ mg Chl } a \text{ m}^{-2}$ measured in the southern Chukchi Sea in August (Walsh *et al.*, 1989). The maximum concentration in the Nansen Basin was similar to the values of $52\text{--}83 \text{ mg Chl } a \text{ m}^{-2}$ found in the marginal ice zone of Fram Strait in June–July (Smith *et al.*, 1987). Elsewhere in the Canadian and Eurasian Basins, the areal Chl *a* varied from 1 to 26 mg m^{-2} and averaged 10 mg m^{-2} . At the International Geophysical Year (IGY) Drifting Station Bravo on Fletcher's Ice Island (T-3), Chl *a* concentration in the euphotic layer varied between 10 and 21 mg m^{-2} in July–August 1957 (Apollonio, 1959), while at the Drift Station Alpha, it varied from 16 to 36 mg m^{-2} in July–August 1958 (English, 1961). These values are comparable to those observed in open ocean waters of the Pacific Ocean ($10\text{--}50 \text{ mg Chl } a \text{ m}^{-2}$; Chavez *et al.*, 1995). The ice algal biomass was also variable, with values ranging from 0.1 to $14 \text{ mg Chl } a \text{ m}^{-2}$. From SCUBA observations, Melnikov (1997) estimated the biomass of ice-bottom algae as $22 \text{ mg Chl } a \text{ m}^{-2}$ at station North Pole-23 in summer of 1977. These concentrations are at the lower end of maximum values reported in arctic coastal waters during the vernal ice–algal bloom ($10\text{--}300 \text{ mg Chl } a \text{ m}^{-2}$; Cota *et al.*, 1991).

Along the transect, rates of algal production in the water column followed the general patterns of pigment concentration. Daily particulate production rates ranged from a high of 2570 mg C m^{-2} in the Chukchi Sea to a low of 9 mg C m^{-2} in the central Arctic Ocean.

Table 4. Average (\pm standard error) areal rates of particulate production, dissolved organic carbon (DOC) release and total (particulate + dissolved) production in the bottom layer of the sea-ice and in the euphotic layer of the water column in four regions of the Arctic Ocean in July–August 1994. The relative contribution of each habitat to the total daily primary production (phytoplankton and ice algae) is also indicated

Latitude	Longitude	Habitat	Particulate production (mg C m ⁻² day ⁻¹)	DOC release (mg C m ⁻² day ⁻¹)	Total production (mg C m ⁻² day ⁻¹)	Relative contribution (%)
70–75° N	169–170° W	Ice	28 \pm 28	19 \pm 18	47 \pm 46	5
		Water column	858 \pm 594	125 \pm 80	983 \pm 674	95
76–80° N	173–178° W	Ice	2 \pm 1	0.3 \pm 0.1	2 \pm 1	2
		Water column	31 \pm 13	21 \pm 3	52 \pm 15	98
81–90° N	31–179° E	Ice	57 \pm 43	12 \pm 6	69 \pm 49	57
		Water column	30 \pm 10	24 \pm 19	53 \pm 27	43
84–86° N	35–38° E	Ice	3 \pm 1	3 \pm 2	5 \pm 1	2
		Water column	272 \pm 249	not detectable	272 \pm 249	98

Particulate ice algal productivity ranged from 0.5 to 310 mg C m⁻² day⁻¹. In the water column, Chl *a* and production decreased in the poleward direction across the Makarov Basin, whereas they increased in the sea ice (Table 4). In the central Arctic Ocean, algal particulate production in the ice was about twice as high as in the water column (Table 4). Our mean daily particulate phytoplankton production of 1140 mg C m⁻² on the ice-covered continental shelf (<200 m) of the Chukchi Sea was lower than the mean value of 2400 mg C m⁻² day⁻¹ published for the open waters of the southern Chukchi Sea during July–October (Walsh *et al.*, 1989), but higher than the values of 102 to 486 mg C m⁻² day⁻¹ (mean = 336 mg C m⁻² day⁻¹) measured during 22–26 h incubation in partly open waters (20–40%) of the southeastern Chukchi Sea in August 1993 (Cota *et al.*, 1996). In the Canadian Basin, our values ranged from 9 to 73 mg C m⁻² day⁻¹, with a mean of 35 mg C m⁻² day⁻¹. In the Canadian Basin south of 75° N, Cota *et al.* (1996) reported primary productivity ranging from 47 to 120 mg C m⁻² day⁻¹ (mean = 74 mg C m⁻² day⁻¹). However, the production rates of Cota *et al.* (1996) were not transformed in order to take into account of changes in the percentage of ice cover. If we multiply their mean areal production rates from the Canadian Basin by 50%, the maximum area with open waters, we obtain the same estimate for this region of the Arctic Ocean. In the continental shelf and slope of the Chukchi Sea, annual variations in the surface ice cover may influence the distribution and the production of the phytoplankton.

In the Nansen Basin, our mean production rate (272 mg C m⁻² day⁻¹) was within the range of values published for the marginal ice zone of Fram Strait (426 mg C m⁻² day⁻¹ of Smith *et al.*, 1987; 7–720 mg C m⁻² day⁻¹ of Hirche *et al.*, 1991) and the Northeast Water Polynya (210 mg C m⁻² day⁻¹ for the entire region and 170 mg C m⁻² day⁻¹ in the region with ice coverage > 80%, Smith, 1995; 212 mg C m⁻² day⁻¹ in the area with mean ice cover of 71% and 544 mg C m⁻² day⁻¹ in the area with 50% ice cover, Pesant *et al.*, 1996). In the central Arctic Ocean (81°–90° N), our mean value of 30 mg C m⁻² day⁻¹ was higher than the mean summer value of 17 mg C m⁻² day⁻¹ measured at the IGY Drifting Station Bravo in 1957 (Apollonio, 1959) and of 12 mg C m⁻² day⁻¹ measured at the Drift Station Alpha (84°31.5′–85°26.5′ N; 128°16′–143°28′ W) in July–August 1958 (English, 1961). Pomeroy (1997) has argued that all ¹⁴C-production rates from the 1950s are now more or less suspect and should be viewed as probable underestimates.

The ice algal total particulate production averaged $33 \text{ mg C m}^{-2} \text{ day}^{-1}$ for the entire transect and $57 \text{ mg C m}^{-2} \text{ day}^{-1}$ for the central Arctic Ocean ($81\text{--}90^\circ \text{ N}$). This rate is within the range of values reported for Arctic first-year ice (mean of $83 \text{ mg C m}^{-2} \text{ day}^{-1}$ in Subba Rao and Platt, 1984 and Legendre *et al.*, 1992) and Antarctic multiyear pack-ice during the autumn bloom ($22\text{--}162 \text{ mg C m}^{-2} \text{ day}^{-1}$ in Fritsen *et al.*, 1994). Within multi-year ice (2.95 m thick), Melnikov (1997) estimated the primary production at station North Pole-23 in a region of the Transpolar Drift Stream ($77\text{--}88^\circ \text{ N}$; $144\text{--}165^\circ \text{ E}$). From the increase in the concentration of particulate organic carbon inside sea ice between June and July 1977, he estimated the ice algal production for the bottom layer of the ice and the entire ice column as 20 and $48 \text{ mg C m}^{-2} \text{ day}^{-1}$, respectively. This value is also very close to our mean particulate production rates for ice algae.

As algal biomass and particulate production, the release rates of DO^{14}C by phytoplankton and ice algae were variable along the transect (Fig. 5a and c). Phytoplankton release of DOC varied from 0 to $356 \text{ mg C m}^{-2} \text{ day}^{-1}$ while ice algal release rates varied from 0 to $45 \text{ mg C m}^{-2} \text{ day}^{-1}$. In the central Arctic Ocean, the total (phytoplankton + ice algae) DOC release rate averaged $36 \text{ mg C m}^{-2} \text{ day}^{-1}$ (Table 4). Assuming that the algal growing season is 120 days, our estimate of total annual primary production (i.e. dissolved plus particulate production by phytoplankton and ice algae) in the central Arctic Ocean is about 15 g C m^{-2} , at least one order of magnitude greater than the estimates of Apollonio (1959) and English (1961). This difference is due in part to the previously unmeasured contribution of the particulate production by ice algae and the release of DOC by both ice and pelagic algae. From the dissolved oxygen data of English (1961) and Mel'nikov and Pavlov (1978), Pomeroy (1997) estimated the annual primary production to be at least 13 and 15 g C m^{-2} at Drift Station Alpha ($85\text{--}86^\circ \text{ N}$, $110\text{--}145^\circ \text{ W}$) and at station North Pole-22 (83° N , $161\text{--}164^\circ \text{ W}$), respectively. Our direct measurements of algal production agree well with calculated production estimates of Pomeroy (1997). During July–August, ice algae contributed up to 57% of the entire primary production (water column + sea ice) in the central Arctic Ocean and 2–5% in the surrounding regions (Table 4). Legendre *et al.* (1992) estimated the contribution of ice algae at 3–25% of the total annual primary production for the arctic waters north of 65° N .

Algal extracellular release of DOC

The percentages of the phytoplankton production released as extracellular carbon were relatively low (6–27%) in the Chukchi Sea, increased significantly (31–65%) in the Canada and Makarov basins, then decreased progressively (from 20 to 0%) toward the Nansen Basin (Fig. 7a). The ice algal release of DOC varied from 0 to 88%, with an average value of 34% (Fig. 7c). Excretion by healthy pelagic microalgae is generally less than 30% of the primary production (Norrman *et al.*, 1995). Only a few studies have measured DOC release by polar algae. In the ice-covered water of the Franz–Joseph Land archipelago ($80\text{--}82^\circ \text{ N}$, $45\text{--}65^\circ \text{ E}$), the photosynthetic extracellular release by phytoplankton in July was always below 3% of the total primary production (particulate + extracellular release) (Müller-Niklas and Herndl, 1996). In this region, the ice cover decreased from 100% at the beginning of July to 50% at the end of the month. At the ice-edge of the Barents Sea, an average of 70% of the total phytoplankton production was released as DOC during the spring bloom (Vernet *et al.*, 1994). During the vernal growth season, measurements of photosynthesis and extracellular release of carbon by ice-bottom algae indicated low rates of DOC production

in annual sea ice, generally 17% or less of the total primary production (7–17%, East Antarctica, McConville and Wetherbee, 1983; <1–10%, McMurdo Sound, Antarctica, Kottmeier *et al.*, 1987; <10%, Resolute Passage, Canadian Archipelago, Smith *et al.*, 1988). High DOC release by ice algae however was reported in Resolute Passage by Smith and Herman (1991), being on average 25 and 55% of the total production during incubator and *in situ* experiments, respectively.

In the present study, the greatest phytoplankton extracellular releases of DOC were observed in the Canadian Basin. This region is characterized by the deepest surface mixed layer, the lowest DIN concentration, and the lowest DIN:PO₄³⁻ ratio (Figs 3c and 4c–e). Correlations between these factors and the percentage of phytoplankton DOC release (Table 1) suggest that deep vertical mixing, which decreased the amount of light received by the phytoplankton and low nitrogen availability, favored the photosynthetic release of DOC.

Laboratory experiments with three phytoplankton species (2 flagellates and 1 cyanobacterium) have shown high percentage (40–55%) of DOC excretion under low light conditions (Zlotnik and Dubinsky, 1989). Recently, Obernosterer and Herndl (1995) showed that batch cultures of the centric diatom *Chaetoceros affinis* released 30% more DOC at a low N:P molar ratio of 5 than when grown under balanced nutrient conditions (N:P = 16). At the low N:P ratio, the mean photosynthetic extracellular release as % of the total primary production was 21% (SE = 9) during the exponential growth phase and 30% (SE = 8) during the stationary phase. In the western part of the Canadian Basin (76°–84° N), the fact that the mean N:P ratio in the euphotic layer varied between 1.3 and 4.7 (Fig. 4e) suggests that nitrogen stress may be involved in the enhanced DOC release. Heterotrophic dinoflagellates and ciliated protozoans were abundant in the upper layer of the water column (Sherr *et al.*, 1997). In addition, all components of the phagotrophic protist community appeared to be active consumers of phytoplankton. Indeed, small-sized flagellates (<5 µm) were frequently observed with picoplanktonic-sized algal cells in their food vacuoles. Heterotrophic dinoflagellates and ciliates were routinely observed to contain a variety of ingested phytoplankton (Sherr *et al.*, 1997). These protists could have grazed on pigmented phytoplankton cells and produced DOC during the incubation (Lampert, 1978). Thus, it is possible that the high % of DOC release by phytoplankton in the Canadian Basin is related to a combination of factors, including light limitation, nitrogen stress and/or grazing by heterotrophic protists.

Many of the dominant ice algae in the Arctic and Antarctic produce extensive extracellular polysaccharide mucilages in addition to low molecular weight metabolites (review by McConville, 1985). These mucilages form a type of matrix material between cells in the ice-bottom communities and are responsible for the tendency of these cells to aggregate into clumps. Two of the main species present in sea ice during this study, the pennate diatom *Nitzschia frigida* and the centric diatom *Melosira arctica*, are known to secrete mucilages (Apollonio, 1985; McConville, 1985). The high extracellular release of the ice algae may explain in part the extremely high concentration of DOC (up to 40 mg C l⁻¹) found in the bottom ice in Frobisher Bay (Bunch and Harland, 1990) and Resolute Passage (Smith *et al.*, 1997a) in the High Canadian Arctic. It was hypothesized that nutrient deficiency was the main factor explaining enhanced DOC release by ice algae (Apollonio, 1985). More studies are needed to explain the factors governing DOC production by ice algae. Metabolites released by ice algae and phytoplankton may constitute an important autochthonous source of carbon for heterotrophic bacteria in sea ice (Vézina *et al.*, 1997) and in the water column (Norrman *et al.*, 1995; Obernosterer and Herndl, 1995; Rich *et al.*,

1997). Across most of the Makarov and Amundsen basins, relatively high DOC concentrations were reported in the surface waters ($> 1.2 \text{ mg C l}^{-1}$) and in the upper 100 m of the water column ($98\text{--}122 \text{ g C m}^{-2}$) (Wheeler *et al.*, 1996, 1997). The preliminary DOC budget of Wheeler *et al.* (1997) suggests that the three major sources of DOC in the central Arctic Ocean are *in situ* production (56%), river run-off (25%), and inputs from Pacific water (19%).

Environmental control of the horizontal distribution of phytoplankton and ice algae.

Along the transect from the Chukchi Sea to the Nansen Basin passing across the North Pole, physical and chemical conditions were highly variable. The regions at both ends of the transect had the lowest ice cover, the shallowest surface mixed layer depth compared to the depth of the euphotic layer and the most nitrogen rich waters. The regions in the middle of the transect ($76^{\circ}\text{--}88^{\circ}\text{N}$) had the highest ice cover, a deeper surface mixed layer and the lowest nitrogen concentration. The two most important factors regulating the large scale distribution of phytoplankton production and biomass across the Arctic Ocean in summer 1994 were the surface ice cover and the depth of the surface mixed layer. These two factors determine the amount of light available to the microalgae in the water column. Nutrients, especially dissolved inorganic nitrogen, were probably not limiting for phytoplankton since DIN was not depleted along the transect and the assimilation number ($P_T:B_T$) did not show any correlation with DIN concentration. This contrasts with the recent results of Cota *et al.* (1996) indicating nitrate depletion at the edge of the Canadian Basin in August 1993. In the upper 100 m of the water column, the C biomass of mesozooplankton was higher in the Canadian Basin than in the Chukchi Sea and the Eurasian Basin (Wheeler *et al.*, 1996; Thibault *et al.*, 1997). The maximum biomass of zooplankton coincided with the minimum phytoplankton biomass (Table 1), suggesting that mesozooplankton grazing may play a secondary role in the distribution of phytoplankton under the permanent pack ice of the Arctic Ocean during the summer.

The relationships between the production and biomass of ice algae and the type of sea ice, the surface water temperature and the surface nitrate concentration suggest that the large scale horizontal distribution of the ice algae is probably governed by processes of ice formation and the associated varying ice structure, ice melting processes and nitrogen supply. At the end of the vernal growth season in Resolute Passage (Smith *et al.*, 1997b) and in the brackish water of southeastern Hudson Bay (Maestrini *et al.*, 1986), nitrogen supply limits the ice algal growth. In the present study, the highest concentrations of the centric diatom *Melosira arctica* were found in areas covered with first-year ice (i.e. $75^{\circ}25' \text{ N}$ and 88° N). Gutt (1995) also observed the occurrence of sub-ice algal aggregations in first-year ice off northeast Greenland in June and July. These observations of the massive growth of *M. arctica* under first-year ice are in contrast to earlier reports from the Barents Sea, where they have been recorded exclusively under multi-year ice (Syvertsen, 1991).

CONCLUSION

Our estimate of total annual primary production (phytoplankton plus ice algae) in the central Arctic Ocean is about 15 g C m^{-2} , at least one order of magnitude greater than the estimates of Apollonio (1959) and English (1961). The difference between the new and old estimates is due in part to the previously unmeasured contribution of the particulate

production by ice algae and the release of DOC by both ice and pelagic algae. It is also possible that the methodology used in the 1950s may have underestimated the phytoplankton production (Pomeroy, 1997). Our new direct estimate is similar to the recent estimates of Pomeroy (1997) based on a re-analysis of historical dissolved oxygen data.

Previous studies of the Arctic Ocean carbon cycle assumed that, since production appeared to be low in the central basins, most organic carbon was either derived from river inputs or imported from the extensive shelf regions (e.g. Walsh, 1995). Our new measurements of primary production suggest a more dynamic carbon cycle in the surface waters of the central Arctic. Higher estimates of primary production result in part from the activity of the ice algae, which had not been sampled in previous studies.

Direct measurements of DOC release by both ice algae and phytoplankton indicate that a significant portion of the high DOC found in the central Arctic Ocean is produced *in situ*. The high release of DOC by phytoplankton in the Canadian Basin is probably due to a combination of factors, including light limitation, nitrogen stress and/or grazing by heterotrophic protists.

Our results and those of Rich *et al.* (1997) on heterotrophic bacteria, Sherr *et al.* (1997) on heterotrophic protists and Thibault *et al.* (1997) on metazooplankton indicate that the central Arctic is not a biological desert, but rather supports an active biological community that contributes to the cycling of organic carbon through dissolved and particulate pools.

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