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Latitudinal carbon productivity in the Bering and Chukchi Seas during the summer in 2007

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ABSTRACT

The Bering and Chukchi Seas are well known to be one of the most productive regions in the world. However, these regions have many climate induced-environmental changes over the last decades. Whether these changes enhance or reduce the overall primary production is important in major ecosystems of the Bering and Chukchi Seas. During the *Oshoro Maru* cruise in 2007 as an IPY (International Polar Year) event of Hokkaido University, nitrogen and carbon uptake rates of phytoplankton were measured at 15 productivity stations in the Bering and Chukchi Seas, using a ^{13}C–^{15}N dual isotope tracer technique. The 2007 mean daily carbon uptake rates of phytoplankton were 0.20 and 0.16 g C m^{-2} d^{-1}, respectively in the southern and northern Bering Sea. These rates are lower than those reported previously in the regions mainly because of the well-known strong seasonal variation of the carbon uptake rate between May (bloom period) and July (post-bloom period; this cruise). In the Chukchi Sea, the mean uptake rates from this study were 1.63 and 0.18 g C m^{-2} d^{-1}, respectively in the central and northern regions which are noticeably lower than those reported previously in decades ago. Based on the enhancement experiments, light is an important controlling factor for the phytoplankton productivity rates in the Bering and Chukchi Seas during the cruise period as indicated by higher carbon uptake rates with increased light conditions. Accordingly, nutrients might not be the controlling factor, given there were only minimal increases of primary productivity rates with higher nitrate concentrations.

1. Introduction

The Bering and Chukchi Seas, which are seasonally sea ice-covered, are an important gateway to the Western Arctic Ocean. These seas are among the most productive regions in the world (Sambrotto et al., 1984; Springer and McRoy, 1993) and have been found to support large number of fishes, marine mammals, and sea birds as well as benthic animals (Springer et al., 1987; Grebmeier and McRoy, 1989). However, over the last decade many climate induced-environmental changes are reported in these regions (Overland and Stabeno, 2004; Grebmeier et al., 2006; Bluhm and Gradinger, 2008). One of the most dramatic changes is the reduced maximum extent and earlier melting of seasonal pack ice in the Bering and Chukchi Seas (Overland and Stabeno, 2004; Serreze et al., 2007). These recent changes in climate and ice conditions could change patterns and the total amount of primary production and consequently the production at higher trophic levels. Grebmeier et al. (2006) reported a major ecosystem shift in the northern Bering Sea because of shifts in regional and atmospheric and hydrographic forcing. In addition, Schell (2000) previously suggested that seasonal primary productivity has decreased by 30–40% in the northern Bering Sea based on a retrospective assessment of primary productivity estimated from stable carbon isotope ratios along the baleen plates of Western Arctic Bowhead whales. Subsequently, Lee et al. (2007) found two or three times lower primary production rates in their study than those previously reported in the Chukchi Sea. One of their hypotheses was that primary production had decreased in the northern Bering and Chukchi Seas and are consistent with the recent lower production rates in the northern Bering Sea (Lee et al., 2012). They reported that the recent lower phytoplankton production in the northern Bering and Chukchi Seas is partly related to a decrease in the phytoplankton biomass transported from lower latitudes such as the central Bering Sea shelf (Lee et al., 2012) by the northward flow in the northern Bering Sea into the Chukchi Sea through Bering Strait (Danielson et al., 2006). However, it is still controversial whether climate change conditions enhance or reduce the overall primary production in the Bering

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and Chukchi Seas as well as the Arctic Ocean. It is very important to know the current status of primary producers in the Bering and Chukchi Seas, since these regions are the conduit of Pacific waters into the entire Arctic Basin and the responses of phytoplankton production to current environmental conditions could be different in different regions in the sub-Arctic seas as well as Arctic Ocean. The objectives of this study were to measure recent carbon and nitrogen productivity of phytoplankton and determine which environmental factors are important for controlling the primary productivity processes in the Bering and Chukchi Seas.

2. Materials and methods

The data were collected from onboard the training ship *Oshoro Maru* as an IPY (International Polar Year) event of Hokkaido University. The dates of the cruise were 25 July-3 August for the first leg in the Bering Sea and 5–14 August for the second leg in the Chukchi Sea in 2007 (Table 1). The primary productivity experiments were executed at 15 selected CTD (conductivity–temperature–depth) stations (Fig. 1) during daylight hours.

2.1. Inorganic nutrient and chlorophyll-a concentration analysis

Water samples for nutrient analysis were collected from six light depths (100, 50, 30, 12, 5, and 1% penetration of the surface photosynthetically active radiation, PAR) determined with a LI-COR underwater 4π light sensor, lowered with a CTD/rosette sampler (Sea-Bird SBE 9). Nutrient samples (100 ml) were frozen at −20 °C without filtering for later analysis of nitrate, ammonium, silicate, and phosphate concentrations using an automated nutrient analyzer (ALPKEM RFA model 300) in the home laboratory, following methods of Whitledge et al. (1981). The accuracies of the nutrient concentration measurements were ± 0.02 μM for phosphate and nitrite and 0.1 μM for nitrate, ammonium, and silicate. The chlorophyll-a (chl-a) concentration data from the cruise were generously provided by Dr. Toru Hirawake (Hokkaido University, Japan).

2.2. Carbon and nitrogen productivity measurements

At selected stations, hourly carbon and nitrogen uptake rates were measured at the six light depths (100, 50, 30, 12, 5, and 1%), using a ^{13}C–^{15}N dual isotope tracer technique previously reported in the northern Bering and Chukchi Seas (Lee et al., 2007, 2012). In brief, seawater samples at each light depth were transferred from the Niskin bottles to acid-cleaned polycarbonate incubation bottles (1 L) covered with stainless steel screens to simulate each light depth. 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. The bottles were incubated in a deck incubator under natural light conditions cooled with surface seawater for 4–5 h. The incubations were terminated by filtration through pre-combusted (450 °C) GF/F filters (24 mm). The filters were immediately preserved at −20 °C until mass spectrometric analysis (Finnigan Delta+XL) at the stable isotope laboratory of the University of Alaska Fairbanks, US. Measured dark uptake rates were subtracted from light carbon uptake values with the assumption that they were due to bacterial processes (Gosselin et al., 1997).

Table 1
Locations and bottom depths of the productivity stations in 2007.

Name	Time	Latitude (°N)	Longitude (°W)	Bottom depth (m)	1% light depth (m)
B04	25 July	56.000	166.994	126	35
B10	26 July	56.494	168.005	115	34
B14	27 July	56.998	166.996	75	35
B21	28 July	57.497	167.004	70	41
B26	30 July	62.000	174.004	60	42
B40	31 July	62.908	173.283	70	40
B42	01 Aug	62.956	166.768	30	–
RC03	13 Aug	67.101	168.834	50	12
C04	06 Aug	67.534	168.837	50	20
C09	07 Aug	68.192	167.234	48	37
C14	08 Aug	68.611	168.563	50	30
C16	09 Aug	70.003	167.992	50	40
C22	10 Aug	70.583	166.026	45	35
C26	11 Aug	70.898	164.563	35	27
C29	12 Aug	69.509	166.002	40	31

In order to determine important controlling factors for phytoplankton growth extra incubations under different light and nutrient conditions were conducted. Since it was difficult to sample surface water using the CTD rosette sampler, the surface waters were sampled at the upper part of the water column which was about at 50% light depths at productivity stations. The water depths $(\text{mean} \pm \text{S.D.} = 3.5 \pm 1.1\ \text{m})$ were not very different from the surface. The waters were incubated under different light conditions (100, 50, 30, 12, 5, and 1%) manipulated by different stainless steel screens. For the nutrient enrichment experiments, the waters from the same depths were placed into different bottles with different nitrate concentrations injected (1, 2, 4, 7, 11, 15, and 20 μM) and incubated under simulated *in situ* light conditions. Before the incubations, the labeled carbon ($NaH^{13}CO_3$) was added into each bottle. The treatments after the 4–5 h incubations were same as normal primary productivity experiments above.

3. Results

3.1. Nutrient and chlorophyll a concentrations on an areal basis

Nutrient concentrations integrated in the euphotic depths from 100 to 1% light depth were shown in Fig. 2. The mean values of phosphate concentrations were 18.7 mmol m^{-2} (S.D.= $\pm$ 5.5 mmol m^{-2}) and 20.8 mmol m^{-2} (S.D.= $\pm$ 5.5 mmol m^{-2}), respectively in the southern and the northern Bering Sea. Similarly, the concentrations in the Chukchi Sea were 22.8 mmol m^{-2} (S.D.= $\pm$ 6.7 mmol m^{-2}) and 21.0 mmol m^{-2} (S.D.= $\pm$ 14.0 mmol m^{-2}), respectively for the central and northern Chukchi Sea. In contrast, the mean values of silicate concentrations were somewhat different in the Bering and Chukchi seas although they were not statistically significant. The concentrations were 218.5 mmol m^{-2} (S.D.= $\pm$ 92.2 mmol m^{-2}) and 520.5 mmol m^{-2} (S.D.= $\pm$ 449.6 mmol m^{-2}), respectively in the southern and northern Bering Sea, whereas 75.5 mmol m^{-2} (S.D.= $\pm$ 68.2 mmol m^{-2}) and 91.1 mmol m^{-2} (S.D.= $\pm$ 36.5 mmol m^{-2}), respectively for the central and northern Chukchi Sea. The highest silicate concentration was 1032.4 mmol m^{-2} at B40 station where the Anadyr Water (salinity $>$ 32.5) was observed (data not shown). The mean ammonium concentrations were 19.9 (S.D.= $\pm$ 37.4 mmol m^{-2}), 20.8 (S.D.= $\pm$ 17.9 mmol m^{-2}), 7.6 (S.D.= $\pm$ 3.3 mmol m^{-2}), and 18.4 (S.D.= $\pm$ 21.3 mmol m^{-2}), respectively in the southern and northern Bering Sea and the central and northern Chukchi Sea. The nitrate concentrations in the southern and the northern Bering Sea were 86.1 mmol m^{-2} (S.D.= $\pm$ 38.0 mmol m^{-2}) and 49.2 mmol m^{-2} (S.D.= $\pm$ 50.3 mmol m^{-2}), respectively, whereas 52.7 mmol m^{-2} (S.D.= $\pm$ 11.5 mmol m^{-2}) and 11.2 mmol m^{-2} (S.D.= $\pm$ 9.8 mmol m^{-2}) in the central and northern Chukchi Sea. At regional basis, the nutrient concentrations of the four different regions in the Bering and Chukchi seas were averaged at each depth from 100 to 1% light depth to check vertical profiles of nutrients (Fig. 3). Generally, major nutrients were low at surface and relatively high at 1% light depth.

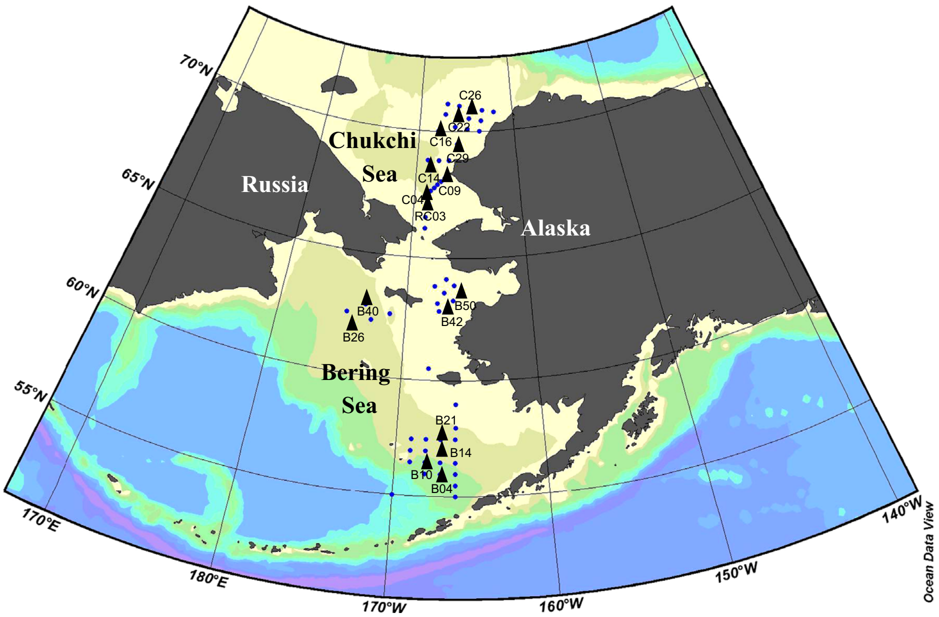

Fig. 1. Sampling stations from *Oshoro-Maru* cruise in the Bering and Chukchi Seas in 2007. The stations for primary production phytoplankton were marked by black triangles.

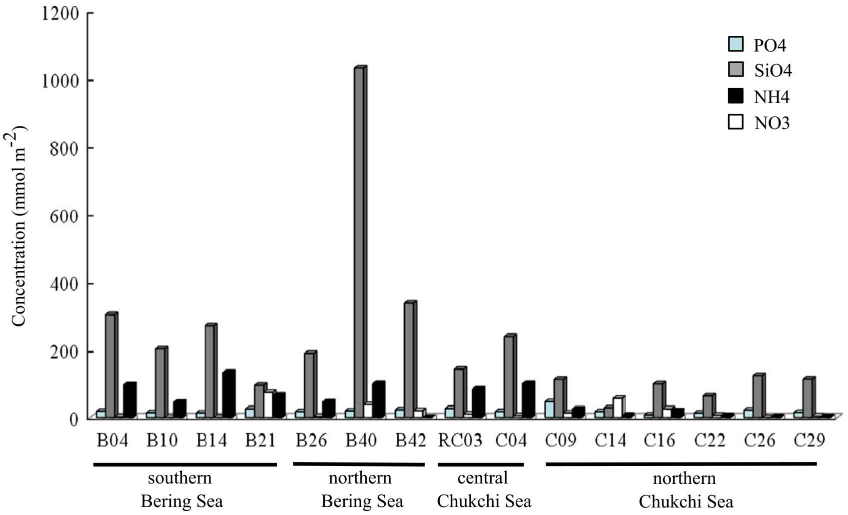

Fig. 2. Inorganic major nutrient concentrations integrated from 100 to 1% light level at all productivity stations.

Chl-a concentrations integrated across the euphotic depths was generally low (<40.0 mg m^{-2}) during the cruise period except stations RC03 and C04 in the central Chukchi Sea where the concentrations were 227.3 and 408.7 mg m^{-2}, respectively (Fig. 4). The averaged chl-a concentrations were 23.0 mg m^{-2} (S.D.= ±8.5 mg m^{-2}), 33.1 mg m^{-2} (S.D.= ±12.0 mg m^{-2}), 318.0 mg m^{-2} (S.D.= ±128.3 mg m^{-2}), and 26.0 mg m^{-2} (S.D.= ±4.9 mg m^{-2}), respectively in the southern and northern Bering Sea and the central and northern Chukchi Sea in 2007. Normally, chl-a concentration was highest at 5 or 1% light depth (Fig. 5a) where the nutrient concentrations were relatively high (Fig. 3).

3.2. *Carbon and nitrogen uptake rates on an areal basis*

Most of the maximum carbon uptake rates occurred at the 100% light depths except stations B04, B26 and C04 during this study (Table 2; Fig. 5b). Carbon uptake rates from the surface to 1% light depth ranged from <0.01 to 36.26 mg C m^{-3} h^{-1} with a mean of 1.64 mg C m^{-3} h^{-1} (S.D.= ±4.93 mg C m^{-3} h^{-1}) in the Bering and Chukchi seas. The average rates of carbon uptake at each light depth were significantly (*t*-test, $p<0.05$) higher in the central Chukchi Sea (Fig. 5b). The mean depth of the euphotic zone was 37.8 m (S.D.= ±3.5 m) for productivity stations in the Bering Sea, whereas the euphotic zone was 29.0 m (S.D.= ±9.3 m) in the Chukchi Sea (Table 1).

Integrated hourly carbon uptake rates ranged from 10.1 to 17.3 mg C m^{-2} h^{-1} with a mean of 13.0 mg C m^{-2} h^{-1} (S.D.= ±3.1 mg C m^{-2} h^{-1}) and 6.4 to 15.7 mg C m^{-2} h^{-1} with a mean of 10.2 mg C m^{-2} h^{-1} (S.D.= ±4.9 mg C m^{-2} h^{-1}) in the southern and northern Bering Sea, respectively (Fig. 6). In comparison, the ranges of uptake rates in the Chukchi Sea ranged from 100.3 to 116.4 mg C m^{-2} h^{-1} with a mean of 108.3 mg C m^{-2} h^{-1} (S.D.= ±11.5 mg C m^{-2} h^{-1}) and 6.0 to 16.3 mg C m^{-2} h^{-1} with a mean of 11.7 mg C m^{-2} h^{-1} (S.D.= ±4.7 mg C m^{-2} h^{-1}), respectively for the central and northern regions.

Uptake rates of nitrate and ammonium had no discernable trends with decreasing light intensity at depth (Tables 3 and 4). The maximum uptake rates for nitrate and ammonium on each

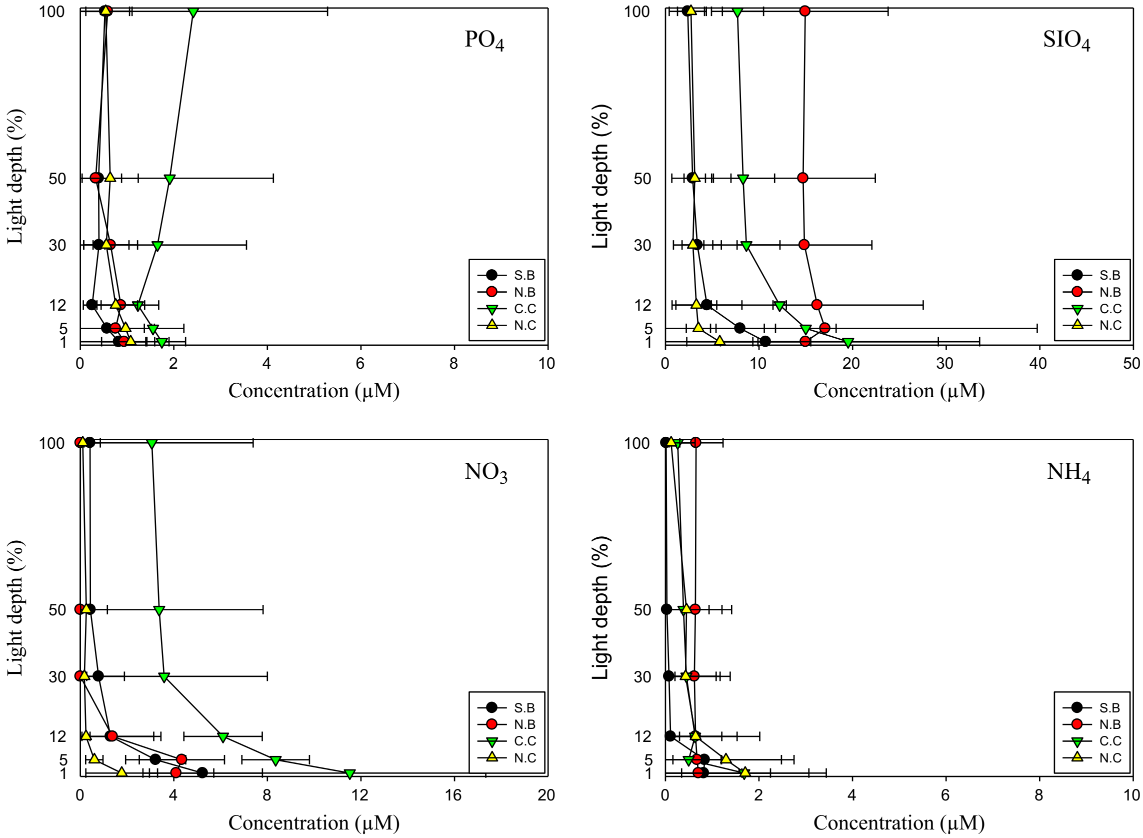

Fig. 3. Vertical profiles of major nutrient concentrations averaged from each region. S. B: Southern Bering Sea, N. B: Northern Bering Sea, C. C: Central Chukchi Sea, and N. C: Northern Chukchi Sea.

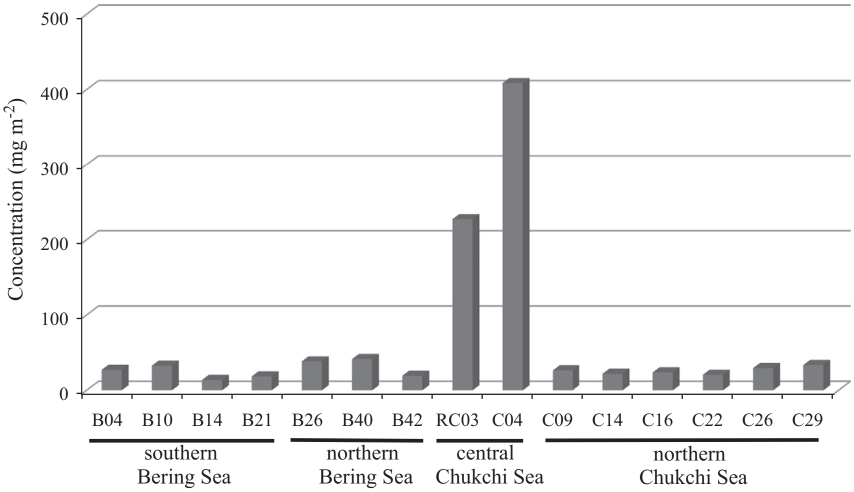

Fig. 4. Chl-a concentrations integrated from 100 to 1% light level at all productivity stations.

station occurred over the full range of light depths of the productivity stations (Fig. 5c and d), not mainly at 100% light depths such as the carbon uptake rate. The nitrate uptake rates of phytoplankton ranged from <0.01 to 4.35 mg N m^{-3} h^{-1} (mean ± S.D. $= 0.27 \pm 0.79$ mg N m^{-3} h^{-1}), whereas ammonium uptake rates ranged from <0.01 to 3.51 mg N m^{-3} h^{-1} (mean ± S.D. $= 0.23 \pm 0.48$ mg N m^{-3} h^{-1}) in the Bering and the Chukchi Seas. The ranges of vertically integrated nitrate and ammonium uptake rates were from 0.21 to 46.90 mg N m^{-2} h^{-1} (mean ± S.D. $= 4.96 \pm 12.14$ mg N m^{-3} h^{-1}) and 0.12 to 18.83 mg N m^{-2} h^{-1} (mean ± S.D. $= 6.17 \pm 6.83$ mg N m^{-3} h^{-1}) in the Bering and the Chukchi Seas. The mean uptake rates of total nitrogen (nitrate+ammonium) were 1.65 mg N m^{-2} h^{-1} (S.D. $= \pm 1.08$ mg N m^{-2} h^{-1}), 12.60 mg N m^{-2} h^{-1} (S.D. $= \pm 9.27$ mg N m^{-2} h^{-1}), 45.24 mg N m^{-2} h^{-1} (S.D. $= \pm 32.69$ mg N m^{-2} h^{-1}), and 5.36 mg N m^{-2} h^{-1} (S.D. $= \pm 2.38$ mg N m^{-2} h^{-1}), respectively in the southern and northern Bering Sea and the central and northern Chukchi Sea (Fig. 7).

3.3. Light and nutrient enhancement effects on carbon uptake rates

Light and nutrient enhancement experiments were executed at 5 productivity stations in the Bering Sea and 4 productivity stations in the Chukchi Sea in 2007 to determine whether nitrogen (nitrate in this study) or light exerts the most direct control on the

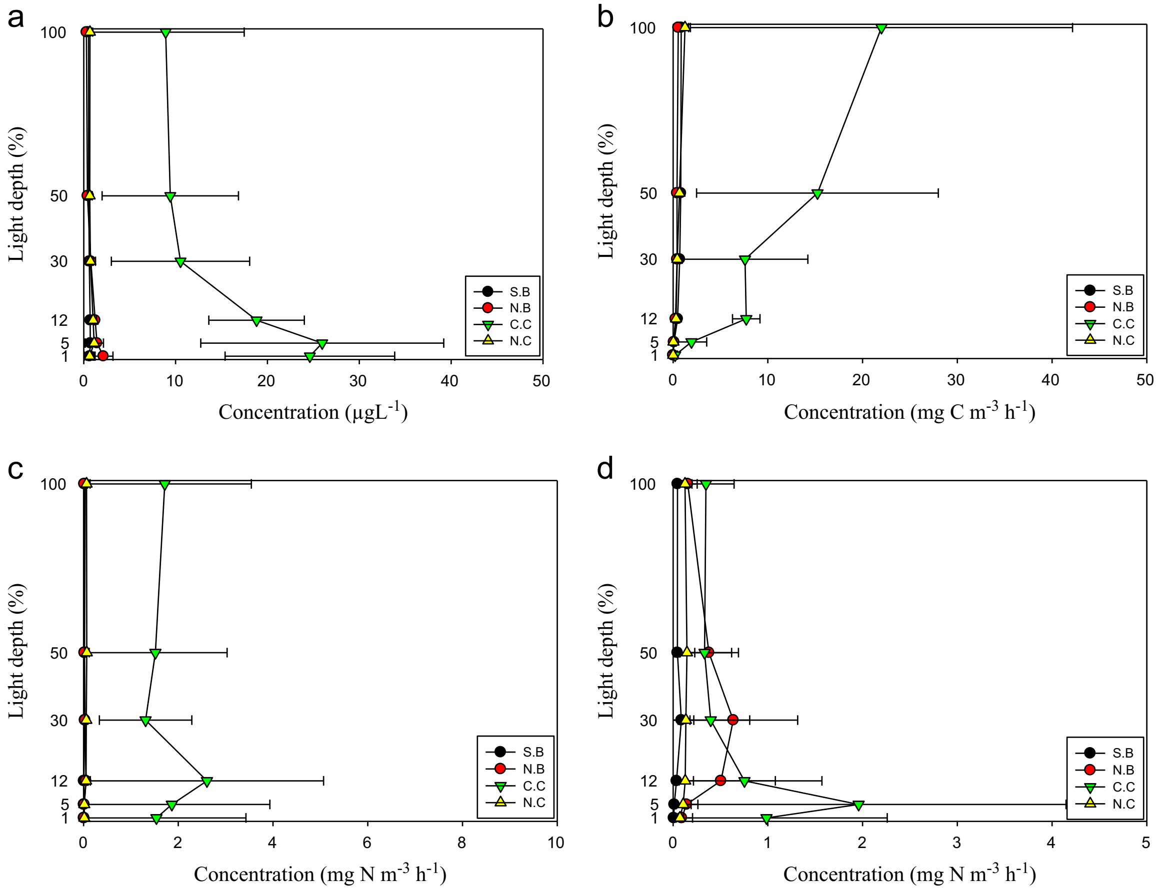

Fig. 5. Vertical profiles of chl-a concentration (a), carbon uptake rate (b), nitrate uptake rate (c), and ammonium uptake rate (d) averaged from each region. S. B: Southern Bering Sea, N. B: Northern Bering Sea, C. C: Central Chukchi Sea, and N. C: Northern Chukchi Sea.

Table 2
Carbon uptake rates (mg C m^{-3} h^{-1}) from different light depth at the productivity stations in 2007.

Light depth (%)	B04	B10	B14	B21	B26	B40	B42	RC03	C04	C09	C14	C16	C22	C26	C29
100	0.707	0.882	0.932	0.885	0.544	0.552	0.520	36.260	7.737	1.369	1.701	1.017	0.666	1.216	1.571
50	0.762	0.880	0.818	0.794	0.528	0.367	0.339	24.259	6.217	0.717	0.684	0.675	0.441	0.880	0.630
30	0.642	0.824	0.652	0.661	0.603	0.156	0.502	12.281	2.904	0.906	0.266	0.522	0.251	0.574	0.135
12	0.544	0.627	0.146	0.589	0.408	0.043	0.316	6.694	8.748	0.569	0.182	0.505	0.124	0.328	0.125
5	0.113	0.269	0.004	0.031	0.052	0.088	–	0.805	3.077	0.019	0.038	0.032	0.027	0.038	0.014
1	0.001	0.015	0.004	0.003	0.004	0.006	–	0.038	0.391	0.009	0.016	0.003	0.003	–	0.005

phytoplankton productivity. The carbon uptake rates of phytoplankton increased as light levels increased in the Bering and Chukchi Seas (Fig. 8). In detail, the carbon uptake rates of phytoplankton had maxima at 50% light level at most of the productivity stations except B50 in the Bering Sea, whereas they had maxima at 100% light level at most of the stations except C09 in the Chukchi Sea. The maxima specific carbon uptake rates (without considering biomass) ranged from 0.004 to 0.008 h^{-1} (mean ± S.D. = 0.006 ± 0.002 h^{-1}) in the Bering Sea, whereas 0.006 to 0.038 h^{-1} (mean ± S.D. = 0.016 ± 0.015 h^{-1}) in the Chukchi Sea. In contrast to the results from light enhancement there were no distinct increases in the carbon uptake rates of phytoplankton under higher nitrate concentrations compared to the low ambient nitrate conditions (Fig. 9).

4. Discussion and conclusions

In general, concentrations of phosphate and ammonium were low, whereas silicate concentration was relatively high in the Bering and Chukchi Seas during the cruise period in 2007. Nitrate concentration was undetectable in the euphotic water column at most of the productivity stations.

Based on a 15-h photo period (Hansell and Goering, 1990) and hourly carbon uptake rates measured in this study, the mean daily carbon uptake rates of phytoplankton were 0.20 and 0.16 g C m^{-2} d^{-1}, respectively in the southern and northern Bering Sea, 2007. Rho and Whitledge (2007) found strong seasonal and spatial variations in the daily carbon uptake rates in the southeastern Bering Sea. The rates in the regions excluding open ocean were minimal in July (Rho and Whitledge, 2007). Their average range in July was from 0.27 to 0.77 C m^{-2} d^{-1} which is higher than our mean uptake rate in the southern Bering Sea from this study. In the northern Bering Sea, our mean rate is much lower than those (0.79–1.35 C m^{-2} d^{-1}) recently reported by Lee et al. (2012). This is probably because of the strong seasonal variation of the carbon uptake rate in the northern Bering Sea. In fact, their measurements were collected in late May and early June, 2007. The rate (0.16 C m^{-2} d^{-1}) in late July during a non-bloom period in the northern Bering Sea is approximately one order lower than a

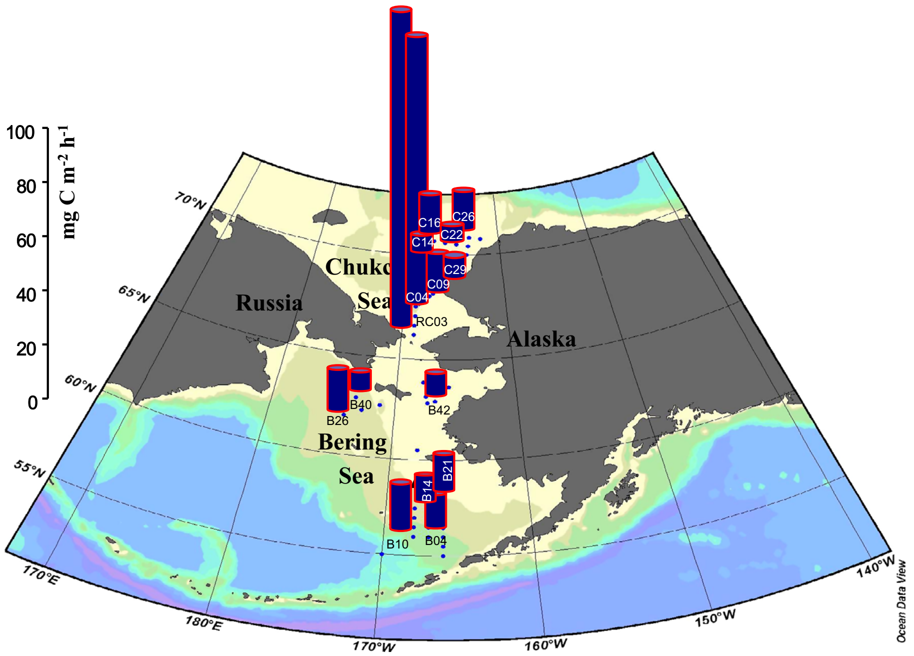

Fig. 6. Integrated hourly carbon uptake rates in the Bering and Chukchi Seas in 2007.

Table 3
Nitrate uptake rates (mg N m^{-3} h^{-1}) from different light depths at the productivity stations in 2007.

Light depth (%)	B04	B10	B14	B21	B26	B40	B42	RC03	C04	C09	C14	C16	C22	C26	C29
100	0.106	0.017	0.012	0.012	0.020	0.008	0.009	3.008	0.423	0.121	0.005	0.030	0.032	0.007	0.188
50	0.035	0.018	0.026	0.004	0.023	0.022	0.011	2.588	0.444	0.106	0.010	0.093	0.036	0.029	0.136
30	0.045	0.025	0.015	0.013	0.015	0.005	0.074	2.000	0.619	0.060	0.008	0.065	0.037	0.070	0.106
12	0.009	0.010	0.004	0.003	0.029	0.017	0.107	0.865	4.347	0.020	0.011	0.054	0.035	0.093	0.105
5	0.002	0.005	0.006	0.004	0.019	0.010	–	0.401	3.327	0.015	0.007	0.035	0.005	0.008	0.018
1	0.003	0.006	0.004	0.003	0.007	0.016	–	0.205	2.875	0.020	0.005	0.015	0.007	–	0.024

Table 4
Ammonium uptake rates (mg N m^{-3} h^{-1}) from different light depths at the productivity stations in 2007.

Light depth (%)	**B04**	**B10**	**B14**	**B21**	**B26**	**B40**	**B42**	**RC03**	**C04**	**C09**	**C14**	**C16**	**C22**	**C26**	**C29**
100	0.070	0.043	0.020	0.053	0.082	0.114	0.268	0.557	0.137	0.091	0.119	0.065	0.236	0.048	0.192
50	0.085	0.055	0.011	0.031	0.033	0.642	0.458	0.534	0.131	0.050	0.236	0.145	0.127	0.070	0.250
30	0.054	0.073	0.004	0.217	0.018	0.523	1.364	0.688	0.106	0.041	0.150	0.166	0.074	0.105	0.276
12	0.024	0.053	0.001	0.065	0.024	0.350	1.141	1.331	0.175	0.068	0.212	0.059	0.064	0.106	0.260
5	0.001	0.004	0.001	0.045	0.056	0.226	–	0.409	3.506	0.029	0.164	0.251	0.060	0.057	0.077
1	0.002	0.002	0.001	0.022	0.009	0.171	–	0.085	1.887	0.028	0.079	0.130	0.053	–	0.073

bloom rate (1.35 C m^{-2} d^{-1}) in late May, 2007 (Lee et al., 2012), although the carbon uptake rates were measured only at 3 stations in late July during this cruise. This difference in the carbon uptake rate between bloom and non-bloom periods is much higher in the northern Bering Sea than in the southeastern Bering Sea shelf where bloom rates were 2–4 times higher than non-bloom rates (Rho and Whitledge, 2007). Previous studies suggest that the northern Bering Sea is a relatively high productivity region in the Arctic Ocean (Hansell and Goering, 1990; Springer and McRoy, 1993; Springer et al., 1996). However, Lee et al. (2012) found recently two or three times lower primary production rates than previous results reported in the northern Bering Sea. In fact, their lower production rates coincided with the decline of benthic biomass and sediment oxygen uptake related to a decrease in the carbon flux in the northern Bering Sea in late 1990s and early 2000s (Grebmeier et al., 2006).

The highest chl-a concentrations integrated from surface to 1% light depth were found in the central part of the Chukchi Sea during the summer in 2007 where the chl-a concentrations were about one order higher than those in other regions (Fig. 4). Consistently, the carbon uptake rate of phytoplankton was one order higher in the central part of the Chukchi Sea than other regions. Previous studies had observed high rates of primary productivity in the region because of high nutrients-loaded Anadyr Water originating along the Bering Shelf break (Coachman et al., 1975; Sambrotto et al., 1984; Springer and McRoy, 1993; Lee et al., 2007). Sambrotto et al. (1984) estimated an annual production of 324 g C m^{-2}, while Hansell et al. (1993) calculated 576–720 g C m^{-2} for the annual production in this region based on nitrate utilization. The annual production estimated by Springer and McRoy (1993) was within their ranges (470 g C m^{-2}). These production rates are unusually large considering the high latitude Arctic location (Sambrotto et al., 1984). However, Lee et al. (2007) recently found much lower rates in the region than those estimated previously based on the *in situ* data from 2002 to 2004. Although only two values of carbon uptake

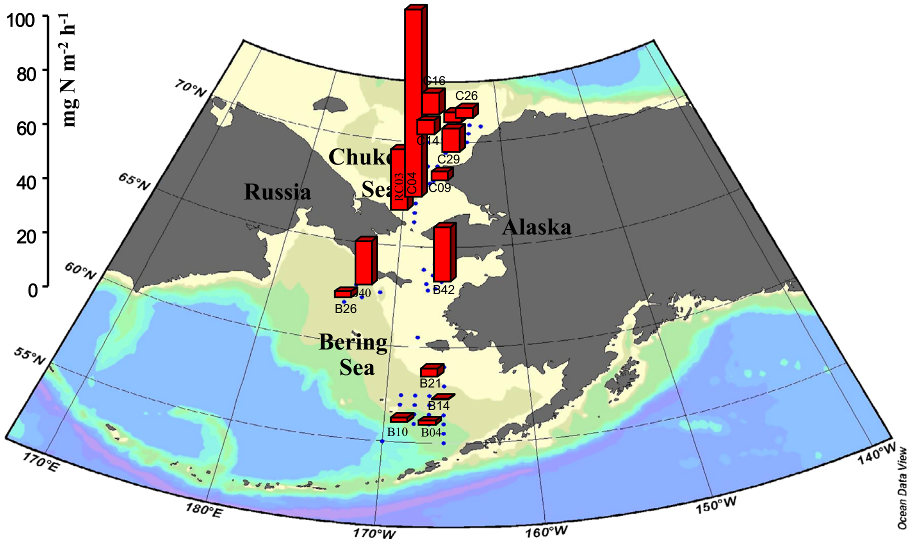

Fig. 7. Integrated hourly nitrogen (nitrate+ammonium) uptake rates in the Bering and Chukchi Seas in 2007.

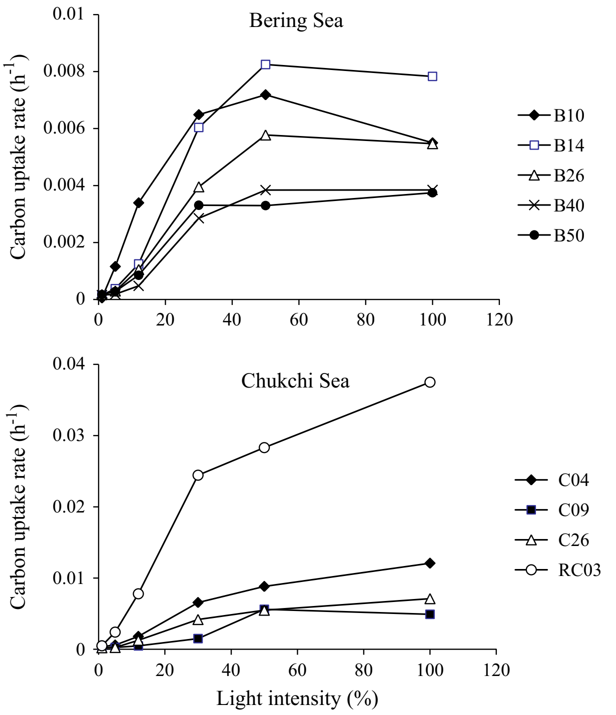

Fig. 8. Carbon uptake rates of phytoplankton under different light conditions in the Bering and the Chukchi Seas in 2007.

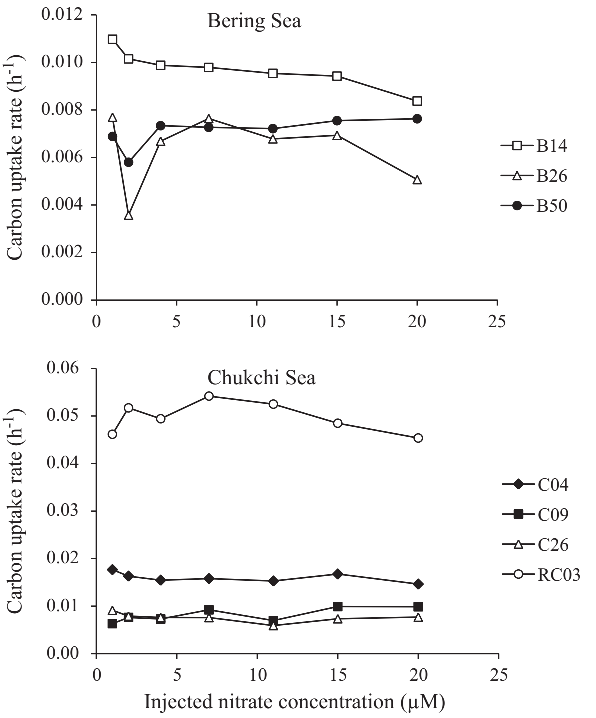

Fig. 9. Carbon uptake rates of phytoplankton under different nitrate concentrations in the Bering and the Chukchi Seas in 2007.

rates were available from this study, the mean daily carbon uptake rate was 1.63 g C m^{-2} d^{-1} in the central Chukchi Sea. This daily carbon uptake rate is somewhat higher than that (1.38 g C m^{-2} d^{-1}) measured recently by Lee et al. (2007) during the similar growing season in August. Previous studies showed much higher rates ranging from 3.0 to 4.7 in the central Chukchi Sea (Hameedi, 1978; Springer and McRoy, 1993). Furthermore, the daily carbon uptake rate (mean ± S.D. = 0.18 ± 0.07 g C m^{-2} d^{-1}) averaged from the rest of the stations in the northern Chukchi Sea is slightly higher than that (mean ± S.D. = 0.16 ± 0.16 g C m^{-2} d^{-1}) reported by Lee et al. (2007) mainly based on the 2004 RUSALCA (**RUS**sian–**A**merican **L**ong-term **C**ensus of the **A**rctic) cruise. The lower productivity in the Chukchi Sea is different from the results of Pabi et al. (2008). They found a recent increase in total annual production from 1998 to 2006 in the Chukchi Sea, based on remotely sensed chl-a concentrations. However, the chl-a concentrations estimated by remote sensing images can be overestimated especially in shelf regions such as the Chukchi Sea because of influence of river discharge and resuspended materials. In conclusion, the carbon uptake rates from this study are considerably lower than those reported previously in the central and northern Chukchi Sea (Hameedi, 1978; Sambrotto et al., 1984; Springer and McRoy, 1993; Hansell et al., 1993), which is a consistent result with that from Lee et al. (2007). One of their hypotheses for the recent lower productivity in the Chukchi Sea is that the apparent difference between their and previous studies might be resulting from large annual and geochemical variations (Lee et al., 2007). The consistent result from this study might prove that the hypothesis could be ruled out from their plausible explanations for the recent lower productivity in the Chukchi Sea.

In contrast to the chl-a concentrations and carbon uptake rates, the nitrogen uptake rates in the northern Bering Sea were relatively higher than those in the southern Bering Sea and northern Chukchi Sea although the central Chukchi Sea had still the highest nitrogen uptake rate (Fig. 7). Based on a 15-h photo period and the hourly uptake rates, the mean daily uptake rates of total nitrogen were 0.03 g N m^{-2} d^{-1} (S.D. = ± 0.02 mg N m^{-2} d^{-1}), 0.19 g N m^{-2} d^{-1} (S.D. = ± 0.14 g N m^{-2} d^{-1}), 0.68 g N m^{-2} d^{-1} (S.D. = ± 0.49 mg N m^{-2} d^{-1}), and 0.08 g N m^{-2} d^{-1} (S.D. = ± 0.04 g N m^{-2} d^{-1}), respectively in the southern and northern Bering Sea and the central and northern Chukchi Sea. The averaged daily uptake rate of total nitrogen in the northern Bering Sea in this study was approximately half of the bloom rates (0.35 g N m^{-2} d^{-1}) in late May, 2007 reported by Lee et al. (2012). This difference in the nitrogen uptake rates between bloom and non-bloom periods is considerably lower than the one order of magnitude difference in the carbon uptake rate in the northern Bering Sea. The carbon uptake rate of phytoplankton appears to be reduced more than the nitrogen uptake rate between the bloom and non-bloom periods.

The daily nitrogen uptake rate in the central Chukchi Sea was about 2 times higher in this study (0.68 g N m^{-2} d^{-1}) than that (0.35 g N m^{-2} d^{-1}) reported in Lee et al. (2007) although the carbon uptake rate was slightly higher in this study. In fact, the average ratios of assimilated carbon and nitrogen uptake rates (C/N ratio) were 3.9 and 5.6, respectively in this and their studies, respectively. The lower C/N ratio suggests relatively less nitrogen limitation of phytoplankton in this study than Lee et al. (2007). The mean *f*-ratio (nitrate uptake rate/nitrate+ammonium uptake rate) of phytoplankton was highest in the central Chukchi Sea followed by the southern Bering Sea (Fig. 10). The averaged *f*-ratios of phytoplankton were 0.43 (S.D. = ± 0.28) and 0.72 (S.D. = ± 0.15), respectively, in the northern Bering Sea and central Chukchi Sea (Fig. 10). The *f*-ratio in the northern Bering Sea in this study was somewhat lower than those (0.74 and 0.65, respectively, in mid May–early June and early June–mid June, 2007) reported by Lee et al. (2012) in the region. In comparison, the *f*-ratio in the central Chukchi Sea in this study was almost identical with that (0.73) calculated from Lee et al. (2007). The high *f*-ratios in the central Chukchi Sea and southern Bering Sea indicate that the total production of the phytoplankton was supported largely by nitrate as a nitrogen source. In fact, Lee et al. (2009) found a high incorporation of carbon into proteins by the phytoplankton in the central Chukchi Sea, which indicates that the phytoplankton have no nitrogen limitation and are in a physiologically healthy condition. Although ambient nitrate concentrations were very low in water columns during this cruise, these regions are well known to be supplied by relatively higher nutrient concentrations of Anadyr and Bering Shelf waters than those of Alaskan Coastal waters (Sambrotto et al., 1984; Grebmeier et al., 1988; Springer and McRoy, 1993; Lee et al., 2007).

Although the carbon uptake rates increased under higher light conditions, light intensity where the maxima uptake rates occurred were larger in the Chukchi Sea (100%) than the Bering Sea (50%). In fact, the euphotic depth was significantly (*t*-test, $p < 0.05$) deeper in the Bering Sea than the Chukchi Sea (Table 1) which indicates relatively more light available to phytoplankton in the Bering Sea. POC (particulate organic carbon)/chl-a concentration ratios from our measurements showed a consistent result. Although they were not statistically different, the averaged POC/chl-a concentration ratio of phytoplankton was higher at the productivity stations in the Bering Sea (mean ± S.D. = 193.6 ± 78.5) than the Chukchi Sea (mean ± S.D. = 121.9 ± 106.6) during our cruise period in 2007. This indicates that phytoplankton had better light conditions in the Bering Sea than in the Chukchi Sea during the study period. Previous studies showed that the strong current from topographic conditions in the narrow and shallow Bering Strait enhances mixing of the water column (Coachman and Shigaev, 1992; Zeeman, 1992) and thus probably increases suspended materials from bottom as well as mixing nutrients back into the upper layer as it passes through the strait. Those suspended materials can reduce the light intensity through the water column and thus reduce the euphotic depth.

In contrast, the carbon uptake rates of phytoplankton from the Bering and Chukchi seas showed no increased rates under enriched nitrate conditions although the rates oscillated slightly up and down at different nitrate concentrations. This suggests that phytoplankton productivity rates were not limited by ambient nitrate concentrations at the sampling depth (50% light depth) in the Bering and Chukchi Seas. This observation may not be the case for all of the phytoplankton from the Chukchi Sea, because the nitrate concentrations were not totally depleted (0.06 to 7.29 μM) at the water depths in the enhancement experiment stations despite low ambient nitrate concentrations. However, it is surprising that there was no increase in the carbon uptake rates of phytoplankton from the Bering Sea under enriched nitrate conditions since the ambient nitrate concentrations were almost undetectable (0.02 μM) at the productivity stations. Currently, we do not have a viable explanation for that. However, we might need to consider longer incubation times to allow enough time to produce an increase trend in the carbon uptake rates of phytoplankton responding to enriched

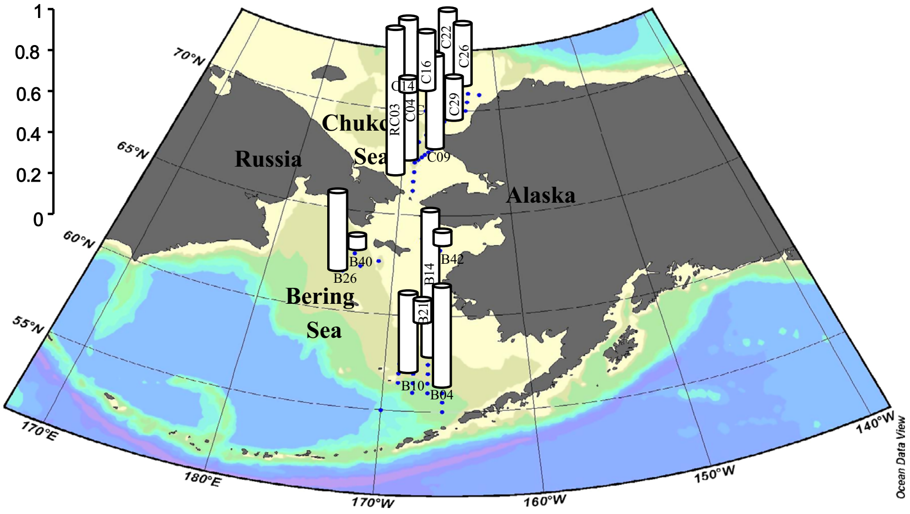

Fig. 10. *f*-ratios in the Bering and Chukchi Seas in 2007.

nutrients (nitrate in this study) because the phytoplankton respond faster to light than nutrients.

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