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Phytoplankton productivity and its response to higher light levels in the Canada Basin

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Abstract Phytoplankton productivity in the Canada Basin was measured in the late summer season, from mid-September to mid-October 2009, using a ^{13}C–^{15}N dual tracer technique. To understand potential production changes associated with sea ice melting in the Arctic Ocean, we examined the effects of light enhancement and nitrate enrichment on the carbon productivity of phytoplankton from the chlorophyll *a* maximum layer. The daily carbon productivity in the Canada Basin in 2009 was very low, with a mean of 4.1 mg C m^{-2} (SD = 3.6 mg C m^{-2}), compared with those reported in previous studies in the region. Among several explanations, the most plausible reason for the large difference in carbon productivity between this and the previous studies was strong seasonal variation in biomass and photosynthetic rate of the phytoplankton in the study region. Based on our results from light enhancement and nitrate enrichment experiments, we found that carbon productivity of phytoplankton in the chlorophyll *a* maximum layer could be stimulated by increased light condition rather than nitrate addition. Thus, potentially increasing light availability from current and ongoing decreases in the sea ice cover could increase the carbon production of the phytoplankton in the chlorophyll *a* maximum layer and produce a well-developed maximum layer at a deeper depth in the Canada Basin.

Introduction

Sea ice is a major factor controlling pelagic and benthic production by modulating water-column stratification and light fields (e.g., Hill et al. 2005; Gradinger 2009). However, the sea ice extent and thickness have been decreasing since the late 1960s, due to melting as a consequence of Arctic Ocean warming (Carmack et al. 1995; Comiso 2006). Recently, sea ice melting in the Arctic Ocean has increased steadily, proceeding faster during the past three summers (2007–2009) (Arrigo et al. 2008; Comiso et al. 2008). It is expected that these sea ice changes will lead to environmental changes and affect not only the physiological status, but also the productivity of primary producers (Lee et al. 2008, 2010) and thus rates of carbon cycling (Arrigo et al. 2008; Bates and Mathis 2009; Cai et al. 2010) in the Arctic Ocean. In fact, Lasternas and Agustí (2010) found major changes in phytoplankton community structure in the North Atlantic sector of the Arctic Ocean during the record Arctic sea ice extent of summer 2007.

Generally, the Arctic Ocean has been categorized as an extremely low primary production region because of the year-round presence of ice and the short

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photosynthetic season (Gosselin et al. 1997). However, some recent studies have suggested signs of primary production increase in the Arctic Ocean (e.g., Rysgaard et al. 1999; Carmack and Macdonald 2002; Arrigo et al. 2008). Rysgaard et al. (1999) found that annual primary production was linearly related to the period of open water and thus expected the annual primary production to be enhanced as a consequence of Arctic sea ice reduction. In addition, increasing the areal extent of open water will intensify wind mixing, upwelling, and win- tertime brine rejection, leading to an increase in the availability of nutrients to phytoplankton (Carmack and Macdonald 2002). In fact, Arrigo et al. (2008) observed a 35 Tg C year^{-1} increase in annual primary production in the Arctic between 2006 and 2007, about 30% of which can be explained by the increased area of open water in 2007, although they found a slight decrease in the Greenland sector. Nonetheless, there are still poten- tial negative feedback between sea ice loss and primary production. The future increase in production resulting from the decreasing sea ice extent will reduce nutrient inventories in the euphotic zone, causing lower primary productivity in Arctic waters (Arrigo et al. 2008). In addition, decreasing ice cover will reduce sea ice algae production (Rysgaard et al. 1999), with consequences for the pelagic and benthic food webs (Carmack and Macdonald 2002).

Whether the loss of sea ice increases or decreases primary production in the Arctic Ocean is still being debated. However, it is clear that these environmental changes will have great effects on the ecosystem, from altering the patterns of primary production to changing the trophic structure and the elemental cycling pathways (Grebmeier et al. 2006). Recently, Li et al. (2009) reported that the abundance of photosynthetic picoeuk- aryotes (<2 μm diameter) is increasing whereas the abundance of nanophytoplankton (2–20 μm diameter) is decreasing in freshening and warming surface layer in the Canada Basin, since the picoplankton with a large surface area-to-volume ratio have effective acquisition of nutri- ents at low concentration levels in the stratified water column. They suggested that an altered food web based on small size community may be expected if recent changes persist in the Arctic Ocean (Li et al. 2009). Thus, it is important to monitor the relationship between cou- pled climate and ecosystem changes in the Arctic to determine the long-term implications of the Arctic sea ice loss (Arrigo et al. 2008).

The Canada Basin has a characteristic geographically isolated from well-ventilated water of other Arctic Ocean basins (Swift et al. 1997). Recently, this region has been affected considerably by increased ice melting, the Atlantic layer thickening, and a decrease in thickness of the Pacific-

origin halocline (Melling 1998; Macdonald et al. 1999; McLaughlin et al. 2004). Some studies on phytoplankton productivity have been conducted in the Canada Basin, primarily during the summer season (Cota et al. 1996; Gosselin et al. 1997; Lee and Whitledge 2005; Lee et al. 2010). Lee and Whitledge (2005) and Lee et al. (2010) found that there was a distinct biomass accumulation up to 30 times higher at the chlorophyll *a* maximum layer in the Canada Basin. Tremblay et al. (2008) proposed that the subsurface chlorophyll maximum layer in the Arctic Ocean was a primary driver of phytoplankton production with potential importance in biogeochemical fluxes. Thus, it is important to determine whether the phytoplankton in this layer are productive under potentially higher light condi- tions with a decreased sea ice thickness or newly ice-free open ocean in the present and near future.

In this study, we measured the primary productivity of phytoplankton in the Canada Basin during the late summer season, a time period when little information has been published. In addition, we examined potential effects of light enhancement and nitrate enrichment on phytoplank- ton productivity in the chlorophyll *a* maximum layer under ongoing changes in the light regime, caused primarily by sea ice melting in the Arctic Ocean.

Materials and methods

Study area

Sampling was conducted in the Canada Basin from September 17 to October 15, 2009, onboard the Canadian Coast Guard Ice Breaker CCGS *Louis S. St. Laurent*. Pri- mary productivities were measured at selected morning stations for deck incubations. Eleven stations were visited: five stations (Stns CB-2a, 4, 9, 10a, and 11b) in the western part (≥150°W) and six (Stns CABOS, CB-23a, MK-7, CB- 21, 48, and 15/17) in the eastern part (≤140°W) of the Canada Basin (Fig. 1). Most of the bathymetric depths in the productivity stations were quite deep, with a mean of >3,000 m (Table 1). Lengths of daylight depended on both latitudes and dates but during the cruise period, the mean daylight was about 10 h.

Sampling

Vertical profiles of water temperature and salinity were obtained from downcast measurements using a calibrated Seabird SBE-911 CTD profiler (s/n 0756) mounted on a rosette. Water samples were collected with the rosette sampler equipped with 10-L Niskin bottles. Incident pho- tosynthetically active radiation (PAR) was measured con- tinuously during the expedition with a Biospherical

Fig. 1 Locations of productivity stations during 2009 JOIS in the Canada Basin
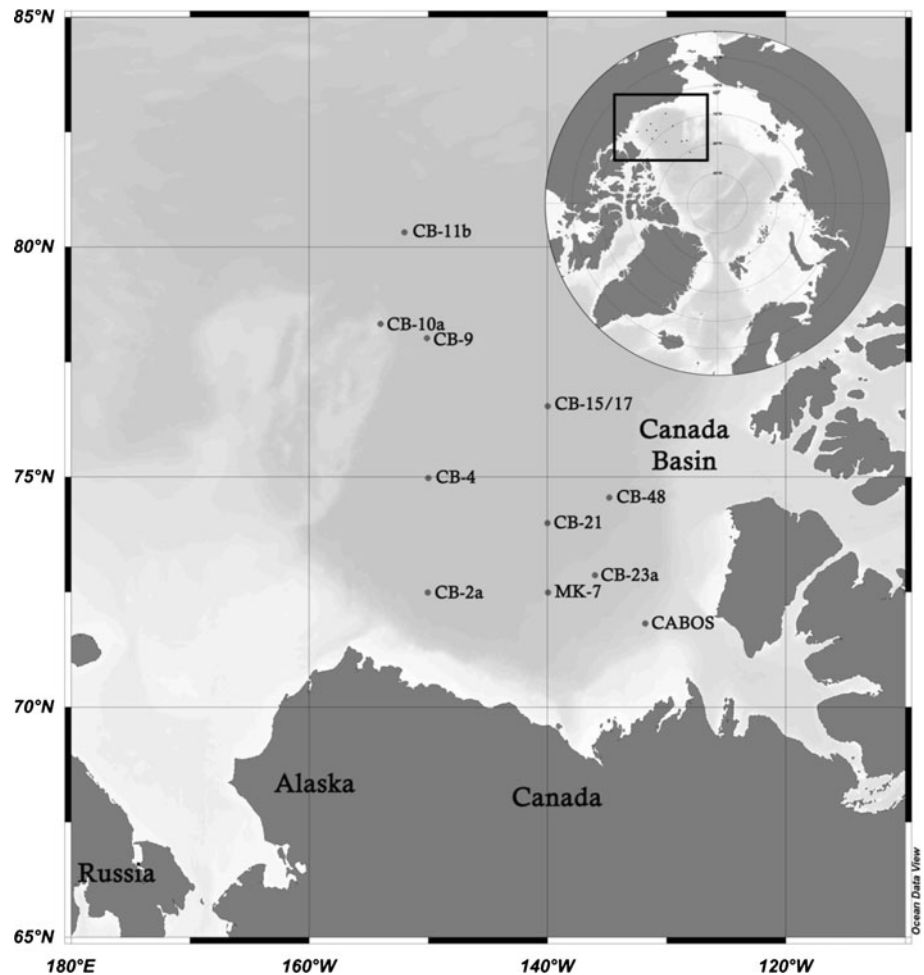
Table 1 Locations, water depths, ice coverage, and the depths of the surface mixed layer and euphotic zone for phytoplankton productivity stations in the Canada Basin in 2009

Station	Location		Water depth (m)	Ice coverage (%)	Surface mixed layer (m)	Euphotic zone (m)
	Latitude (°N)	Longitude (°W)				
CABOS	71.8188°	131.7953°	1,130	0	14	73
CB-23a	72.8677°	136.0057°	2,786	80	25	68
MK-7	72.4908°	139.9517°	3,025	90	20	76
CB-2a	72.4930°	150.0465°	3,691	60	16	70
CB-4	74.9788°	150.0043°	3,825	0	17	69
CB-9	78.0190°	150.1240°	3,825	50	20	68
CB-10a	78.3290°	154.0083°	1,066	90	17	64
CB-11b	80.3147°	152.0092°	3,812	90	15	62
CB-15/17	76.5382°	139.9795°	3,690	100	18	56
CB-48	74.5518°	134.8095°	3,267	90	27	72
CB-21	73.9958°	139.9940°	3,527	80	24	67

Instruments Analog Quantum Reference Sensor (QSR-2200, s/n 20279) next to our incubator. Underwater PAR profiles were obtained after conversion via a Profiling Reflectance and Radiometer (PRR) made by Biospherical Instruments, Inc. (BSI, USA) (Zhao et al. 2010).

Chemical and biological measurements

Seawater samples for dissolved nutrients (nitrate and ammonium) were analyzed immediately onboard after collection, using AutoAnalyzer methods (Barwell-Clarke and

Whitney [1996]). In vivo chlorophyll *a* fluorescence was measured with an in situ fluorometer (Seapoint Sensors, Inc., s/n 2745) connected to the CTD probe. A quadratic polynomial was used to calibrate fluorometer data against extracted chlorophyll *a* measurements (Parsons et al. [1984]) from discrete water samples ($n = 115$; $r^2 = 0.979$). Samples for the extracted chlorophyll *a* measurements were filtered onto glass fiber filters (Advantec; diameter = 25 mm). Chlorophyll *a* concentrations were measured using a Turner Designs model 10-AU field fluorometer.

Carbon and nitrogen uptake rate measurements

In situ carbon and nitrogen uptake rates of phytoplankton were measured from six photic depths (100, 50, 30, 12, 5, and 1%), which determined from the underwater PAR profiles, using a ^{13}C–^{15}N dual tracer technique (Lee and Whitledge [2005]; Lee et al. [2010]). Water samples were screened through a 200-μm Nitex mesh to remove large grazers (Sakshaug [1980]; Carmack et al. [2004]) and taken in polycarbonate incubation bottles (0.5 L). Labeled carbon ($NaH^{13}CO_3$), nitrate ($K^{15}NO_3$), and ammonium ($^{15}NH_4Cl$) substrates were inoculated immediately in the bottles after water sampling. The concentrations of each heavy isotope-enriched (98–99%) solutions were 0.17 mM, 0.22 μM, and 0.04 μM for $^{13}CO_2$, $^{15}NO_3$, and $^{15}NH_4$, respectively. The added ^{13}C concentration was approximately 7–14% (mean: 9%) of the total inorganic carbon in the ambient seawater as determined by titration with 0.01 N HCl during this expedition (Anderson et al. [1999]). The concentrations of added $^{15}NO_3$ and $^{15}NH_4$ were generally 10–120% of the ambient concentrations because they were very low (<0.1 μM) in the water. Although this might elevate the in situ uptake rates of nitrate and ammonium (Garneau et al. [2007]), Lee et al. ([2010]) found no relationship between specific carbon or nitrogen uptake rate and the percent of enriched nutrient isotopes at comparable light levels in their study in the Arctic Ocean.

Along with carbon and nitrogen uptake measurements, we conducted light enhancement and nitrate enrichment experiments with the phytoplankton from the chlorophyll *a* maximum layer, which was located at about 1% light level of surface irradiance, in every productivity station except the nitrate enrichment experiments at stations CB-23a and MK-7 because water samples were not available. For the light enhancement experiments, waters from the chlorophyll *a* maximum depths were distributed into bottles with different light conditions (0.5 L) from 100 to 1% light level (control) with the different mesh screens and inoculated with labeled carbon ($NaH^{13}CO_3$) in each bottle. For the nitrate enrichment experiments, the waters from the chlorophyll *a* maximum depths were placed into different bottles with different nitrate concentrations (0, 1, 5, and 10 μM), and labeled carbon ($NaH^{13}CO_3$) was added.

After inoculation, the water samples were incubated in a water bath on the top deck of the ship for approximately 4 h. The temperature of incubator was monitored and generally similar with in situ surface water temperature (around −1°C). After the incubation, all productivity samples were terminated by low-vacuum (<100 mmHg) filtration onto precombusted (450°C, 4 h) glass fiber filters (Whatman GF/F; diameter = 25 mm); the filters were then rinsed with 0.45-μm-filtered seawater. They were immediately frozen at −20°C until analysis. Upon return to the laboratory at the Korea Polar Research Institute, the filters were treated with HCl fumes overnight to remove carbonate (Hama et al. [1983]). Finally, the abundances of ^{13}C and ^{15}N as well as total amounts of particulate organic carbon (POC) and nitrogen (PON) were determined in the Thermo Finnigan Delta + XL mass spectrometer at the stable isotope laboratory of the University of Alaska, Fairbanks.

Calculations

The measured dark carbon uptake rates were subtracted from carbon uptake rates in each light depth, assuming that the dark uptake rates were from bacterial processes (Gosselin et al. [1997]). However, the nitrogen uptake rates were not subtracted from the dark uptake rates because this is a highly controversial procedure for nitrogen uptake measurements (Smith and Harrison [1991]). The carbon and nitrogen production rates were calculated based on Hama et al. ([1983]) and Dugdale and Goering ([1967]), respectively. Corrections for isotope dilution effects were not applied because of the short incubation time (<6 h; Dugdale and Wilkerson [1986]) and minimal effect on NH_4^+ uptake rates in the Barents Sea (Kristiansen et al. [1994]) and *f*-ratios in the Gulf of St. Lawrence (Tremblay et al. [2000]).

To correct the effects of light attenuation by ice, all integrated carbon productivity values were transformed with the equation presented by Gosselin et al. ([1997]):

$$P_{corrected} = (P_{uncorrected} \times (100 - \emptyset)/100)) + (P_{uncorrected} \times \emptyset)/100 \times E_s/E_o$$

where $P_{corrected}$ and $P_{uncorrected}$ are the integrated productivity values corrected and uncorrected for ice cover, and $\emptyset$ is the percentage of ice cover for each station. E_s/E_o is the light attenuation by the ice and is assumed to the average value (0.11) measured by Gosselin et al. ([1997]). For values from light enhancement and nitrate enrichment experiments, they were not corrected for ice cover and dark uptake rate since we used only specific carbon uptake rates (not integrated productivity) of phytoplankton from the chlorophyll *a* maximum layer for a comparison among themselves under different light and nitrate conditions. To compare the effects of light and nitrate on primary
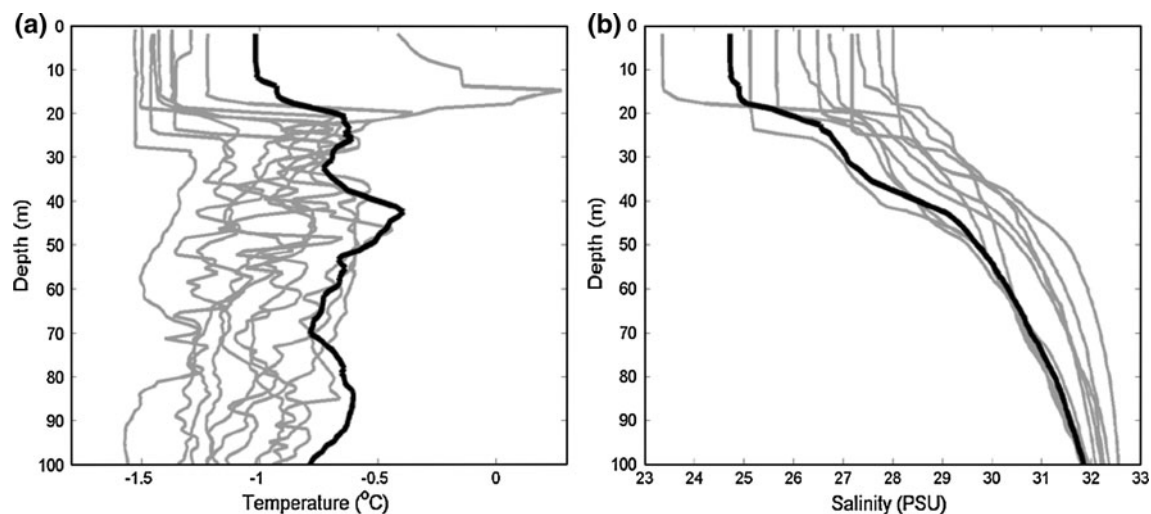
Fig. 2 The vertical structures of temperature (**a**) and salinity (**b**) at all the productivity stations in the Canada Basin in 2009. A single cast (CB-4), representing a typical profile, is overlain in bold

productivity under different sea ice conditions, the productivity stations were simply split into two different groups, defined as ice-free and intermediate (50–60%) regions and ice-heavy (>80%) regions depending on the ice conditions.

Results

Physical condition of study area

Similar to 2008, but quite different from the years prior to 2007, open water extended east almost to 140°W in the center of the Canada Basin (Fig. 1). Of the productivity stations, CABOS and CB-4 were in ice-free regions, and CB-2a and CB-9 were partially covered (50–60%) (Table 1). The rest of the stations were in ice with concentrations of at least 80%. Due to freezing air temperature, new sea ice was formed throughout the cruise.

The temperature and salinity of the upper 100 m are shown in Fig. 2. All surface waters were at the freezing temperature except for the ice-free stations CABOS and CB-4 and had mixed surface waters 12–28 m thick due to wind mixing and convection from brine rejection during sea ice formation. The temperature ranged from −1.6 to 0.4°C with one to two temperature maximums of 0.2–0.5°C between 20 and 50 m (Fig. 2a), resulting from the interplay of low-salinity summer-heated waters from the Pacific and once in the Canada Basin, both summer heating due to solar radiation and winter cooling (Jackson et al. 2010). Salinity in the upper 100 m waters ranged from 23.3 to 32.5 psu (Fig. 2b), with the lowest salinity at the surface due to summer sea ice melt, runoff from both Eurasian and North American rivers, and low-salinity Pacific Summer

Water. Beneath the surface mixed layer, salinity increased with depth, with haloclines of 0.5–4 psu coincident with the thermoclines of the temperature maximums.

### Nutrient and chlorophyll *a* patterns in the water column

Nitrate concentration was mostly depleted (<0.1 μM) in the upper 30 m, in which there existed strong stratifications, but gradually increased from the 30 m depth (Fig. 3a) below the surface mixed layer. Beneath 50 m, nitrate concentration rapidly increased, and between 100 and 150 m, it slowly reached to the nitrate maximum (12–16 μM) in the Pacific Winter Water (data not shown; See Carmack and McLaughlin 2011). In contrast, ammonium concentration was consistently low throughout the water column. The maximum ammonium concentration was 0.5 μM at 40 m.

Chlorophyll *a* concentration from extracted chl *a* measurement was very low (<0.20 mg m^{-3}) throughout the water column above 80 m (Fig. 3b). The chlorophyll *a* concentration at the surface ranged from 0.01 to 0.12 mg m^{-3}, with a mean of 0.05 mg m^{-3} (SD = 0.04 mg m^{-3}). In general, the chlorophyll *a* maximum layer was at a depth of 50-60 m, where the mean chlorophyll *a* concentration was 0.12 mg m^{-3} (SD = 0.06 mg m^{-3}) in this study. During the cruise, the mean chlorophyll *a* concentration integrated from 100 to 1% light depth was 6.03 mg m^{-2} (SD = 1.87 mg m^{-2}).

Carbon and nitrogen productivities

The carbon uptake rates from the surface to 1% light depth ranged from <0.001 to 0.077 mg C m^{-3} h^{-1} (Table 2). Generally, the maximum carbon uptake rates occurred at
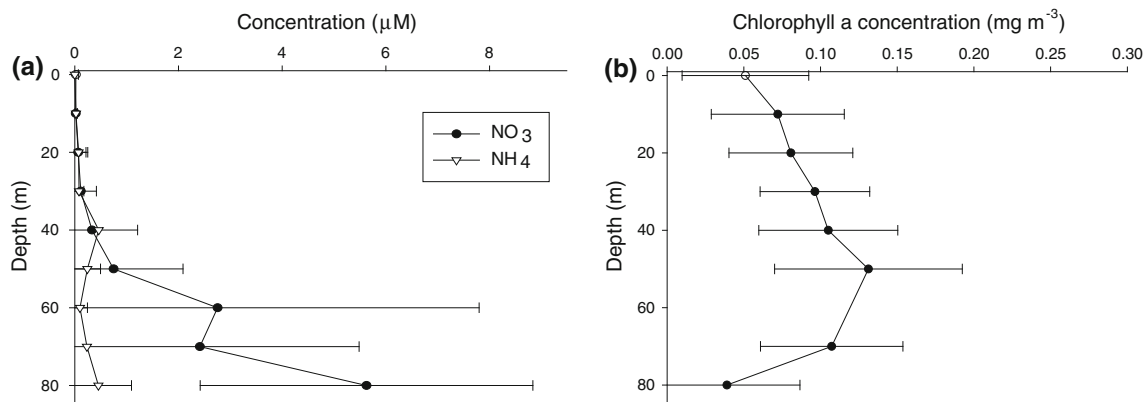
Fig. 3 The vertical structures of NO_3 and NH_4 concentrations (**a**) and chlorophyll *a* concentration (**b**) averaged from all the productivity stations in the Canada Basin in 2009. *Error bars* indicate standard deviations

Table 2 In situ carbon uptake rates (mg C m^{-3} h^{-1}) at different light levels of the phytoplankton productivity stations in the Canada Basin in 2009

Light level (%)	CABOS	CB-23a	MK-7	CB-2a	CB-4	CB-9	CB-10a	CB-11b	CB-15/17	CB-48	CB-21
100	0.077	0.042	0.048	0.067	0.044	0.035	0.071	0.055	0.028	0.053	0.019
50	0.036	0.019	0.020	0.017	0.024	0.019	0.022	0.015	0.014	0.019	0.004
30	0.011	0.013	0.008	0.011	0.017	0.017	0.008	0.006	0.005	0.008	0.001
12	0.005	0.006	0.001	0.004	0.007	0.006	0.002	0.002	0.001	0.005	<0.001
5	0.008	0.003	<0.001	0.003	0.003	0.005	<0.001	<0.001	<0.001	<0.001	–
1	0.004	0.001	<0.001	0.003	0.001	0.003	<0.001	<0.001	<0.001	<0.001	–
P	1.26	0.53	0.20	0.51	0.78	0.46	0.20	0.13	0.09	0.31	0.07
Daily *P*	12.59	5.30	1.97	5.11	7.78	4.64	1.96	1.27	0.86	3.10	0.66
B	10.19	3.80	5.05	4.01	6.29	6.23	7.19	5.20	5.52	8.05	4.85
P/B	1.24	1.39	0.39	1.28	1.24	0.74	0.27	0.24	0.16	0.39	0.14

P is the hourly primary productivity (mg C m^{-2} h^{-1}) integrated from 100 to 1% light level

Daily *P* is the integrated daily primary productivity (mg C m^{-2} day^{-1}). *B* is the integrated chlorophyll *a* concentration (mg chl *a* m^{-2}). *P/B* is the ratio of daily productivity/chlorophyll *a* concentration (mg C (mg chl *a*)$^{-1}$ day^{-1}). (–) indicate not available data

100% light depths of all stations. The carbon uptake rates in the euphotic zone decreased progressively with depth, consistent with the vertical decrease in light in the water column. Primary productivity integrated over the euphotic zone from six light depths ranged from 0.07 to 1.26 mg C m^{-2} h^{-1}, with a mean of 0.41 mg C m^{-2} h^{-1} (SD = 0.36 mg C m^{-2} h^{-1}) after the correction for the effects of ice cover (see the "Materials and methods"). The integrated daily primary productivity was calculated using a 10-h photoperiod per day based on the mean day length recorded during our study. The mean value was 4.1 mg C m^{-2} day^{-1} (SD = 3.6 mg C m^{-2} day^{-1}). The production/biomass ratio ranged from 0.14 to 1.39 mg C (mg chl *a*)$^{-1}$ day^{-1} (Table 2).

The vertical uptake rates of both nitrate and ammonium are shown in Table 3. Most of the maximum nitrate uptake rates occurred at a depth of 100% light level. The vertically integrated nitrate uptakes (uncorrected for irradiance effects according to Smith 1995) ranged from 0.022 to 0.130 mg

NO_3 m^{-2} h^{-1}, with a mean of 0.061 mg NO_3 m^{-2} h^{-1}. In contrast, the maximum ammonium uptake rates occurred primarily at the 5 and 1% light levels, although there was no unique vertical pattern of ammonium uptake rates of phytoplankton in this study (Table 3). The vertically integrated ammonium uptake rates ranged from 0.157 to 0.716 mg NH_4 m^{-2} h^{-1}, with a mean of 0.400 mg NH_4 m^{-2} h^{-1}. The ammonium uptake rates were considerably higher than the nitrate uptake rates at all depths. The vertically integrated uptake of total nitrogen (nitrate + ammonium) ranged from 0.180 to 0.716 mg N m^{-2} h^{-1}, with a mean of 0.451 mg N m^{-2} h^{-1}.

Light enhancement and nitrate enrichment effects on the phytoplankton in the chlorophyll *a* maximum layer

The specific carbon uptake rates of phytoplankton from the chlorophyll *a* maximum layer generally increased as the

Table 3 In situ nitrate and ammonium uptake rates at different light levels of the phytoplankton productivity stations in the Canada Basin in 2009

Light level (%)	CABOS	CB-23a	MK-7	CB-2a	CB-4	CB-9	CB-10a	CB-11b	CB-15/17	CB-48	CB-21
(a) Nitrate uptake rates (mg N–NO$_3$ m^{-3} h^{-1})											
100	0.0021	0.0004	0.0003	0.0007	–	0.0021	0.0029	0.0014	0.0007	0.0014	<0.0001
50	0.0021	0.0003	0.0004	0.0005	–	0.0013	0.0023	0.0007	0.0005	0.0009	–
30	0.0006	0.0004	0.0006	0.0005	–	0.0022	0.0012	0.0005	0.0004	0.0004	–
12	0.0002	0.0003	0.0004	0.0004	–	0.0015	0.0009	0.0003	0.0001	0.0008	–
5	<0.0001	0.0002	0.0001	0.0001	–	0.0009	0.0004	–	–	–	–
1	–	–	0.0001	0.0001	–	<0.0001	–	–	–	–	–
P	0.091	0.038	0.036	0.042	–	0.130	0.101	0.030	0.022	0.063	–
(b) Ammonium uptake rates (mg N–NH$_4$ m^{-3} h^{-1})											
100	0.0049	0.0025	0.0012	0.0028	0.0009	0.0011	0.0040	0.0011	0.0012	0.0013	0.0013
50	0.0056	0.0027	0.0034	0.0045	0.0034	0.0020	0.0032	0.0011	0.0014	0.0010	0.0013
30	0.0016	0.0040	0.0054	0.0045	0.0085	0.0025	0.0020	0.0011	0.0008	0.0012	0.0017
12	0.0027	0.0031	0.0052	0.0055	0.0051	0.0029	0.0038	0.0019	0.0021	0.0012	0.0012
5	0.0055	0.0050	0.0064	0.0052	0.0073	0.0030	0.0015	0.0023	0.0012	0.0041	0.0022
1	–	0.0013	0.0031	0.0018	0.0022	0.0040	0.0029	0.0032	0.0020	0.0015	0.0032
P	0.522	0.522	0.611	0.581	0.716	0.302	0.278	0.170	0.157	0.285	0.262

P is the integrated hourly nitrate or ammonium uptake rate (mg N m^{-3} h^{-1}). (–) indicate not available data

light level increased, although carbon uptake rates at the 100% light level were similar to those at the 50% light level (Fig. 4). The specific carbon uptake rates at the 5% light level were not significantly (*t*-test, $P > 0.05$) different from the values at the control light level (1%). However, the carbon uptake rates in >5% light level were significantly (*t*-test, $P < 0.05$) greater than the rates in the control light level. The average specific carbon uptake rate under higher light levels was 0.0006 h^{-1} (SD = 0.0002 h^{-1}) in the ice-free and intermediate regions, whereas the average uptake rate in the ice-heavy regions was 0.0003 h^{-1} (SD = 0.0001 h^{-1}) (Fig. 4a, b). The specific carbon uptake rates in the ice-free and intermediate regions were significantly (*t*-test, $P < 0.05$) different from those in the ice-heavy regions. In contrast, the specific carbon uptake rates of phytoplankton from the nitrate enrichment experiments were not statistically different (*t*-test, $P > 0.05$), regardless of injected nitrate concentrations (Fig. 5a, b).

Discussion

### Carbon productivity of phytoplankton

In this study, the mean daily carbon productivity was 4.1 mg C m^{-2} (SD = 3.6 mg C m^{-2}) in the Canada Basin in 2009 (Table 2). This is a very low rate compared with those reported from previous studies in the region (Gosselin et al. 1997; Lee and Whitledge 2005; Lee et al. 2010). Gosselin et al. (1997) found that their mean daily carbon

uptake rate was 35.0 mg C m^{-2} in the western Canada Basin. The daily uptake rate (11.3 mg C m^{-2}) estimated by Lee and Whitledge (2005) is about threefold higher than our result. In addition, Lee et al. (2010) reported that the mean daily uptake rate was 59.5 mg C m^{-2}, considerably higher than the rate in this study. The difference in the daily carbon uptake rate between this and the previous studies could have been caused by several factors. Compared with the previous studies conducted from July to early September, our study was carried out from mid-September to mid-October (i.e., early fall). The shorter day length during this study could be part of the reason for the lower daily carbon uptake rate because day length has a pronounced effect on algal growth rate (Smith and Sakshaug 1990). In fact, the daily rates from Lee and Whitledge (2005) and Lee et al. (2010) were estimated based on a 24-h day length in the Canada Basin during July–August. On the other hand, the daily rate from this study was based on a mean 10-h day length during the cruise. Above all, we suggest that strong seasonal variation in the phytoplankton biomass and photosynthetic rate caused the large difference in daily carbon productivity between this and the previous studies. In this study, the chlorophyll *a* concentrations were extremely low, with a mean of 0.05 and 0.12 mg chl *a* m^{-3} at the surface and chlorophyll *a* maximum layer, respectively (Fig. 3b). In comparison, the mean concentrations in the study of Lee et al. (2010) were 0.1 mg chl *a* m^{-3} at the surface and 0.5 mg chl *a* m^{-3} in the chlorophyll *a* maximum layer, which are twofold to fourfold higher than those in this study. In addition, the ratio of carbon production to chl *a* concentration (P/B ratio) in our
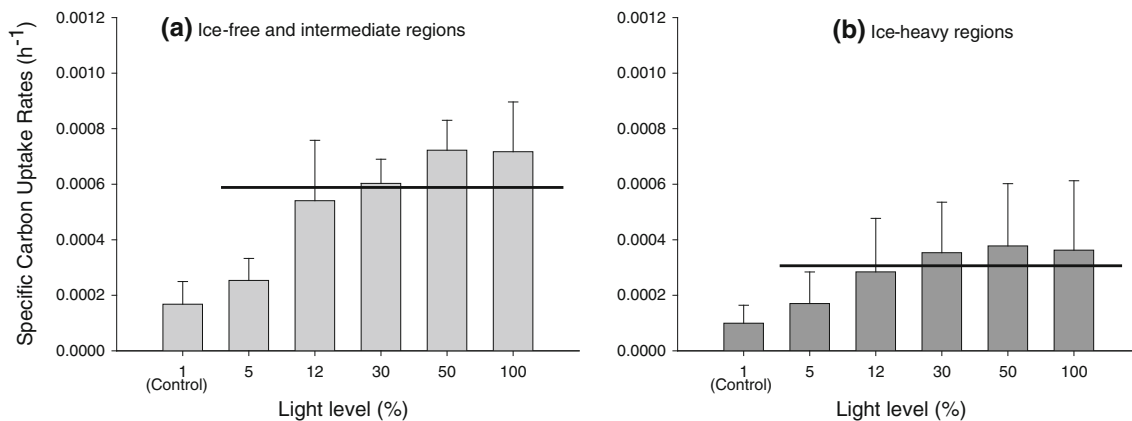
Fig. 4 Specific carbon uptake rates of phytoplankton in the chlorophyll *a* maximum layer under different light conditions. **a** Ice-free and intermediate regions (50–60% ice coverage) ($n = 4$) and **b** ice-heavy regions (>80% ice coverage) ($n = 7$). Values shown are means ± SD. *Black lines* show mean values of all uptake rates in each region. Control: 1% light levels where sampled waters were actually collected
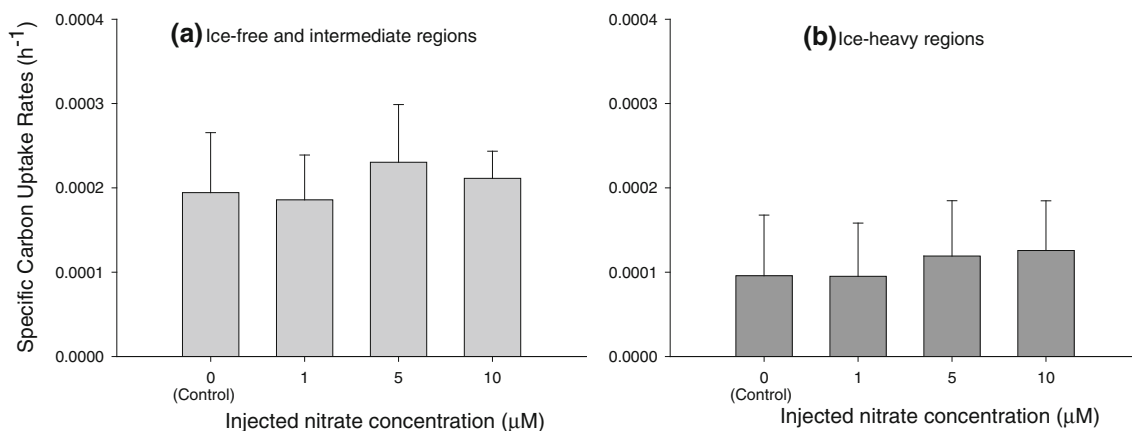
Fig. 5 Specific carbon uptake rates of phytoplankton in the chlorophyll *a* maximum layer under different additions of nitrate concentrations. **a** Ice-free and intermediate regions (50–60% ice coverage) ($n = 4$) and **b** ice-heavy regions (>80% ice coverage) ($n = 5$). Values shown are means ± SD

study ranged from 0.14 to 1.39, with a mean of 0.68 mg C (mg chl *a*)$^{-1}$ day^{-1} (Table 2), which is considerably lower than the range (from 5.54 to 16.67) in polar waters reported by Harrison and Cota (1991). This indicates that phytoplankton during this late summer season produced less carbon per unit chlorophyll *a*. English (1961) and Pautzke (1979) found that there was strong seasonal variation in phytoplankton biomass and photosynthetic rate in the Arctic Ocean. In fact, phytoplankton biomass in July and August was fivefold to tenfold higher than that in September and October, and productivity also decreased sharply after mid-August in the central Arctic Ocean (English 1961). In addition, Pautzke (1979) reported that the *P/B* ratio of phytoplankton in the Canada Basin was highest in July and declined in August and September.

Without considering other factors such as sea ice conditions and inter-annual variations of phytoplankton productivity in the Canada Basin, Lee et al. (2010)

measured the highest average daily production rate (59.5 mg C m^{-2} day^{-1}) of phytoplankton during late June to mid-July, whereas Gosselin et al. (1997) obtained the second-highest average rate (35.0 mg C m^{-2} day^{-1}) during late July to early August, although the productivity stations from the two studies were mostly in the western part of the Canada Basin. Later in the summer season, Lee and Whitledge (2005) found a much lower rate (11.3 mg C m^{-2} day^{-1}) during mid-August to early September, and then we obtained the lowest average rate (4.1 mg C m^{-2} day^{-1}) in this study from mid-September to mid-October. This seasonal pattern of phytoplankton productivity in the Canada Basin is almost identical to that reported by English (1961) in the central Arctic Ocean.

The previous studies roughly estimated the annual carbon production rate of phytoplankton, assuming a 120-day growing season and the same daily production rates over the season in the Arctic Ocean (Gosselin et al. 1997; Lee

and Whitledge 2005; Lee et al. 2010) because of logistic problems in measuring the primary productivity of phytoplankton over the whole growing season in a year. The annual carbon production rates in the Canada Basin were 4.2, 1.4, and 7.1 g C m^{-2} for Gosselin et al. (1997), Lee and Whitledge (2005), and Lee et al. (2010), respectively. Thus, the annual production might be overestimated or underestimated, depending on the season in which measurements were conducted. For example, the estimated annual carbon production of phytoplankton ranged from 0.1 to 1.5 g C m^{-2} (mean = 0.5 g C m^{-2}), based on our measurement during the late summer season in the Canada Basin in 2009. This value is about one order of magnitude lower than the production (7.1 g C m^{-2}) reported by Lee et al. (2010) during late June to mid-July. Thus, it is important to consider strong seasonal variation in phytoplankton productivity in estimating annual production in the Arctic Ocean. Based on the four different daily productivity measurements (Gosselin et al. 1997; Lee and Whitledge 2005; Lee et al. 2010; this study) of phytoplankton in each season, the annual production in the Canada Basin was estimated to be approximately 3.3 g C m^{-2}, which is less than half of the value (7.1 g C m^{-2}) reported by Lee et al. (2010).

Nitrogen productivity of phytoplankton

The total daily nitrogen productivity (NO$_3$ + NH$_4$ uptake rates) in the Canada Basin in 2009 ranged from 1.80 to 7.16 mg N m^{-2}, with a mean of 4.51 mg N m^{-2}, based on the assumption that the nitrate and ammonium uptake occurred during only a 10-h photoperiod per day. This value is comparable with that of Pautzke (1979) in the northern Canada Basin (5.0 mg N m^{-2} day^{-1}). However, this value is lower than the value (20.2 mg N m^{-2} day^{-1}) reported by Lee et al. (2010), but higher than that (0.8 mg N m^{-2} day^{-1}) of Lee and Whitledge (2005). Carbon/nitrogen (C/N) ratios of the particulate material have been used to evaluate phytoplankton nutrient status, although temperature and light may also affect the ratios (Smith and Sakshaug 1990). For example, high C/N ratios of the particulate material in the low irradiance zone below the ice are often indicative of nitrogen deficiency (Smith and Sakshaug 1990). In our study, the mean C/N uptake ratio was 1.6 g:g, which is much lower than those of Lee and Whitledge (2005) and Lee et al. (2010) (3.9 and 13.8, respectively), suggesting little nitrogen stress for their growth at the sampling time in this study (Smith and Sakshaug 1990; Lee et al. 2010). Thus, the difference in the nitrogen productivities between this and the previous studies might be explained by the different degree of nitrogen limitation as well as seasonal and regional variations, such as carbon productivity, as discussed above. However, this low C/N

ratio might be affected by the potential effect of substrate enhancement on nitrogen uptake rates (Garneau et al. 2007). The substrate enhancement effects on nitrate and ammonium uptake rates were estimated by the methodology from MacIsaac and Dugdale (1972). To calculate the effects, we used the K_s (half-saturation constants) and V_{max} (the maximum rate of nutrient uptake) values reported in surface waters of the eastern Canadian Arctic (Smith and Harrison 1991). The rates of nitrate and ammonium uptake were overestimated by about 35 and 70%, respectively, although some of the overestimated ammonium uptake rate may have been balanced by a potential isotope dilution effect (Kanda et al. 1987), which ranged from 5 to 11% in this study. Another potential explanation for the low C/N ratio is that heterotrophic bacteria may take up a large part of the total dissolved inorganic nitrogen in the euphotic zone of the Arctic waters (Fouilland et al. 2007). Moreover, the nitrogen uptake rates with no correction for the percentage of ice coverage (see "Materials and methods") could induce the low C/N ratio.

An ecologically important parameter of nitrogen uptake is the f-ratio, which is the ratio of nitrate uptake to total nitrogen uptake (Eppley and Peterson 1979). This parameter can be used to evaluate the relative importance of ammonium and nitrate as sources of nitrogen for the cell (Dugdale and Goering 1967). In our study, the mean f-ratio was 0.22 (SD = 0.17). This value is quite comparable with 0.25 obtained by Lee and Whitledge (2005) in the Canada Basin, but rather lower than the value (0.36) of Lee et al. (2010). Like the variation in the carbon productivity mentioned above, the f-ratio might have a seasonal variation (highest in June to July and low thereafter) in the Arctic Ocean. It is also noted that a considerable utilization of ammonium, compared with nitrate, was shown at the low light depths with relatively high ambient nitrate concentrations. This might be because of more active ammonium uptake than nitrate uptake under low light conditions in the Canada Basin during the sampling season in 2009, because nitrate uptake by phytoplankton is more strongly coupled to light than ammonium uptake (Dortch and Postel 1989). In fact, the average f-ratio decreased with depth in this study (data not shown), although nitrate was more available to the phytoplankton at deep layers than at the surface.

Effects of light enhancement and nitrate enrichment on phytoplankton productivity under different sea ice conditions

Irradiance, because of its extreme seasonal variation, is considered to be a major environmental factor controlling phytoplankton growth in polar region (Smith and Sakshaug 1990). However, some recent studies have suggested that nitrogen supply is the primary factor controlling the

production of primary producers in the seasonally ice-covered Arctic Ocean (Tremblay et al. 2002, 2006; Codispoti et al. 2009).

Our experiments showed that light enhancement increased carbon productivity of the phytoplankton in the chlorophyll *a* maximum layer (Fig. 4), while nitrate enrichment did not lead to a significant increase in productivity (Fig. 5). The productivity increase under higher light levels indicates that the phytoplankton in this layer is light-limited, and thus their productivity can be increased by increasing light conditions. In contrast, no significant increase in the productivity by nitrate addition indicates that the phytoplankton growth in the chlorophyll *a* maximum layer was not limited by nitrate. Similarly, Lee and Whitledge (2005) found that light can be a major factor limiting phytoplankton productivity in the chlorophyll *a* maximum layer, whereas nutrients are a main limiting factor at the surface, based on different C/chl *a* ratio. However, the carbon uptake of phytoplankton might not be stimulated by the addition of major inorganic nutrients because of our short-term incubations (T. Whitledge, pers. comm.).

The phytoplankton productivity in the chlorophyll *a* maximum layer responded differently to the increased light level depending on the different sea ice conditions. The specific carbon uptake rates in the ice-free and intermediate regions were significantly (t-test, $P < 0.05$) higher than those in the ice-heavy regions. These different responses of the phytoplankton to the sea ice conditions can be explained by light availability, because the interception of light by sea ice cover causes poor light conditions for phytoplankton productivity in the water column under the sea ice cover (Rysgaard et al. 1999; Sakshaug 2004). Thus, the phytoplankton under the heavier sea ice regions are acclimated to relatively lower light conditions, whereas those under lower ice concentrations would have been exposed to higher irradiance (Hill et al. 2005). Normally, low-light-adapted algae have a lower P/B ratio than do those adapted to high-light conditions (Smith and Sakshaug 1990). In this study, the P/B ratios (mean = 1.12) in the ice-free and intermediate regions (50–60%) were significantly (t-test, $P < 0.05$) higher than those (mean = 0.43) in the ice-heavy regions (>80%). These results suggest that the phytoplankton under the heavy-ice regions were more shade-adapted and thus responded more slowly to the increased light conditions than the phytoplankton under the lower sea ice coverage regions.

Summary and conclusions

This study reported that phytoplankton productivity was very low because of low biomass and photosynthetic activity of phytoplankton during the late summer season in the Canada Basin in 2009. From light enhancement and nitrate enrichment experiments, we found that the phytoplankton in the chlorophyll *a* maximum layer was limited primarily by light and that their productivity could be increased by greater light conditions, although their responses differed depending on the sea ice conditions above. Based on our result, we expect that ongoing sea ice melting could cause some increases in carbon production of the phytoplankton in the chlorophyll *a* maximum layer in the ice-covered Arctic Ocean. However, our findings from light enhancement and nitrate enrichment experiments might be different in other seasons since the experiments were executed in late Arctic growth season.

In fact, light penetration through the sea ice can be greater and deeper within the water column under current less sea ice thickness than the previous conditions (Perovich and Richter-Menge 2009; Lee et al. 2010). This change in the light condition could produce a well-developed chlorophyll maximum layer at deeper depths due to a more active phytoplankton productivity with potentially increasing light levels. However, this scenario assumes that the major change induced by sea ice melting is light, because the major effect of sea ice is a marked reduction in the quantity of PAR at the surface of the water column below the sea ice (Smith and Sakshaug 1990; Lee et al. 2010). Recently, McLaughlin and Carmack (2010) found that the chlorophyll maximum and nutricline were deepening in the Canada Basin interior because anticyclonic Ekman pumping and downwelling in the Beaufort Gyre were increased as a result of recent increase in inputs of sea ice meltwater and ice-drift velocities (references therein). They suggested that light limitation play an important role in determining the depth at which primary production occurs as a consequence of the deepening chlorophyll maximum and nutricline in the Canada Basin (McLaughlin and Carmack 2010). However, they did not consider a potential increase in light availability under recent reduction of sea ice extent and thickness in the Arctic Ocean (Lee et al. 2010). Thus, to better understand the processes and changes in Arctic primary production under ongoing environmental changes, we need to obtain more seasonal and annual data under a variety of conditions in different regions with considering more factors such as algal physiology and community structure, as well as light dependence to sea ice and nutrient dynamics at the chlorophyll *a* maximum layer in the Arctic Ocean.

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