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Uptake rates of dissolved inorganic carbon and nitrogen by under-ice phytoplankton in the Canada Basin in summer 2005

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Abstract The Ocean Exploration cruise in June–July 2005 allowed detailed description of the in situ under-ice primary productivity of phytoplankton in the Canada Basin. On the basis of a ^{13}C–^{15}N dual isotope tracer technique, the estimated daily carbon production rate of under-ice phytoplankton ranged from 20.4 to 178.3 mg C m^{-2} day^{-1}, whereas the daily nitrogen production rate ranged from 5.5 to 50.9 mg N m^{-2} day^{-1}. These ranges are much higher than those recorded in previous studies, probably due to high seasonal and regional differences in the basin. Reduced nitrogen limitation for phytoplankton and the relative light attenuation through different sea-ice conditions may also be factors influencing the higher carbon and nitrogen uptake rates in 2005. Based on this study, new carbon production by phytoplankton growing beneath sea ice is estimated to range from 0.66 to 6.75 g C m^{-2} $year^{-1}$, indicating that 25.2–66.4% of total annual primary production might potentially be exported from the euphotic zone in the deep Canada Basin.

Keywords Canada Basin · C/N ratio · Nitrogen uptake rate · Phytoplankton · Primary productivity · Sea ice

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Introduction

Higher temperatures, along with a possible increase in ice export, have decreased the extent and thickness of perennial sea ice in the Arctic Ocean over the past 40 years and produced more open water (Rothrock et al. 2003; Nghiem et al. 2007; Perovich and Richter-Menge 2009). Perovich and Richter-Menge (2009) found that the extent of Arctic sea ice in 2007 was at its lowest level recorded since 1978. These changes in ice thickness and extent may alter the light available under sea ice and thus influence the carbon and nitrogen production rates of phytoplankton. As a consequence of changes in phytoplankton production rates, the seasonal distributions, geographic ranges, and nutritional structure of zooplankton may be altered (Tynan and DeMaster 1997).

Since several physical and chemical factors limit the primary production of phytoplankton in the water column under ice in polar oceans (Arrigo 2003), it is difficult to determine the specific factors controlling primary production during the summer. Recent studies have shown that the carbon production of phytoplankton in surface waters under sea ice is limited by light in the Canada Basin (Lee and Whitledge 2005). Therefore, the ongoing decrease in sea-ice thickness might favor an increase in primary production in the Arctic Ocean. However, we still cannot predict whether ongoing climate change will lead to reduced or increased production in arctic regions because very little is known about the critical limits of in situ physical/chemical environmental conditions for phytoplankton growth under sea ice.

A few studies of pelagic primary productivity in the Canada Basin (Cota et al. 1996; Gosselin et al. 1997; Chen et al. 2003; Lee and Whitledge 2005) have revealed that recent rates of primary production in this region are

higher than those previously measured (Apollonio 1959; English 1961; Pautzke 1979). However, it is difficult to attribute these higher rates to specific changes in environmental conditions, since earlier studies did not conduct intensive and comprehensive measurements of phytoplankton primary productivity under sea ice in the basin. The NOAA Ocean Exploration program in the Canada Basin in 2005 presented an opportunity for additional measurements of in situ under-ice primary productivity in the Canada Basin, forming a basis for the discussion of possible future impacts resulting from decreased sea-ice thickness.

Materials and methods

Study sites

The Canada Basin, one of the deepest and least-known areas in the Arctic Ocean, is covered with sea ice for most of the year (Fig. 1). Data were collected in this basin from on board the US Coast Guard icebreaker *Healy* from 27 June to 26 July 2005 (Table 1). The study area was covered with sea ice of 1.2–2.5 m thickness (Table 1).

Field data

Shipboard measurements of temperature and salinity were conducted using a Sea Bird model 911 plus conductivity-temperature-depth (CTD) profiler deployed about 100 m away from the ice floe water sampling and incubation sites. Water samples for macronutrient analyses were collected using 10-l Niskin sampling bottles with integrated 24-place rosette samplers. Immediately after water sampling, inorganic nitrate (NO_3^-), ammonium (NH_4^+), silicate (SiO_4^-), and phosphate (PO_4^+) concentrations were analyzed on board the ship using an automated nutrient analyzer (ALPKEM RFA model 300). The accuracy of nutrient concentrations in water samples for the analytical system was ±0.02 μM for phosphate and nitrite and 0.1 μM for nitrate, ammonium, and silicate.

Light intensity was measured one time before incubation. Each light depth was determined from observed underwater radiation using a LI-COR 4π light sensor (LI-193) facing upward through a 9–10 cm-diameter ice hole and a surface radiation reference (LI-190 quantum sensor) that was used to correct the light intensity for clouds. However, because the measured light intensities could have been elevated relative to ambient levels due to the effect of the hole, the measured intensity values (Table 1) were only used as a relative reference.

Chlorophyll-*a* analysis

Samples for the determination of total chlorophyll-*a* (Chl-*a*) were filtered onto Whatman GF/F glass fiber filters (24 mm). The filters were kept frozen until their analysis on board. They were extracted in a 3:2 mixture of 90% acetone and DMSO (Webb et al. 1992), placed in a freezer at −5°C for 24 h and centrifuged following the procedure of Parsons et al. (1984). Chl-*a* concentrations were measured using a Turner Designs model 10-AU fluorometer which had been calibrated with commercially purified Chl-*a* preparations.

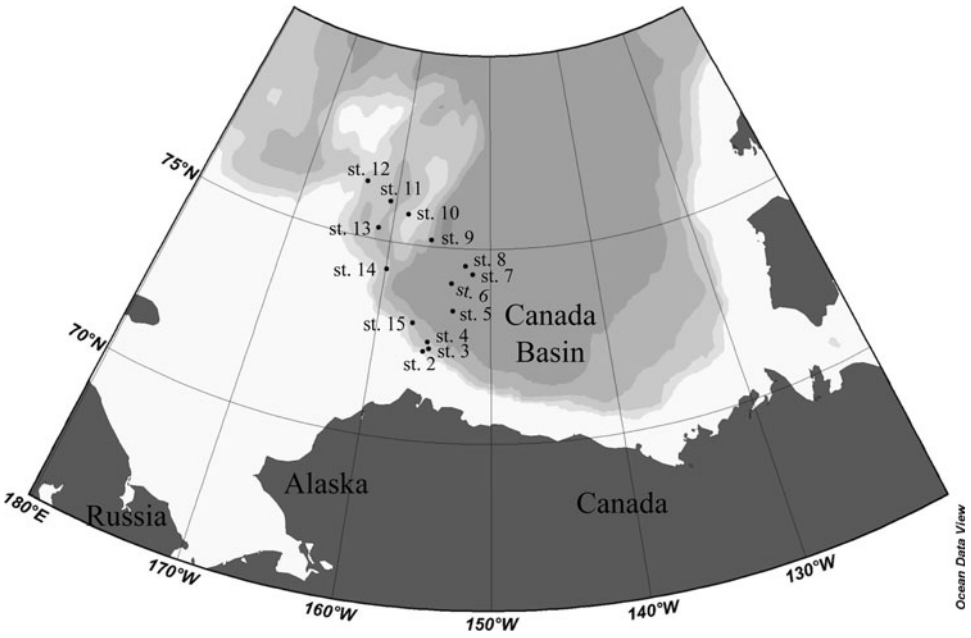

Fig. 1 Productivity stations in the Canada Basin in 2005. All the stations in 2005 were ice productivity stations, at which in situ production was conducted under sea ice

Table 1 Description of the sea ice productivity stations in the Canada Basin in 2005

Station	Location		Date	Ice thickness (cm)	Air surface light intensity ($\mu E\ m^{-2}\ s^{-1}$)	Bottom light intensity ($\mu E\ m^{-2}\ s^{-1}$)	1% light depth at bottom ice (m)
	Latitude (°N)	Longitude (°W)					
2i	72 19. 36	155 44. 96	28/06	128	–	452	40
3i	72 20. 87	155 18. 37	29/06	143	1,220	259	50
3Ai	72 20. 87	155 18. 37	30/06	123	–	–	40
3Bi	72 20. 87	155 18. 37	01/07	–	–	211	50
4i	72 32. 59	155 30. 94	03/07	128	1,595	210	40
5i	73 26. 69	153 26. 48	05/07	154	1,294	82	52
6i	73 53. 98	153 36. 24	07/07	156	1,484	98	54
8i	74 34. 49	152 04. 90	11/07	175	1,215	67	56
9i	75 11. 13	155 56. 80	13/07	154	1,542	72	52
10i	75 42. 56	158 30. 79	15/07	167	530	76	46
11i	76 01. 95	160 37. 35	16/07	140	660	76	48
13i	75 17. 87	161 20. 37	20/07	144	–	66	60
14i	74 17. 38	159 53. 56	22/07	145	221	29	46
15i	73 01. 10	156 53. 53	23/07	245	1,135	56	50

Ice thickness was provided by Dr. R. Gradinger (Institute of Marine Science, UAF)

Carbon and nitrogen productivity

In situ carbon and nitrogen uptake experiments were conducted at 14 different ice floe stations with an average thickness of 1.5 m of ice covered with 2–3 cm of snow. Small holes ($\varnothing = \sim 10$ cm) were drilled with a SIPRE ice corer for in situ incubation experiments in water under sea ice, and large holes ($\varnothing = \sim 25$ cm) drilled with an ice auger were used for lowering a 5-l Niskin bottle to collect water samples for nutrients, Chl-*a* concentration, and primary production under the ice floes.

Daily carbon and nitrogen uptake rates were estimated from six light depths (100, 50, 25, 10, 5, and 1% of light at bottom ice) under the sea ice using a ^{13}C–^{15}N dual isotope tracer technique (Cota et al. 1996; Lee and Whitledge 2005). Since the phytoplankton under the sea ice were considered to be shade adapted, in situ incubations were executed at depths relative to the profiles of light below the ice. Hereafter all light-depth percentages refer to the percentage of light that penetrated the ice cover so that 100% was located at the bottom edge of the sea ice. To measure the uptake rates of carbon and nitrogen by phytoplankton, two clear and one dark Nalgene polycarbonate bottles (1.2 l) were filled with water from each light depth and then heavy isotope-enriched (98–99%) solutions of $H^{13}CO_3$ and $K^{15}NO_3$ or $^{15}NH_4Cl$ were added to the samples at concentrations of ~ 0.2 mM ($^{13}CO_2$), ~ 0.8 μM ($^{15}NO_3$), and ~ 0.2 μM ($^{15}NH_4$) (Dugdale and Goering 1967; Hama et al. 1983). The ^{13}C enrichment was about 5–10% of the total inorganic carbon in the ambient water, as determined by titration with 0.01 N HCl (Anderson et al. 1999) during the cruise. Because the ambient concentrations of nutrients were so low (<0.1 μM), the concentrations of isotope additions were generally 60–150% of the ambient nitrate and ammonium concentrations for most samples. Although the final concentrations of nitrate and ammonium were lower than the estimated half-saturation constants for nitrate (0.87) and ammonium (0.17) in polar regions reported by Smith and Harrison (1991), this might have elevated the in situ uptake rates of nitrate and ammonium (MacIsaac and Dugdale 1972; Garneau et al. 2007).

We evaluated the potential isotope dilution effect for the ammonium uptake measurements using the equations derived by Kanda et al. (1987). The average underestimation for ammonium uptake ranged from 20 to 60% (assuming a = 1 and 2, where "a" is the ratio of regeneration and uptake). This underestimation might have been balanced by the $^{15}NH_4$ enrichment that has been reported to be as much as 50% in the Arctic Ocean (Garneau et al. 2007).

After isotope inoculations were completed in a shaded box, the incubation bottles were tied to an anchor rope with a weight at the bottom, lowered to the depth from which they were originally collected, and kept at their in situ temperature and light under the sea ice with snow cover for 4–6 h. The incubation hole was covered by three layers of sea-ice cubes on top of the hole to reduce the possibility that light would be transmitted to the uppermost samples (Lee et al. 2008). However, the incubation irradiances could have been elevated through the ice hole covered by ice cubes. Since phytoplankton under sea ice are

shaded-adapted (Andersen 1989), they can respond strongly to variations in under-ice irradiance. Therefore, the uptake values measured in this study might represent maximum- or over-estimates. After incubation, the bottles were retrieved and brought to the ship in a dark, insulated box for filtration through precombusted Whatman GF/F filters. The filters were immediately frozen at −20°C and preserved for mass spectrometric analysis at the stable isotope laboratory of the University of Alaska Fairbanks. Total amounts of particulate organic carbon (POC) and nitrogen (PON) as well as the abundance of ^{13}C and ^{15}N were determined using a ThermoFinnigan Delta + XL mass spectrometer after HCl fuming overnight to remove carbonate. Carbon and nitrogen production rates were calculated following the procedures of Hama et al. (1983) and Dugdale and Goering (1967). All carbon uptake rates were corrected by subtraction of dark uptake rates from corresponding light values. We subtracted dark carbon uptake values from light carbon uptake values assuming that the measured dark uptake rates are from bacterial processes (Gosselin et al. 1997). For consistency, with the carbon uptake rates, we subtracted dark nitrogen uptake rates from the light nitrogen uptake rates of phytoplankton, although subtracting dark bottle values is a highly debatable procedure for nitrogen uptake rates (Smith and Harrison 1991). This method follows the method used to calculate nitrogen uptake rates in our previous work (Lee and Whitledge 2005).

Results

Physical structures and major inorganic nutrient concentrations in the Canada Basin in 2005

In 2005, the temperature above depths of 100 m ranged from −1.35 to −0.65°C (Fig. 2a). In the upper zone, from the surface to about 30 m, all of the profiles were nearly uniform (−1.35°C) (Raskoff et al. 2005). Below the upper zone, the temperature increased to about 50 m and then decreased to 100 m. In contrast, the salinity and density were low in the mixed zone, but below this, they increased with depth (Fig. 2b, c).

The major nutrients in the upper zone above the nutricline (~30 m depth) had fairly uniform profiles (Fig. 3). Below the nutricline, concentrations increased with depth, except those of ammonium, which was usually present in low concentrations throughout the water column, and nitrate concentrations, which were about 0.1–0.2 μM in the water column above the nutricline. In contrast, the concentrations of phosphate (>0.7 μM) and silicate (2.0 μM) were relatively high throughout the water column.

Light intensity under sea ice

Air surface light intensity ranged from 221 to 1,595 μE m^{-2} s^{-1}, whereas the light intensity at the bottom edge of the ice ranged from 29 to 452 μE m^{-2} s^{-1} (Table 1). The mean light level beneath the sea ice was 9.6% (SD = ±5.5%) of the incident light at the surface in 2005 (Fig. 4). From the bottom of the ice, light continually dissipated down to a depth of 25 m, which was the maximum depth at which light intensity was measured. At 25 m under the sea ice, the light level was 1.2% (SD = ±0.4%) of the incident light at the surface in 2005.

Distribution of phytoplankton in the water column under sea ice

In general, the phytoplankton biomass under sea ice represented by Chl-*a* concentration was low (<0.5 mg Chl-*a* m^{-3}) throughout the water column above 60 m depth in the basin (Fig. 5). The deep Chl-*a* maximum layer (DCM) was located at ~40 m depth at most stations in 2005. The Chl-*a* concentration at the surface ranged from <0.1 to 0.3 mg Chl-*a* m^{-3}, with an average of 0.1 mg Chl-*a* m^{-3}. In contrast, Chl-*a* at the DCM ranged from 0.2 to 1.0 mg Chl-*a* m^{-3}, with an average of 0.5 mg Chl-*a* m^{-3}. The mean integrated concentration from 0 to 60 m depth was 10.8 mg Chl-*a* m^{-2} (SD = ±5.7 mg Chl-*a* m^{-2}).

Carbon and nitrogen uptake rates by phytoplankton under sea ice

The carbon uptake rates from just below the bottom of the ice (100% light depth) to the 1% light depth ranged from 0.002 to 0.396 mg C m^{-3} h^{-1} with a mean of 0.053 mg C m^{-3} h^{-1} (SD = ±0.073 mg C m^{-3} h^{-1}) (Table 2). There was no general vertical pattern in carbon uptake rates by phytoplankton in the Canada Basin in 2005. However, the maximum uptake rates obtained from this study generally occurred near 5 or 1% under sea-ice light levels, which were located at 30–50 m below the sea ice. The integrated carbon uptake rates in the water column ranged from 0.85 to 7.43 mg C m^{-2} h^{-1} with an average of 2.48 mg C m^{-2} h^{-1} (SD = ±1.87 mg C m^{-2} h^{-1}) (Fig. 6a).

The maximum uptake rates of nitrate and ammonium under the sea ice in the Canada Basin occurred near 5 or 1% light depth, and ranged from <0.001 to 0.044 mg N m^{-3} h^{-1} for nitrate and from <0.001 to 0.082 mg N m^{-3} h^{-1} for ammonium among stations (Table 3). In general, ammonium uptake rates were higher than nitrate uptake rates at all depths, except the 1% light depth at ~50 m (Table 3). The vertically integrated uptake

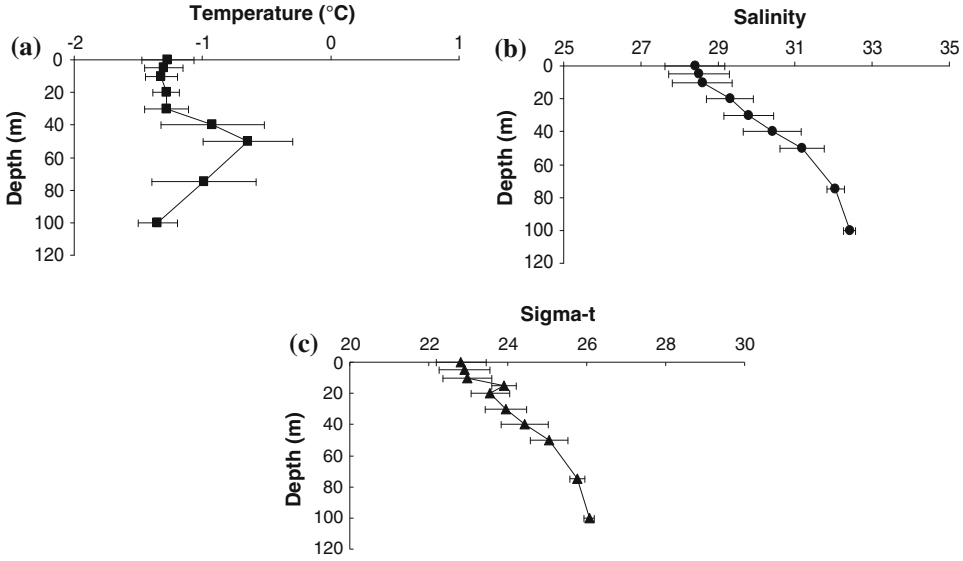

Fig. 2 The vertical structures of temperature (**a**), salinity (**b**), and sigma-*t* (**c**) averaged from the sampling stations in the Canada Basin in 2005. *Error bars* represent standard deviations

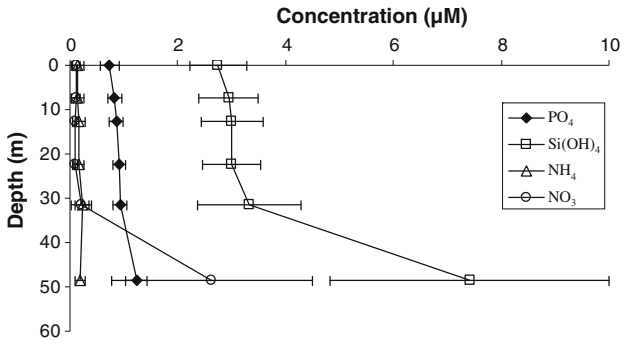

Fig. 3 The vertical concentrations of inorganic macronutrients averaged from the sampling stations in the Canada Basin in 2005. *Error bars* represent standard deviations

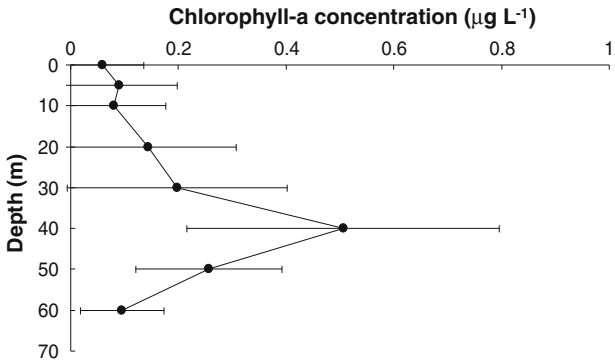

Fig. 5 The vertical Chl-*a* concentration of phytoplankton under sea ice in 2005. *Error bars* represent standard deviations

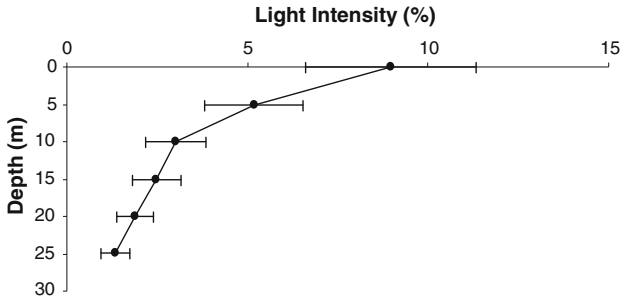

Fig. 4 The vertical structure of the relative light intensity under sea ice to the air surface irradiance averaged from the sampling stations in the Canada Basin in 2005. *Error bars* represent standard deviations

rates of total nitrogen (nitrate + ammonium) from 100 to 1% light depth under bottom ice ranged from 0.23 to 2.12 mg N m^{-2} h^{-1} (Fig. 6b) with an average of 0.84 mg N m^{-2} h^{-1} (SD = ±0.63 mg N m^{-2} h^{-1}).

Discussion

Environmental conditions under sea ice

General vertical profiles of temperature and salinity in the deep Canada Basin in 2005 were different from those recorded in 2002 (Lee and Whitledge 2005). This was mainly caused by the different amount of melted sea-ice water on the surface in the 2 years. Since the cruise in 2002 was from mid-August to early September (when the surface water is warmed during the summer), the surface water in 2002 was warmer than that in 2005. Thus, more melted sea-ice water was added into the surface water column, and hence the salinity at the surface in 2002 was lower than that in 2005. The average molar ratio of total ambient dissolved inorganic total nitrogen to phosphate was 0.64 (±0.84), whereas the nitrogen to silicate ratio was 0.14 (±0.12) in 2005. These ratios were substantially lower than the Redfield ratios (Redfield et al. 1963), implying a strong deficiency in ambient nitrogen concentrations relative to

Table 2 Carbon uptake rates (mg C m^{-3} h^{-1}) at different light depths under the sea ice of the productivity stations in the Canada Basin in 2005

Light depth (%)	2i	3i	3Ai	3Bi	4i	5i	6i	8i	9i	10i	11i	13i	14i	15i
100	0.268	0.136	0.083	0.053	0.073	0.011	0.170	0.026	0.012	0.013	0.010	0.011	0.013	0.031
50	0.396	0.114	0.091	0.050	0.026	0.011	0.011	0.019	0.013	0.022	0.007	0.009	0.011	0.021
25	0.288	0.132	0.088	0.052	0.033	0.016	0.011	0.016	0.014	0.016	0.009	0.008	0.013	0.018
10	0.250	0.100	0.108	0.087	0.030	0.017	0.011	0.016	0.014	0.016	0.015	0.019	0.011	0.018
5	0.078	0.073	0.148	0.050	0.034	0.017	0.023	0.017	0.088	0.012	0.258	0.167	0.015	0.017
1	0.008	0.008	0.005	0.007	0.069	0.027	0.022	0.033	0.013	0.036	0.002	0.007	0.045	0.041

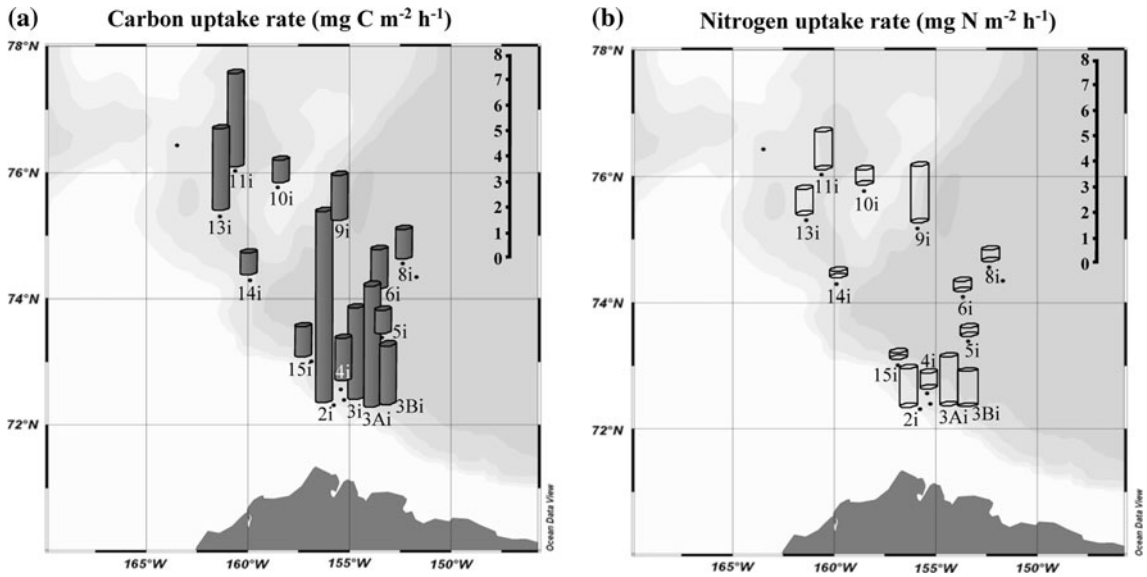

Fig. 6 The vertically integrated carbon uptake rates (**a**) and nitrogen (nitrate + ammonium) uptake rates (**b**) under the sea ice in the Canada Basin in 2005

Table 3 Nitrate and ammonium uptake rates at different light depths under the sea ice of the productivity stations in the Canada Basin in 2005

Light depth (%)	2i	3i	3Ai	3Bi	4i	5i	6i	8i	9i	10i	11i	13i	14i	15i
(a) Nitrate uptake rates (mg N–NO_3 m^{-3} h^{-1})														
100	0.012	0.011	0.010	0.005	0.004	<0.001	0.024	0.001	0.001	<0.001	0.002	0.001	<0.001	0.001
50	0.012	–	0.012	0.016	0.003	0.001	0.001	0.002	0.002	0.001	0.002	0.001	<0.001	<0.001
25	0.010	–	0.010	–	0.006	<0.001	0.001	0.001	<0.001	0.002	0.002	0.001	0.001	0.001
10	0.023	–	0.018	0.015	0.003	0.001	0.001	0.001	0.001	0.003	0.002	0.002	<0.001	0.001
5	0.013	–	0.009	–	0.010	0.002	0.008	0.002	–	0.001	0.044	0.020	0.001	<0.001
1	–	–	–	–	0.003	0.002	0.002	0.006	0.007	0.011	0.006	0.012	0.013	0.013
(b) Ammonium uptake rates (mg N–NH_4 m^{-3} h^{-1})														
100	0.008	0.011	0.021	0.038	0.002	0.001	0.001	0.002	0.003	0.003	0.001	0.001	0.001	–
50	0.011	–	0.018	0.061	0.002	0.001	0.001	0.007	0.003	0.004	0.002	0.005	<0.001	–
25	0.012	0.002	0.016	0.072	0.003	0.001	0.001	0.004	0.009	0.006	0.009	0.005	0.001	<0.001
10	0.035	0.033	0.001	0.070	0.007	0.006	0.003	0.007	0.008	0.017	0.011	0.005	0.002	0.001
5	0.045	0.038	0.066	0.004	0.017	0.010	0.005	0.007	0.082	0.015	0.042	0.019	0.003	0.001
1	–	–	–	–	0.010	0.005	0.001	0.008	0.001	0.005	<0.001	0.001	0.006	0.010

phosphate and silicate in the Canada Basin in 2005. The most obvious difference in the environmental variables between 2005 and 2002 was in the light intensity beneath the sea ice, which is mainly due to the different ice thicknesses. The mean light levels beneath the sea ice were 2.9% (SD = ±0.8%) and 9.6% (SD = ±5.5%) of the

incident light at the surface, respectively, in 2002 and 2005. The mean thickness in 2002 was 2.3 m (Lee and Whitledge 2005), whereas the mean thickness in 2005 was 1.5 m, a 35% decrease. Although sediments trapped in sea ice (Horner and Schrader 1982) or snow cover (Andersen 1989) are often the most important variables affecting light attenuation through sea ice, the different ice thicknesses between the two studies are believed to be the main cause of the different light intensities under the sea ice, since the snow covers were similar (2–3 cm) and there were no visible sediments trapped in the sea ice. The amount of light predicted from Andersen (1989) may increase from ~6.2% of surface irradiance at the bottom of 2.3-m sea ice to ~16.3% at the bottom of 1.5-m sea ice without snow cover. Since there were small amounts of snow cover on the ice during both years, the mean light intensities at the sea-ice bottoms were actually 2.9% (±0.8%) and 9.2% (±5.6%) of the incident light at the air surface for 2002 and 2005, respectively, which were lower than those without snow cover.

Carbon uptake rates of phytoplankton under sea ice

Assuming a constant uptake rate by phytoplankton and a 24-h cycle of sunshine during the summertime in the Arctic Ocean (Subba Rao and Platt 1984; Lee and Whitledge 2005), the daily carbon production rate of phytoplankton under the sea ice in the Canada Basin in 2005 was found to range from 20.4 to 178.3 mg C m^{-2} day^{-1} (Fig. 6a), with a mean of 59.5 mg C m^{-2} day^{-1}. This value is about fivefold higher than the mean uptake rate (11.3 mg C m^{-2} day^{-1}) in 2002 (Lee and Whitledge 2005). Like other high-latitude ecosystems, the Arctic has seasonal variations in photosynthetic rate (English 1961; Pautzke 1979). Our measurements were conducted from late June to July in 2005 when carbon assimilation is highest, whereas in 2002, measurements were carried out from mid-August to early September, when activity is relatively low in the Canada Basin (Pautzke 1979). In addition to the seasonal difference in photosynthetically active radiation, the relative light attenuation through different sea-ice conditions may be an important determinant for carbon uptake rates by phytoplankton under sea ice. To understand the factors that affected the carbon uptake rates of phytoplankton under the sea ice in 2005, linear regression models relating the integrated carbon uptake rates of phytoplankton under the sea ice to different factors in the deep Canada Basin are summarized in Table 4. There were no significant relationships between the different nutrient concentrations and the carbon uptake rates in the basin. In contrast, ice thickness and light intensity were highly correlated with the uptake rates of the phytoplankton under the sea ice in the basin (Table 4). In fact, the averaged

Table 4 Summary of linear regression models relating the integrated carbon uptake rates (Y) of phytoplankton to different environmental factors (X) from the cruise in 2005

	a	b	R^2	P	n
PO_4	0.742	0.038	0.22	0.609	14
$Si(OH)_4$	0.111	0.013	0.11	0.245	14
NH_4	1.729	0.090	0.05	0.460	14
NO_3	1.645	0.028	0.09	0.297	14
Light intensity	0.638	0.011	0.57	<0.001*	14
Ice thickness	5.119	−0.019	0.27	0.040*	14

All models are of the form $Y = a + bX$. P is probability value and n is sample number. Light intensity was measured beneath bottom of the ice at the productivity stations. Ice thickness from each station was provided by R. Gradinger (IMS, UAF). * Indicates a significant linear relationship between integrated carbon uptake rates and factors

POC/Chl-*a* and PON/Chl-*a* of phytoplankton were much higher in 2005 than in 2002 (data not shown), indicating that phytoplankton were under relatively less light limitation in 2005 (Hegseth 1997).

Since there are seasonal and annual changes in the photosynthetic rate of phytoplankton in the Arctic Ocean (English 1961; Pautzke 1979), estimates of annual primary production must be made with caution. However, for comparison purposes with results from previous studies, the annual carbon production was roughly estimated with the assumption of a 120-day growing season in the Arctic (Subba Rao and Platt 1984; Gosselin et al. 1997; Lee and Whitledge 2005). The annual carbon production rate of phytoplankton under a mean sea-ice thickness of 1.5 m was found to range from 2.5 to 21.4 g C m^{-2}, with a mean of 7.1 g C m^{-2} in the Canada Basin in 2005. This primary production range is significantly higher (Student's t test, P-value $< \alpha = 0.05$) than that of the phytoplankton under 2.3-m sea ice in the same basin in 2002, which had values of 0.3–3.2 g C m^{-2}, with a mean of 1.4 g C m^{-2} (Lee and Whitledge 2005). Moreover, our annual production rate was still higher than the estimates reported by Pautzke (1979) for phytoplankton production under drifting pack ice, which were 2.1 g C m^{-2} in the southern Canada Basin in 1975 and 3.2 g C m^{-2} for the average of different areas in the Canada Basin during 1971–1975. In the Canada Basin, where ice cover reached a maximum of about 90–100%, Gosselin et al. (1997) found that the mean daily carbon uptake rate of phytoplankton was 35 mg C m^{-2} day^{-1}. If this daily uptake is used for estimating the annual uptake in the Canada Basin, it would be 4.2 g C m^{-2}, which is nearly half of our mean rate in 2005. Although the annual carbon production rate had a large range in 2005, the mean rate under sea ice in this study was comparable with that in the open water column (8.9 g C m^{-2}) (Cota et al. 1996). However, our rate was

somewhat lower than that recorded for the water column by Lee and Whitledge (2005), which ranged from 9.5 to 17.4 g m^{-2} with a mean of 12.7 g m^{-2} in the basin in 2002. Compared with other areas in the deep Canada Basin, our under-ice productivity in the Canada Basin in 2005 was about one order of magnitude greater than that estimated by English (1961) (about 0.6 g C m^{-2}) under 2.5–3.0 m pack ice in the central Arctic Ocean. However, the rate of annual production (7.1 g C m^{-2}) determined from our study might be an underestimate, as we did not correct for the percentage of the total phytoplankton production released as extracellular carbon, which has been found to range from 31 to 65% in the Canada Basin (Gosselin et al. 1997). The relative contribution of ice algae to total daily primary production is low (2%) in the basin (Gosselin et al. 1997). If this contribution and the rerelease of extracellular carbon are combined with our under-ice rates, the annual production rate of primary producers under 1.5-m-thick sea ice could have ranged from 9.4 to 11.9 g C m^{-2} in the Canada Basin in 2005, which is much higher than measurements for the central Arctic Ocean (Apollonio 1959; English 1961). This difference might be caused by the unmeasured release of dissolved organic carbon (DOC) by both ice and pelagic algae (Gosselin et al. 1997) and the larger rates of phytoplankton production under the thinner sea ice.

Nitrogen uptake rates of phytoplankton under sea ice

The daily total nitrogen production rate of under-ice phytoplankton in the Canada Basin in 2005 ranged from 5.5 to 50.9 mg N m^{-2} day^{-1} (Fig. 6b), with a mean of 20.2 mg N m^{-2} day^{-1}. The estimated mean uptake rate from this study is much higher than the mean rates recorded by Pautzke (1979) (5.0 mg N m^{-2} day^{-1}) for the northern Canada Basin and by Lee and Whitledge (2005) (0.8 mg N m^{-2} day^{-1}) for the eastern Canada Basin. This is probably because of the seasonal and regional variations in the different studies conducted in the basin, e.g., similar to those described above for carbon uptake rates. An alternate possibility is that weaker nitrogen (especially nitrate) limitation occurred in 2005 than in 2002. The mean assimilated C/N ratio under the sea ice was 3.9 (SD = ±2.26) in this study, which is much lower than that (13.8) in 2002 (Lee and Whitledge 2005) and lower than the Redfield ratio of 6.6:1 (Redfield et al. 1963), suggesting less nitrogen stress in 2005 than in 2002 (Gosselin et al. 1997). Therefore, the phytoplankton might have obtained more nitrate, which could have caused the higher mean *f*-ratio observed in 2005 (discussed in detail below). The possible overestimation of nitrogen uptake rates of the phytoplankton by the additions of nitrate and ammonium isotopes must also be considered since the ambient concentrations of nitrate and ammonium in the water were very low. The mean C/N ratio of particulate organic matter was 13.3 (SD = ±1.0) which was much higher than the mean assimilated C/N ratio (3.9) in this study but similar to the mean assimilated C/N ratio (13.8) in 2002 (Lee and Whitledge 2005). Although C/N ratios of particulate organic matters are generally different from assimilated C/N ratios in phytoplankton uptake experiments because of detritus effects in the water column, the actual assimilated C/N ratio in this study might be an underestimate due to the excess nitrogen added to the incubations compared to the ambient depleted nutrient concentrations. However, there was no relationship between specific carbon or nitrogen uptake rates and percentage of enriched nutrient isotopes at comparable light levels in this study.

It is important to distinguish between the relative importance of regenerated and new sources of nitrogen. Regenerated nitrogen (ammonium) maintains cells in a healthy state, whereas new nitrogen (nitrate) increases the population size (or rate of primary production), which is passed onto higher trophic levels (Dugdale and Goering 1967). The ratio of new production (normally nitrate uptake) to total primary production (generally the sum of nitrate, ammonium, and sometimes urea uptakes) is the *f*-ratio which is an ecologically important parameter of nitrogen uptake, providing qualitative information on the nature of the sinking POC (Eppley and Peterson 1979). In our study, the mean *f*-ratio (nitrate uptake/nitrate + ammonium uptakes) was 0.36 (SD = ±0.24), indicating that about 36% of the total under sea-ice production was new production in the study area. Tremblay et al. (2000) found that overall *f*-ratios were not significantly biased by nitrogen isotopic dilution in arctic regions. However, our *f*-ratio could be overestimate, as it was estimated based solely on the relative uptake rates of nitrate and ammonium (Yool et al. 2007; Tremblay et al. 2008). Regenerated nitrate can form more than 70% of the total nitrate pool in the euphotic zone (Yool et al. 2007). Although the exclusion of regenerated nitrate changes least in high latitudes among various regions (Yool et al. 2007), nitrification could be important under the ice, since nitrifying bacteria are usually inhibited by light close to the surface (Ward et al. 1984), which would not be the case under low light conditions beneath the ice. In the Arctic Ocean, about 22% of the net nitrate uptake is considered to be regenerated production by nitrification in the euphotic layer (Tremblay et al. 2008). If we considered this amount in our nitrate uptake, then our revised estimated *f*-ratio was 0.31 (SD = ±0.18) which is rather smaller than our previous ratio. For comparison with previous studies, nitrification was not considered when calculating the *f*-ratio. The *f*-ratio (0.36) from this study is comparable with that obtained in Prudhoe Bay ($f = 0.40$) during summer

(Horner et al. 1974) as well as with the highest values (0.05–0.38) obtained in the southeastern Chukchi Sea during August (Cota et al. 1996). However, the present ratio is somewhat higher than that obtained from the deep Canada Basin in 2002 (Lee and Whitledge 2005) and is much higher than that estimated by Cota et al. (1996), whose mean *f*-ratio was 0.12 in the Canadian Basin and Northwind Ridge and Plain, based on the assumption of an ammonium concentration of 0.1 μM.

The daily nitrate uptake rates (new production) of phytoplankton ranged from 1.39 to 14.45 mg N m^{-2} day^{-1}, with an average of 5.47 mg N m^{-2} day^{-1} in 2005. Thus, using those values, the range of annual new production was estimated to be from 0.17 to 1.73 g N m^{-2}, with an average of 0.66 g N m^{-2}, based on 120 growing days. If nitrogen productivity is converted into carbon production using the mean assimilated C/N ratio (3.9) observed in this study, the annual new carbon production of under-ice phytoplankton can be estimated to range from 0.66 to 6.75 g C m^{-2}, which was about 25.2–66.4% (mean ± SD = 49.9 ± 15.6%) of the total annual primary production (2.5–21.4 g C m^{-2}) in the deep Canada Basin in 2005. This suggests that 25.2–66.4% of the total annual primary production might potentially be exported from the euphotic zone (Eppley and Peterson 1979). This range is relatively higher than both the level recorded in 2002 (20.8%; Lee and Whitledge 2005) and the range obtained by Cota et al. (1996), who estimated mean new production to be 16.1% in the Canadian Basin and Northwind Ridge and Plain. However, the mean percentage from this study can be compared with that of Garneau et al. (2007), who found that the annual new production was about 60% of the total annual production in an Arctic polynya region (North Water region, NOW). It should be noted that all of the above discussion assumes that the nitrification of ammonium to nitrate in the upper water column is not a significant process. However, future research should consider evaluating the validity of that assumption.

Summary and conclusions

The mean rates of daily carbon and nitrogen uptake by phytoplankton under the sea ice in the Canada Basin were much higher in 2005 than in previous studies. In addition to the seasonal variations in photosynthetically active radiation during the different study periods, the relative light attenuation through different sea-ice conditions may be an important determinant of these differences. Since light intensity had a significant linear relationship with the carbon uptake rate of phytoplankton under the sea ice in the basin, an increased quantity of light passing through thinner sea ice could be the principal factor increasing the primary production of phytoplankton under the sea ice in the Canada Basin in 2005, compared to earlier studies. Based on the mean assimilated C/N ratio observed in this study, reduced nitrogen limitation could be another reason for the higher rates in 2005. Compared to previous studies, it appears that nitrate fueled larger amounts of phytoplankton growth under the sea ice in the Canada Basin in 2005, based on the observed higher *f*-ratios and new production estimates. This suggests that a larger percentage of the total carbon production might be exported from the euphotic zone.

In conclusion, the decreasing sea-ice thickness in the Canada Basin (Rothrock et al. 2003; Nghiem et al. 2007; Perovich and Richter-Menge 2009) might be favorable for increased phytoplankton growth under the sea ice because the degree of light intensity governed by different sea-ice thicknesses was the most important factor affecting the carbon production of the phytoplankton in the Canada Basin in 2005. However, more seasonal and annual data under a variety of environmental conditions in different regions should be obtained to improve the understanding of arctic primary production processes and marine ecosystem responses to changes in sea-ice thickness in the Arctic Ocean. This is particularly important since the Arctic has pronounced seasonal and annual variations in photosynthetic rate (English 1961; Pautzke 1979) as well as regional variations.

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