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Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea

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Abstract

Cruises to Bering Strait and the Chukchi Sea in US waters from late June in 2002 to early September in 2004 and the Russian–American Long-term Census of the Arctic (RUSALCA) research cruise in 2004 covered all major water masses and contributed to a better understanding of the regional physics, nutrient dynamics, and biological systems. The integrated concentration of the high nitrate pool in the central Chukchi Sea was greater in this study than in previous studies, although the highest nitrate concentration (~22 μM) in the Anadyr Water mass passing through the western side of Bering Strait was consistent with prior observations. The chlorophyll-*a* concentrations near the western side of the Diomede Islands ranged from 200 to 400 mg chl-*a* m^{-2} and the range in the central Chukchi Sea was 200–500 mg chl-*a* m^{-2} for the 2002–2004 *Alpha Helix* (HX) cruises. Chlorophyll-*a* concentrations for the 2004 RUSALCA cruise were lower than those from previous studies. The mean annual primary production of phytoplankton from this study, using a ^{13}C–^{15}N dual-isotope technique, was 55 g C m^{-2} for the whole Chukchi Sea and 145 g C m^{-2} for the plume of Anadyr–Bering Shelf Water in the central Chukchi Sea. In contrast, the averages of annual total nitrogen production were 13.9 g N m^{-2} (S.D. = ±16.2 g N m^{-2}) and 33.8 g N m^{-2} (S.D. = ±14.1 g N m^{-2}) for the Chukchi Sea and the plume, respectively. These carbon and nitrogen production rates of phytoplankton were consistently two-or three-fold lower than those from previous studies. We suggest that the lower rates in this study, and consequently more unused nitrate in the water column, were caused by lower phytoplankton biomass in the Bering Strait and the Chukchi Sea. However, we do not know if the lower rate of production from this study is a general decreasing trend or simply temporal variations in the Chukchi Sea, since temporal and geographical variations are substantially large and presently unpredictable.

Keywords: Primary production; Phytoplankton; Carbon; Nitrogen; Bering Strait; Chukchi Sea

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1. Introduction

Bering Strait is the only conduit of water masses and organic matter between the North Pacific and Arctic Oceans. The mean annual transport through Bering Strait is about 0.8 Sv (Coachman and Aagaard, 1988; Roach et al., 1995). The basic driving force of this flow is a ~0.5 m height difference between the Bering Sea and the Arctic Ocean (Coachman et al., 1975; Coachman and Shigaev, 1992). The transport through the strait has a pronounced seasonal cycle with a summer

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maximum and a winter minimum and large inter-annual variations (Coachman and Aagaard, 1988; Woodgate et al., 2005). The observed strong variability in the northward flow is caused mainly by the regional wind conditions (Coachman et al., 1975).

The three different water masses passing northward through Bering Strait are Anadyr Water (AW), Bering Shelf Water (BSW), and Alaska Coastal Water (ACW). These are distinguished primarily by their salinity differences (Coachman et al., 1975; Aagaard, 1987). ACW has a low salinity (<approximately 31.8 psu) due to fresh water input from rivers flowing into the southeastern Bering Sea combined with Alaskan Coastal Water from the Gulf of Alaska (Coachman et al., 1975; Stabeno et al., 1995). BSW, which is colder (0–3 °C) and more saline (31.8–32.5 psu) than ACW, originates primarily in the middle shelf south of St. Lawrence Island. AW originates along the Bering Shelf break and is a high salinity (32.5–33.0 psu) northern branch of the Bering Slope Current (Coachman et al., 1975; Kinder et al., 1975; Coachman and Shigaev, 1992). Of these water masses, AW supplies the Chukchi continental shelf with high nutrients that promote abundant phytoplankton growth throughout the summer and transports oceanic zooplankton onto the shallow northern shelf and into the Chukchi Sea through the western Bering Strait (Sambrotto et al., 1984; Springer et al., 1989; Springer and McRoy, 1993). Usually, the ratio of the three different water masses is 6:3:1, respectively, for AW, BSW, and ACW (Coachman et al., 1975). However, the ratio varies seasonally and inter-annually, mostly due to local influences of the wind (Coachman et al., 1975). Consequently, the location and direction of these water masses moving through the strait have a strong influence on the physical conditions, nutrient concentrations, and phytoplankton activity observed in this important gateway to the Arctic Ocean (Springer, 1988; Springer and McRoy, 1993).

The Bering Strait region and Chukchi Sea are important feeding grounds for the western Arctic bowhead whale population, as indicated by stable carbon isotope ratios (Schell et al., 1989; Lee et al., 2005), as well as for many seabird populations (Springer et al., 1987). The high pelagic primary productivity provides the basis for enhanced local secondary production, and the huge biomass of zooplankton transported into the region in the Anadyr Current contributes a major portion of the energy used at higher trophic levels (Springer et al., 1989).

In addition to the pelagic environment, a strong pelagic–benthic coupling of biological processes sustains some of the highest benthic faunal biomass in the Arctic, and consequently supports large populations of benthic-feeding marine mammals and seabirds at higher trophic levels in the food chain (Grebmeier and McRoy, 1989; Highsmith and Coyle, 1992; Springer et al., 1987; Springer and McRoy, 1993). Based on the recent decline from 1977 to 1997 in average $\delta^{13}C$ values on the baleen plates of bowhead whales, which reflects their food sources, Schell (2000) suggested that seasonal primary productivity has decreased by 30–40% in the northern Bering Sea and presumably the Chukchi Sea over several decades.

The quantity of nutrients and organic matter flowing through this major passage into the Chukchi Sea and subsequently, into the Arctic Ocean must be determined to understand the present functioning of the Arctic system, especially that related to production and biogeochemical processes. Input through Bering Strait is of particular interest as it is the dominant nutrient source and a major source of buoyancy to the upper layer in the Arctic Ocean (Jones and Anderson, 1986; Guay and Falkner, 1997; Cooper et al., 1997; Coachman and Aagaard, 1988). An accurate assessment of nutrient concentrations and fluxes north of Bering Strait in the Chukchi Sea is essential in assessing and understanding the status and health of the Bering and Western Arctic ecosystems, as well as the changing contribution to regional and global issues of production cycles and biogeochemical cycling (Walsh et al., 1989).

We conducted a productivity study in the region every year from early June 2002 to early September 2004 as a part of the long-term monitoring of the effect of inflow into the Arctic Ocean via Bering Strait to advance our understanding of physical structures, nutrient dynamics, and biological systems in the strait and Chukchi Sea (Fig. 1). This study covered mainly US waters in those regions, however, the Russian–American Long-term Census of the Arctic (RUSALCA) program, which is a joint US–Russian research program, provided the ideal sampling across all major water masses including territorial waters of the Russian Federation in the strait and Chukchi Sea in 2004 (Fig. 2). In this paper, we report results of this work in 2002–2004. Our primary objective was to quantify

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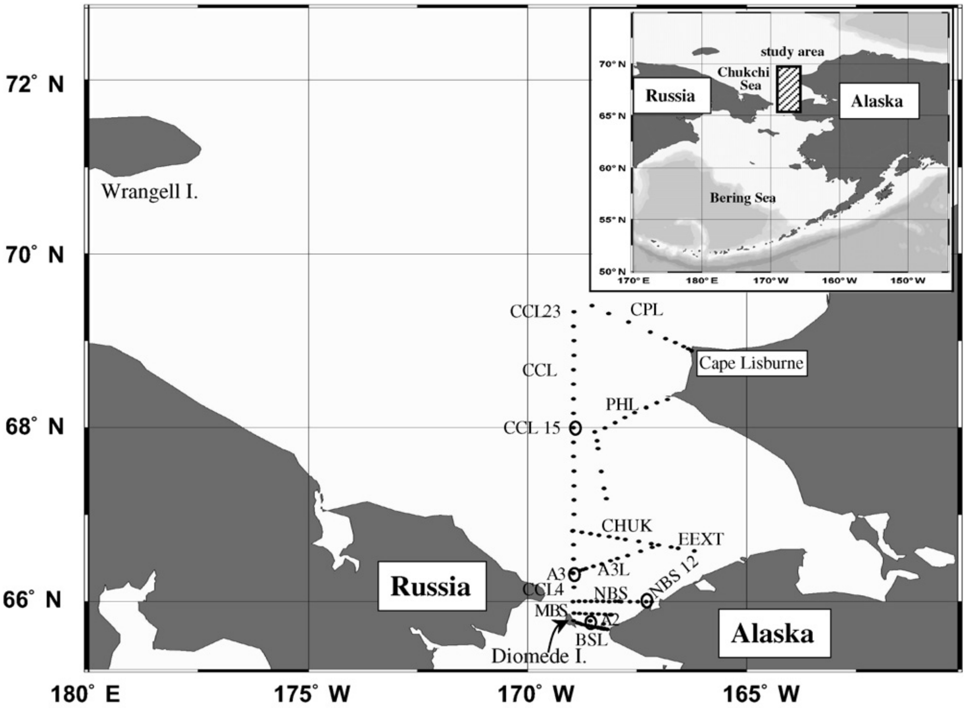

Fig. 1. Sampling locations in Bering Strait and the Chukchi Sea during 2002–2004 *Alpha Helix* cruise. Carbon and nitrogen uptake rates measured at the stations identified by circles.

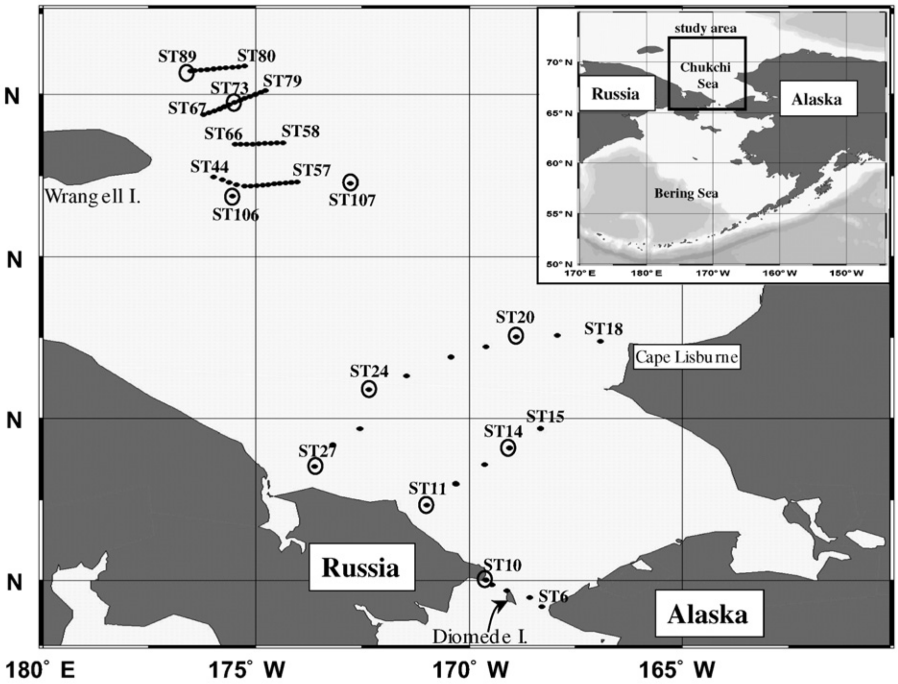

Fig. 2. Sampling locations in Bering Strait and the Chukchi Sea during 10–22 August 2004 RUSALCA cruise. Carbon and nitrogen uptake rates measured at the stations identified by circles.

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the contemporary ranges of nutrients, phytoplankton biomass, and primary productivity in different water masses distributed in the strait and Chukchi Sea. The second objective was to compare contemporary ranges with those obtained in the previous decade for assessment of rate changes under recent conditions in the Bering Sea and Chukchi Sea.

2. Materials and methods

The data were collected from three different cruises during 2002–2004 aboard the R/V *Alpha Helix* (HX) and one cruise in 2004 aboard on R/V *Professor Khromov* (RUSALCA). For the HX cruises, data were collected only in the US territorial waters of Bering Strait and the Chukchi Sea. More extensive sampling of the strait and Chukchi Sea was conducted in 10–22 August 2004 from the RUSALCA cruise. The dates of the HX cruises were 21–29 June 2002, 30 June–8 July 2003, and 29 August–6 September 2004.

2.1. Inorganic nutrient analysis

Water samples for inorganic nutrients (nitrate, nitrite, ammonium, silicate, and phosphate) were obtained from Niskin bottles mounted on CTD/rosette samplers and analyzed on shipboard using an automated nutrient analyzer (ALPKEM RFA model 300) following methods of Whitledge et al. (1981). The accuracy for the nutrients of water samples is ±0.2% with a full-scale range of 5 V.

2.2. Chlorophyll-*a* analysis

Samples for the determination of total chlorophyll-*a* were filtered onto Whatman GF/F glass fiber filters (24 mm). Size-fractionated chlorophyll-*a* was determined on samples passed sequentially through 20 and 5 μm Nucleopore filters (47 mm) and 0.7 μm Whatman GF/F filters (47 mm). The filters were kept frozen and returned to the laboratory for analysis. The filters were subsequently extracted in a 3:2 mixture of 90% acetone and DMSO in a freezer for 24 h and centrifuged (Shoaf and Lium, 1976). Concentrations of chlorophyll-*a* were measured using a Turner Designs model 10-AU fluorometer, which had been calibrated with commercially purified chlorophyll-*a* preparations. After measuring total fluorescence, 100 μl of 10% HCl solution was added into the extracted solution and stored in a test-tube rack for about 90 s to degrade chlorophyll into phaeopigments. A final fluorescence reading was taken after the acidification. The methods and calculations for chlorophyll-*a* and phaeopigments were based on Parsons et al. (1984).

2.3. Carbon and nitrogen uptake rates of phytoplankton

Daily carbon and nitrogen uptake rates were estimated from six light depths (100%, 50%, 30%, 12%, 5%, and 1% penetration of the surface photosynthetically active radiation, PAR), using a ^{13}C–^{15}N-dual isotope tracer technique. Each light depth was determined from an underwater PAR sensor lowered with CTD/rosette samplers on the HX cruises, while a LICOR 4π light sensor (LI-193SB model) was used for the light depth determinations on the RUSALCA cruise. Seawater samples of each light depth were transferred from the Niskin bottles to 1L polycarbonate incubation bottles, which were covered with stainless-steel screens for each light depth. Water samples were inoculated with labeled nitrate ($K^{15}NO_3$), ammonium ($^{15}NH_4Cl$), and carbon ($NaH^{13}CO_3$) substrates (Dugdale and Goering, 1967; Hama et al., 1983). Bottles were incubated in a deck incubator cooled with surface seawater. Although the running surface seawater in the incubator was 2–3 °C warmer than temperatures at in situ depths below the surface, the influence of the warmer temperature on the carbon and nitrogen uptakes of phytoplankton from lower euphotic water depths is generally considered to be small (Dunbar, 1968). The 4–7 h incubations were terminated by filtration through pre-combusted (450 °C) GF/F glass–fiber filters (24 mm). The filters were immediately frozen and preserved for mass spectrometric analysis at the stable isotope laboratory of the University of Alaska Fairbanks. Particulate organic carbon and nitrogen, and abundance of ^{13}C and ^{15}N were determined in the Finnigan Delta+XL mass spectrometer after HCl fuming overnight to remove carbonate. Corrections for the isotope dilution effect were not applied to the measurement of ammonium uptake rates (Glibert et al., 1982) because the incubation periods were relatively short (4–7 h) (Dugdale and Wilkerson, 1986). However, this protocol might underestimate the uptake rate of ammonium. The isotope dilution effect was estimated by using the equations from Kanda et al.

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(1987). The average underestimation for ammonium uptake ranges from 5% (S.D. = ±0.1%) to 12% (S.D. = ±0.2%), assuming $a = 1$ and $a = 2$ ("a" is the ratio of regeneration and uptake), since the value of "a" is reasonably assumed to be in the range of 1–2 (Glibert, 1982; Glibert et al., 1985). The isotope dilution effect on NH_4^+ uptake was estimated to be small at productivity stations in the Chukchi Sea probably because of relatively brief incubations and high ammonium concentration in the water column.

3. Results

3.1. Salinity and nitrate structure on an areal basis

In general, the low salinity ACW (<31.8 psu) was located along the eastern coastline and higher salinity water (>32.5 psu) was found on the western side of the southern Chukchi Sea (Figs. 3–5). However, the surface current flows tended to be displaced by local wind conditions of the southern Chukchi Sea in 2002 and 2004 (Figs. 3a and 5a). The structure of the surface salinity in 2002 showed a rather similar pattern to 2004, whereas the bottom salinity distributions were quite similar in 2002, 2003, and 2004 (Figs. 3b, 4b, and 5b).

The nitrate concentration of the surface water was mostly depleted where the water was vertically stratified (Figs. 3a, 4a, and 5a). There was residual nitrate content at the surface in the western part of Bering Strait, which had an origin from AW and the water column was well mixed. The near bottom layer provided a substantial amount of nitrate from the western to the eastern side during a northward flow of water (Figs. 3b, 4b, and 5b).

3.2. Integrated nitrate concentration in the Chukchi Sea

There were three distinct regions of particularly high nitrate concentrations in the water column of the Chukchi Sea. One was just north of the Diomede Islands, another was in the central Chukchi Sea (Fig. 6), and the last was in Herald Canyon near Wrangell Island (Fig. 6c). The maximum values of the integrated nitrate concentration in those pools were 681 mg-at NO_3–N m^{-2} in the Chukchi pool from the 2003 HX cruise, 858 mg-at NO_3–N m^{-2} near the Diomede Islands from the 2004 HX cruise, and 1328 mg-at NO_3–N m^{-2} in Herald Canyon from the RUSALCA cruise. Although the sizes of the high nitrate pool in the central Chukchi Sea from this study were somewhat different among years, the location and nitrate concentration were quite similar among years for the HX cruises. However, the nitrate concentration in the central Chukchi Sea was somewhat higher from the RUSALCA cruise than from the HX cruises. The low nitrate concentrations (<50 mg-at NO_3–N m^{-2}) were located on the eastern side of the Chukchi Sea, where the typical nitrate-depleted ACW occurred throughout the water column.

3.3. Chlorophyll-*a* concentration in Bering Strait and the Chukchi Sea

The highest integrated chlorophyll-*a* concentrations found during the cruises were 734 mg chl-*a* m^{-2} at station CCL4 north of the Diomede Islands in 2002, 509 mg chl-*a* m^{-2} at CCL13 in 2003, and 492 mg chl-*a* m^{-2} at CCL15 from the HX cruise and 450 mg chl-*a* m^{-2} at station 74 from the RUSALCA cruise in 2004. The distribution of chlorophyll-*a* (in Fig. 7) closely matched the distribution of nitrate concentrations in the Chukchi Sea (Fig. 6). That is, there were three distinct areas of high nitrate and chlorophyll-*a* concentrations in the Chukchi Sea compared to the low chlorophyll-*a* (<50 mg chl-*a* m^{-2}) in the nitrate-depleted water mass on the eastern side of the Chukchi Sea.

3.4. Size-fractionated chlorophyll-*a* in Bering Strait and the Chukchi Sea

There were two distinctly different phytoplankton communities based on size in the two different water masses (determined by bottom salinities at 40 m depth) in the strait and Chukchi Sea (Fig. 8). Phytoplankton >20 μm contributed about 42% (S.D. = ±16.0%) and 94% (S.D. = ±5.0%) of biomass in the water columns of ACW and AW, respectively. The cells <20 μm and >5 μm contributed 18% (S.D. = ±5.5%) and small cells (<5 μm and >0.7 μm) made up 40% (S.D. = ±19.2%) in ACW, whereas 3% (S.D. = ±2.6%) and 3% (S.D. = ±3.1%), respectively in AW.

3.5. Nitrogen uptake rates of phytoplankton in the Chukchi Sea

Generally, there were no discernable trends for nitrate and ammonium uptake rates of phytoplankton

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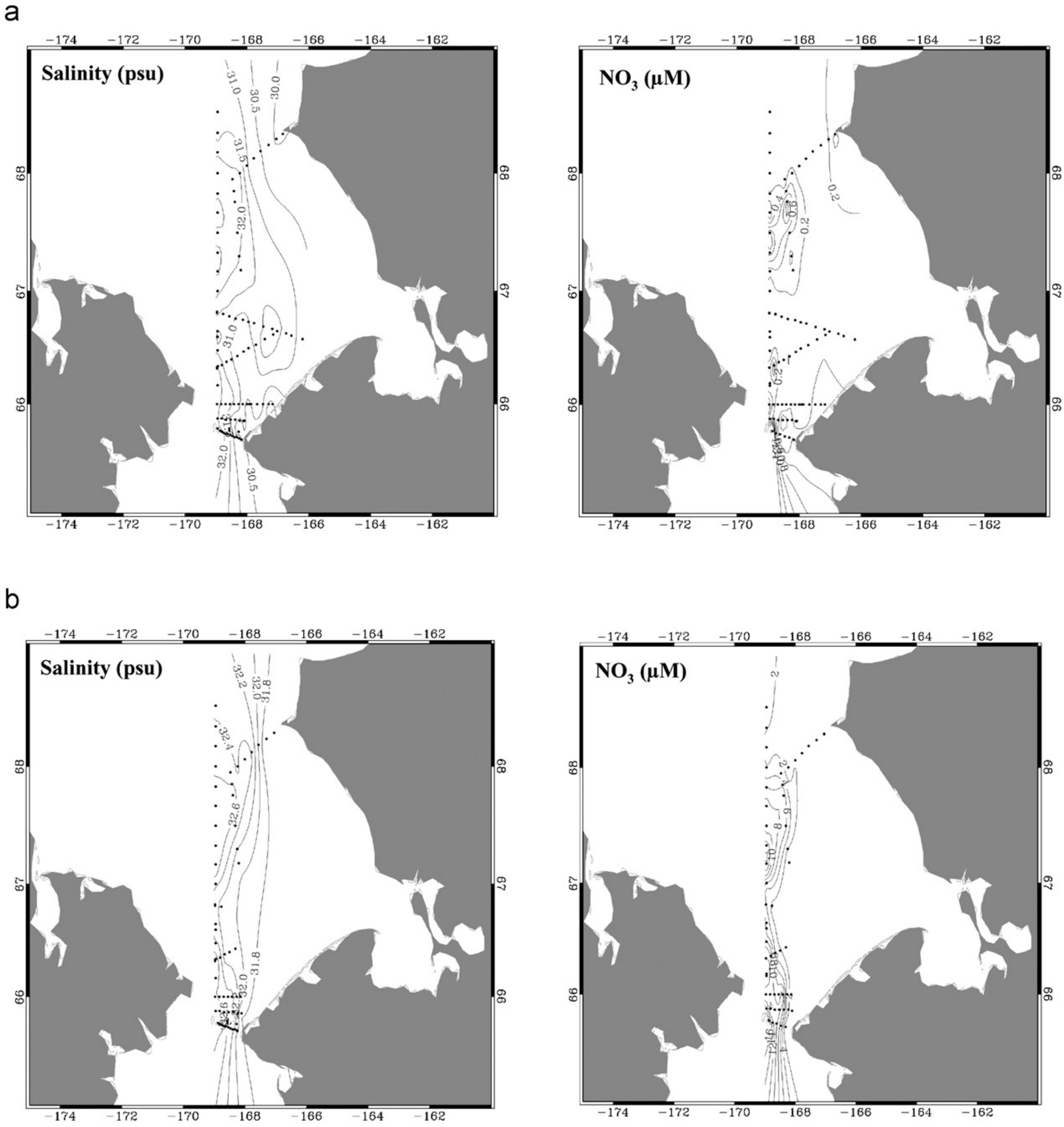

Fig. 3. Areal distributions of salinity and nitrate at (a) surface (b) bottom layer (40 m) of Bering Strait and the Chukchi Sea (US waters). 21–29 June 2002 *Alpha Helix* cruise.

with decreasing light intensity at depth (Table 1). The nitrate uptake rates of phytoplankton ranged from undetectable to as high as 4.40 mg N m^{-3} h^{-1} at station 14 with a mean of 0.24 mg N m^{-3} h^{-1} (S.D. = ±0.60 mg N m^{-3} h^{-1}). Ammonium uptake rates ranged from 0.01 to 8.34 mg N m^{-3} h^{-1} (mean ± S.D. = 0.47 ± 1.37 mg N m^{-3} h^{-1}) for the RUSALCA and HX cruises in the Chukchi Sea. The ranges of vertically integrated nutrient uptake rates at different stations were from 0.14 to 15.95 mg N m^{-2} h^{-1} and from 0.95 to 34.45 mg N m^{-2} h^{-1}, respectively for nitrate and ammonium.

The uptake rates of total nitrogen ($NO_3^- + NH_4^+$) in the Chukchi Sea ranged from 1.37 to 36.47 mg N m^{-2} h^{-1} (Fig. 9) with an average of 9.24 mg N m^{-2} h^{-1} (S.D. = ±10.68 mg N m^{-2} h^{-1}).

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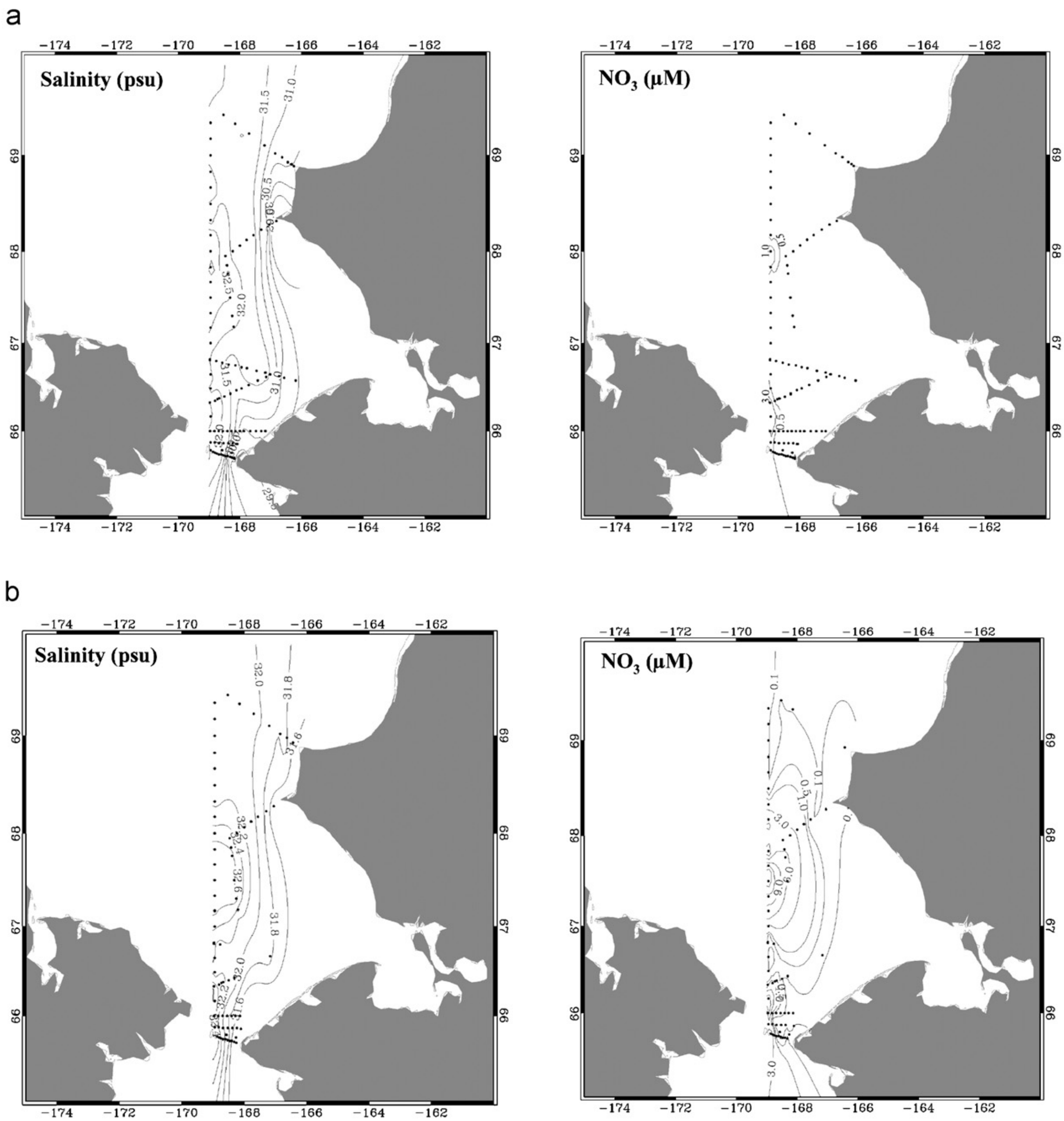

Fig. 4. Areal distributions of salinity and nitrate at (a) surface (b) bottom layer (40 m) of Bering Strait and the Chukchi Sea (US waters). 30 June–8 July 2003 *Alpha Helix* cruise.

3.6. *Carbon uptake rates of phytoplankton in the Chukchi Sea*

The carbon uptake rates for the RUSALCA productivity stations were collected only during the summer of 2004, while the uptake rates of A3 and CCL15 from the HX cruises were measured for 3 years from 2002 to 2004. The uptake rates from the surface to 1% light depth ranged from 0 to 38.3 mg C m^{-3} h^{-1} with a mean of 3.1 mg C m^{-3} h^{-1} (S.D. = ±6.6 mg C m^{-3} h^{-1}) in the Chukchi Sea (Table 2). Generally, the maximum rates from the RUSALCA cruise occurred at the 100% light depths except stations 10, 89, and 73B in the Chukchi Sea. The maximum uptakes at those stations occurred at subsurface. The depths of

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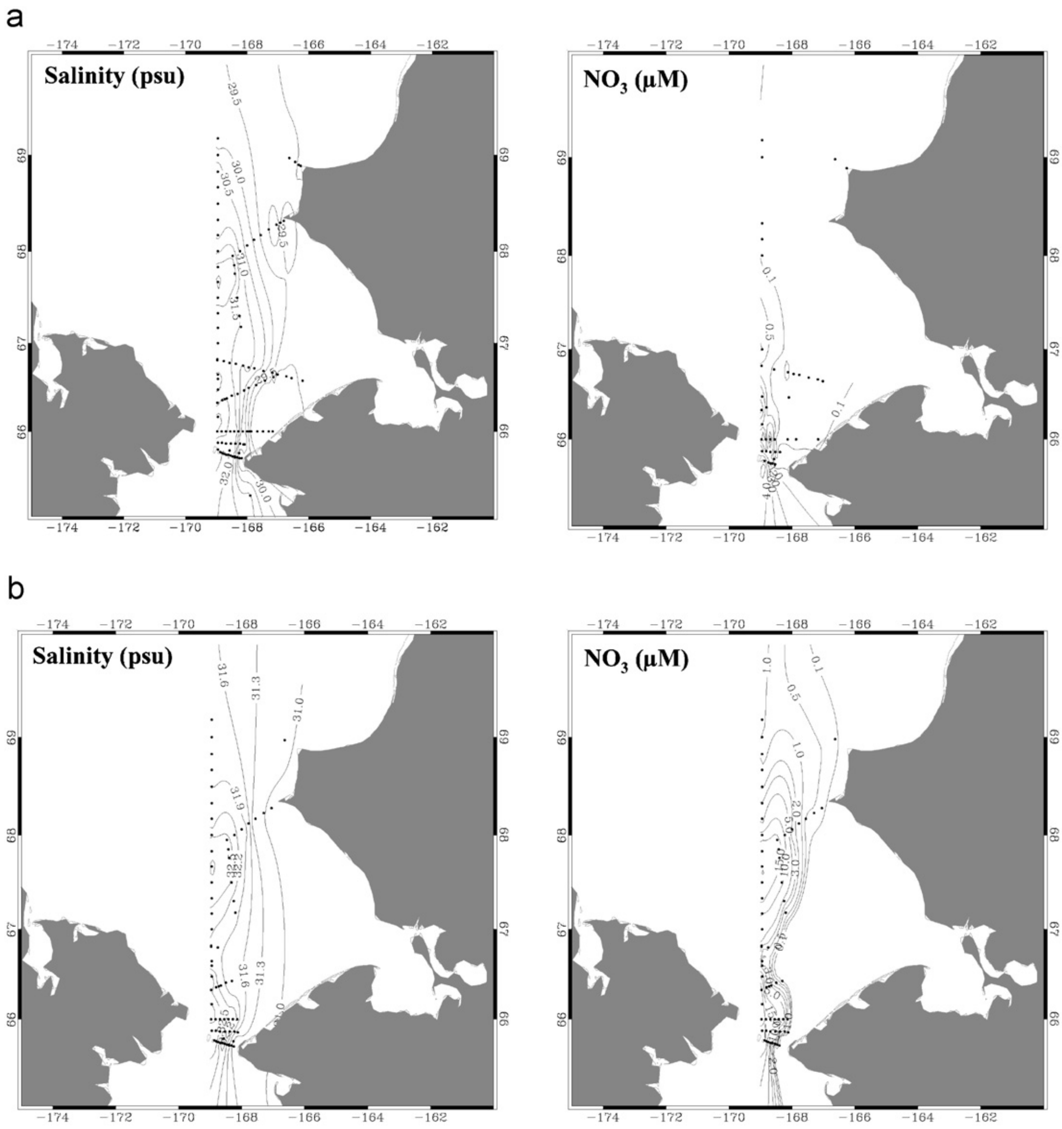

Fig. 5. Areal distributions of salinity and nitrate at (a) surface (b) bottom layer (40 m) of Bering Strait and the Chukchi Sea (US waters). 29 August–6 September 2004 *Alpha Helix* cruise.

the euphotic zone from 100% to 1% of surface irradiance were 23 m for productivity stations from the RUSALCA cruise in 2004 and 33 m from the HX cruises for 3 years. Integral hourly carbon uptake rates (in Fig. 10) ranged from 2.90 to 99.73 mg C m^{-2} h^{-1} with a mean of 34.64 mg C m^{-2} h^{-1} (S.D. = ±40.44 mg C m^{-2} h^{-1}). Station A2 in the eastern Bering Strait had a low uptake rate since the station was dominated by ACW, which is normally depleted in major nutrients concentrations through the water column. In contrast, station 10 in the western Bering Strait where the water mass is typical of AW had a relatively high rate. After phytoplankton passed through Bering Strait, the production rates were substantially higher at stations 11, 14, A3, and CCL15 in the central Chukchi Sea (Fig. 10) because the strong current from topographic conditions in the strait enhanced mixing of the water column as it passed through the strait and the nutrients were mixed back into the upper layer (Coachman and Shigaev, 1992; Zeeman, 1992).

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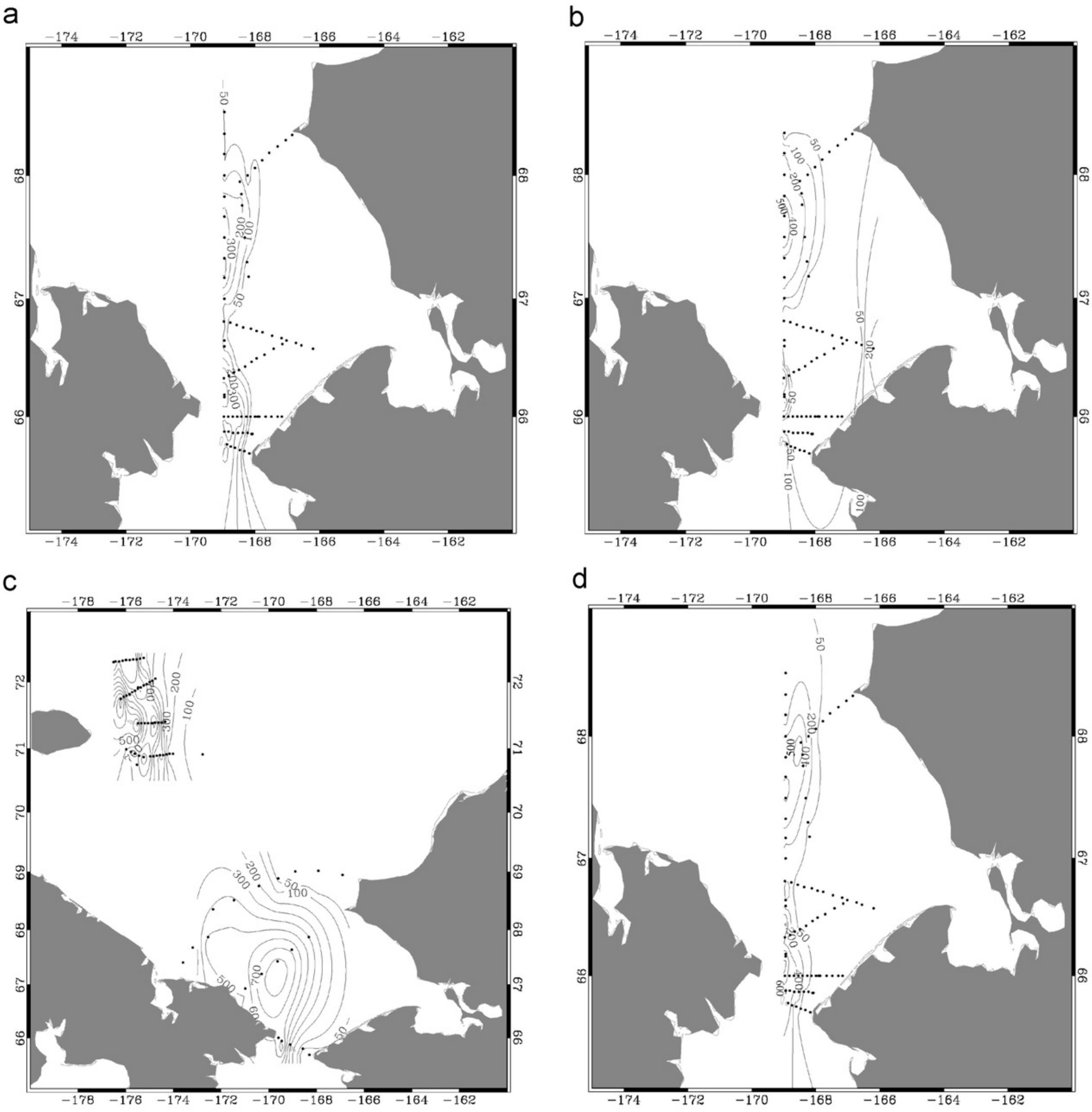

Fig. 6. Areal distribution of integrated nitrate concentration (mg at N–NO_3 m^{-2}) in Bering Strait and the Chukchi Sea.

4. Discussion

4.1. Inorganic nitrate content in the Chukchi Sea

The highest observed nitrate concentration was ~22 μM in the western side of Bering Strait and the central Chukchi Sea. This high nitrate concentration is consistent with that reported from Whitledge et al. (1992). The presence of this high bottom nitrate concentration may indicate that some nitrification occurs in the Chirikov Basin and Chukchi Sea (Whitledge et al., 1992). The range of the high integrated nitrate pool was from 300 to 500 mg-at NO_3–N m^{-2} in the central Chukchi Sea for the 2002 and 2003 HX cruises (Figs. 6a and b). Springer (1988) reported between 200 and 400 mg-at NO_3–N m^{-2} from 1985 to 1987. A somewhat higher range (600–860 mg-at NO_3–N m^{-2}) was found from

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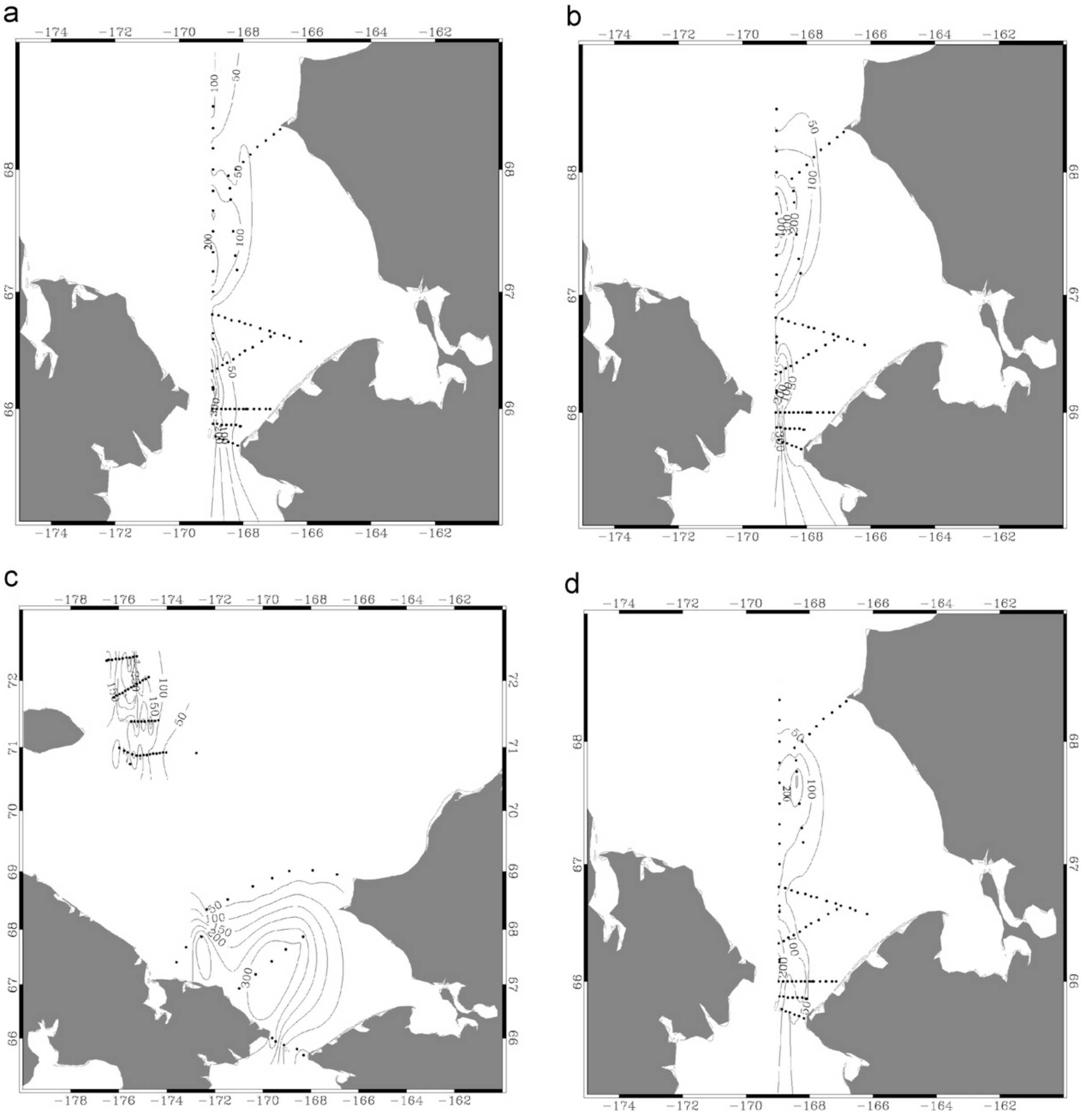

Fig. 7. Areal distribution of integrated chlorophyll-a (mg chl-a m^{-2}) in Bering Strait and the Chukchi Sea.

the cruises in 2004 (Figs. 6c and d). Springer and McRoy (1993) also found this high range of nitrate in 1988. The higher nitrate concentrations observed from 2002 to 2003 HX cruises in this study might be due to seasonal and/or interannual variations in nitrate concentration (Springer and McRoy, 1993) or lower nitrate uptake by reduced phytoplankton biomass (this point is discussed in more detail later).

4.2. *Chlorophyll-a concentration in Bering Strait and the Chukchi Sea*

The distribution of integrated chlorophyll-a concentrations in the Chukchi Sea displayed no large differences among years in this study (Fig. 7). Normally, high levels (>200 mg chl-a m^{-2}) of chlorophyll-a occurred in the western part whereas low

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values ($<50\,\mathrm{mg\,chl\text{-}}a\,\mathrm{m}^{-2}$) occurred in the eastern part as a result of the different nutrient concentrations in the different water masses. There were three distinct regions of particularly high chlorophyll-*a* concentrations in Bering Strait and the Chukchi Sea. One was located in the west of the Diomede Islands, another one was in the central Chukchi Sea, and the final one was in Herald Canyon in the northwestern part of the Chukchi Sea (Fig. 7c). The high chlorophyll-*a* concentration near the Diomede Islands ranged from 200 to $400\,\mathrm{mg\,chl\text{-}}a\,\mathrm{m}^{-2}$ and the pool in the central Chukchi Sea ranged from 200 to $500\,\mathrm{mg\,chl\text{-}}a\,\mathrm{m}^{-2}$ for the 2002–2004 HX cruises and 2004 RUSALCA cruise. The chlorophyll-*a* pool ranged from 200 to $300\,\mathrm{mg\,chl\text{-}}a\,\mathrm{m}^{-2}$ in Herald Canyon where high chlorophyll-*a* concentrations were present below the surface layer (~30 m) in 2004.

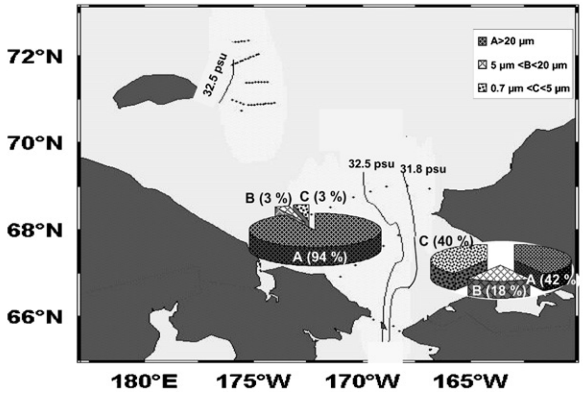

Fig. 8. Averaged compositions of different size phytoplankton in two different water masses determined by bottom salinities (40 m) in Bering Strait and the Chukchi Sea.

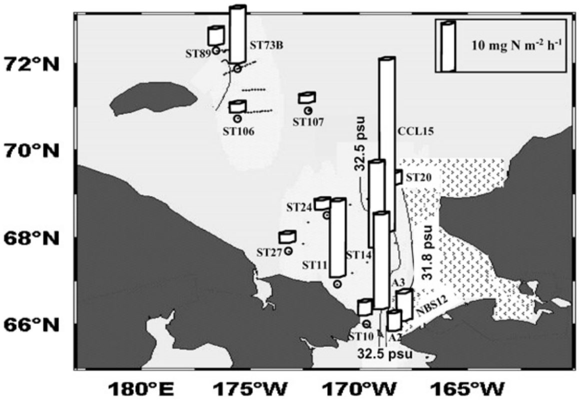

Fig. 9. Areal distribution of nitrogen (nitrate and ammonium) uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. The production rates at all stations from the RUSALCA cruise were measured in 2004. The rates from A2, A3, NBS12, and CCL15 were averaged from 2002 to 2004 *Alpha Helix* cruises. The shaded area stands for Alaskan Coastal Water mass (<31.8 psu) determined by bottom salinities (40 m) in 2004.

Table 1
Nitrate and ammonium uptake rates at different light depths of productivity stations in the Chukchi Sea

Light depth (%)	ST 10	ST 11	ST 14	ST 20	ST 24	ST 27	ST 106	ST 89	ST 73B	ST 107	NBS12	A2	A3	CCL15
(a) *Nitrate uptake rates* ($mg\,N\text{–}NO_3\,m^{-3}\,h^{-1}$)														
100	0.05	0.39	1.52	0.04	0.01	0.01	0.01	0.06	0.01	0.03	0.06	0.06	0.51 (±0.37)	0.44 (±0.46)
50	0.07	1.46	1.91	0.04	0.01	0.01	0.01	0.06	0.01	0.03	0.06	0.05	0.47 (±0.42)	0.48 (±0.59)
30	0.07	1.08	4.40	0.03	0.01	0.00	0.01	0.04	0.05	0.03	0.05	0.04	0.50 (±0.44)	0.50 (±0.64)
12	0.09	0.13	0.82	0.01	0.01	0.00	0.01	0.03	0.07	0.01	0.04	0.02	0.41 (±0.34)	0.40 (±0.42)
5	0.12	0.10	0.21	0.01	0.00	0.02	0.01	0.23	0.67	0.00	0.03	0.04	0.03 (±0.01)	0.22 (±0.35)
1	0.03	0.09	0.04	0.02	0.01	0.05	0.04	0.10	0.02	0.00	–	0.01	0.01 (±0.01)	0.17 (±0.29)
P	1.10	8.84	15.95	0.42	0.14	0.39	0.37	2.32	8.49	0.36	0.72	1.18	6.85 (±2.69)	7.35 (±8.10)
(b) *Ammonium uptake rates* ($mg\,N\text{–}NH_4\,m^{-3}\,h^{-1}$)														
100	0.09	0.51	0.33	0.10	0.15	0.15	0.04	0.05	0.04	0.06	0.53	0.06	0.95 (±1.36)	1.98 (±3.14)
50	0.16	0.64	0.19	0.21	0.19	0.07	0.04	0.05	0.02	0.08	0.71	0.07	0.87 (±1.20)	0.64 (±0.82)
30	0.08	0.77	0.19	0.09	0.11	0.03	0.03	0.04	0.05	0.08	0.48	0.08	0.79 (±1.05)	2.90 (±4.72)
12	0.12	0.34	0.25	0.06	0.02	0.02	0.02	0.05	0.09	0.04	0.21	0.08	0.60 (±0.62)	2.44 (±3.89)
5	0.10	0.13	0.04	0.07	0.01	0.03	0.01	0.05	0.15	0.01	0.08	0.07	0.14 (±0.13)	0.63 (±1.02)
1	0.11	0.12	0.08	0.02	0.06	0.11	0.27	0.02	0.01	0.01	–	0.04	0.08 (±0.04)	0.53 (±0.86)
P	1.53	7.15	1.89	1.82	1.61	1.24	1.49	0.95	2.93	1.01	6.14	2.98	13.0 (±16.17)	29.11 (±44.39)

The uptakes for all stations from the RUSALCA cruise were one time measurements in 2004, while the uptakes of A3 and CCL15 from the *Alpha Helix* cruises were averaged for 3 years from 2002 to 2004. *P*: integrated hourly production ($\mathrm{mg\,N\,m^{-2}\,h^{-1}}$) and ±: S.D.

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Table 2

Carbon uptake rates (mg C m^{-3} h^{-1}) at different light depths of productivity stations in the Chukchi Sea

Light depth (%)	ST 10	ST 11	ST 14	ST 20	ST 24	ST 27	ST 106	ST 89	ST 73B	ST 107	NBS12	A2
100	2.54	14.79	25.38	1.46	0.71	0.49	0.30	0.34	0.31	0.9	1.03	0.50
50	2.10	13.03	17.64	1.04	0.55	0.39	0.26	0.32	0.12	0.57	0.66	0.48
30	2.60	9.84	12.00	0.62	0.37	0.27	0.16	0.23	0.18	0.34	0.45	0.46
12	3.80	3.23	2.55	0.22	0.10	0.12	0.07	0.11	0.55	0.13	0.18	0.33
5	1.04	0.28	0.73	0.03	0.01	0.10	0.05	0.41	1.97	0.03	0.01	0.15
1	0.06	0.11	0.08	0.01	0.00	0.21	0.08	0.05	0.02	0.00	–	0.05
P	387	1487	1269	129	68	72	45	81	432	90	98	179
B	139	154	170	12	8	73	104	106	282	12	6	34
P/*B*	2.78	9.66	7.47	10.75	8.50	0.99	0.43	0.76	1.53	7.5	16.35	5.26

Light depth (%)	A3				CCL15			
	2002	2003	2004	Average	2002	2003	2004	Average
100	1.01	15.8	4.11	6.97 (±7.81)	3.22	2.34	38.31	14.62 (±20.52)
50	1.20	18.1	2.47	7.24 (±9.39)	0.88	2.27	27.74	10.63 (±14.82)
30	6.27	14.7	2.47	7.83 (±6.28)	1.54	2.02	25.38	9.65 (±13.63)
12	2.49	9.76	3.74	5.33 (±3.89)	1.10	1.75	7.69	3.51 (±3.63)
5	0.71	0.52	0.30	0.51 (±0.20)	0.01	1.19	0.86	0.68 (±0.61
1	0.16	0.07	0.04	0.09 (±0.06)	0	0	0.02	0.01 (±0.01)
P	1428	2141	765	1444 (±687.90)	524	387	3578	1496 (±1803.92)
B	98	147	119	121 (±24.58)	136	148	246	177 (±60.34)
P/*B*	14.57	14.57	6.43	11.86 (±4.70)	3.85	2.62	14.55	7.01 (±6.56)

The uptake rates for all stations from the RUSALCA cruise were one time measurements in 2004, while the uptakes of A3 and CCL15 from the *Alpha Helix* cruises were measured for three times from 2002 to 2004. ±: S.D.; *P*: integrated daily primary production (mg C m^{-2} d^{-1}), based on 15-h photo period per one day; *B*, integrated chlorophyll-*a* (mg chl-*a* m^{-2}) from 100% to 1% light depth; and *P*/*B*: production/biomass of phytoplankton.

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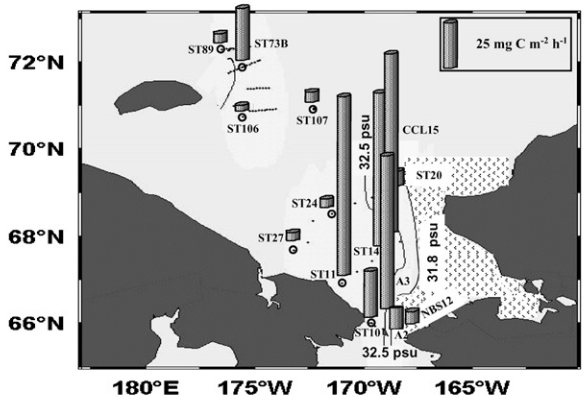

Fig. 10. Areal distribution of carbon uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. The production rates at all stations from the RUSALCA cruise were measured in 2004. The rates from A2, A3, NBS12, and CCL15 were averaged from 2002 to 2004 *Alpha Helix* cruises. The shaded area stands for Alaskan Coastal Water mass (<31.8 psu) determined by bottom salinities (40 m) in 2004.

The range of integrated chlorophyll-*a* concentration in the pool near the Diomede Islands is somewhat lower, whereas the highest range from the central Chukchi Sea pool is much lower in this study than in previous studies. In the mid-1980s, chlorophyll-*a* ranged from 400 to 600 mg chl-*a* m^{-2} and 600 to over 1500 mg chl-*a* m^{-2} for the pools near the Diomede Islands and the central Chukchi Sea, respectively (Robie et al., 1992; Springer, 1988; Springer and McRoy, 1993). The lower concentration of chlorophyll-*a* from this study might have resulted from small sample sizes that were not necessarily taken from the highest production areas. Or, this difference might be caused by the interannual variations in chlorophyll-*a* concentrations as reported previously (Springer and McRoy, 1993). For example, it might be a result of slower growth rates of phytoplankton transported into these regions due to nutrient or light limitation. Nitrate and ammonium were nearly depleted in the euphotic layers of most of the productivity stations. Moreover, phytoplankton might have more light limitation in this study than previous studies, since the maximum carbon uptakes occurred mostly at the surface (0 m) in this study (Table 2) whereas the maximum uptakes were usually found at the depths between 5 and 15 m in Korsak (1992). An alternative explanation is that less phytoplankton biomass was transported through Bering Strait during the years of this study. The flow of AW into the Chukchi Sea carrying high nutrients and phytoplankton biomass from the productive regions upstream in the Chirikov Basin creates the large chlorophyll pool in the central Chukchi Sea (Robie et al., 1992; Springer and McRoy, 1993). Thus, lower chlorophyll-*a* concentrations reported here might indicate lower phytoplankton biomass transported through the strait. Actually, the highest concentration of chlorophyll-*a* at the end of the western Bering Strait was somewhat lower in 2004 ($\sim$20 mg chl-*a* m^{-3}) than in Robie et al. (1992) who reported values of >30 mg chl-*a* m^{-3}. However, the large interannual variation of the chlorophyll-*a* concentrations in this region (Springer, 1988) makes it difficult to conclude if the lower chlorophyll-*a* concentrations in this study are from a few observations at different times during an annual variation or from a longer term decreasing trend in phytoplankton biomass of the Chukchi Sea. Unfortunately, frequent cloudy weather conditions limit the utility of satellite remote sensing of chlorophyll in this region.

4.3. *Areal distribution of size-fractionated chlorophyll-a*

There are some implications for marine ecosystems from the size composition of phytoplankton at the base of the food web. For example, the different size compositions could influence the number of trophic levels in pelagic food chains and thus transfer efficiency in the food chains (Malone, 1980), the extent of coupling between pelagic and benthic environments (Grebmeier and McRoy, 1989; Joint et al., 1993), and the relative partitioning of nitrate or ammonium utilization in the ecosystem.

Generally, large cells ($>5\,\mu$m), which grow best under eutrophic conditions, were dominant in Bering Strait and the Chukchi Sea. Even in ACW where nitrate is normally depleted, large cells $>5\,\mu$m dominated ($\sim$60%). The dominance of larger phytoplankton in the strait and Chukchi Sea indicates a shorter, and consequently, more efficient food chain (Parsons, 1972). However, because of their fast sinking rates in this shallow basin, these large cells are an advantage to the benthic food web (Grebmeier and McRoy, 1989). A major vertical flux of carbon to the bottom occurs when the food web is based on large phytoplankton cells (Joint et al., 1993). Grebmeier et al. (1988) found low C/N ratios (5.8–7.6) at the surface sediment under Anadyr–Bering Shelf Water,

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indicating a high quality, nitrogen-rich marine carbon supply to the benthos. In contrast, they found lower quality organic matter (higher C/N ratios = 7.7–14.0) and much lower benthic biomass in sediment under ACW. The quality and quantity of organic matter that sinks to the bottom as potential food for the benthos depend on a number of major factors such as the rate of primary production, sinking rate of phytoplankton, zooplankton grazing rate, overall water column depth, and proximity to land runoff sources (Grebmeier et al., 1988). Because the zooplankton grazing rate is low (~1% of the daily phytoplankton production) here (Shuert and Walsh, 1993), grazing might be ruled out as the reason for the different rates of production and qualities in sediments under the two different water masses. The water column depth is shallower under ACW than under Anadyr–Bering Shelf Water and there are more effects of fluvial runoff sources on the sediment under ACW (Naidu et al., 1993). Therefore, different primary productivities and thus cell size structure of phytoplankton communities (presumably different sinking rates) are believed to be a major reason for two distinct benthic ecosystems in the Chukchi Sea.

4.4. Nitrogen uptake rates in Bering Strait and the Chukchi Sea

For the uptake rates in different areas, the average uptake rate of total nitrogen from low-nutrient areas was 3.41 mg N m^{-2} h^{-1} (S.D. = ±3.34 mg N m^{-2} h^{-1}), whereas the average total nitrogen for the high nutrient AW in the Chukchi Sea (stations 11, 14, A3, and CCL15) was 22.55 mg N m^{-2} h^{-1} (S.D. = ±9.42 mg N m^{-2} h^{-1}) in Fig. 9. The ranges of total nitrogen uptake rate for the Chukchi Sea are lower than those from previous studies (Hansell and Goering, 1990; Sambrotto et al., 1984; McRoy et al., 1972). In particular, the mean total nitrogen uptake for the high-nutrient AW from this study is about four-fold lower than that from Hansell and Goering (1990). The range of mean values reported by Hansell and Goering (1990) for the Chukchi Sea was from 9.10 to 86.80 mg N m^{-2} h^{-1} and their mean value of total nitrogen uptake rate only for the central Chukchi Sea was 85.54 mg N m^{-2} h^{-1}. However, they included urea uptake in the total nitrogen uptake calculation, and urea contributed about 27% to total nitrogen uptake rate in the area of the Chukchi Sea. If this percentage of urea uptake was added to the average of total nitrogen uptake rate for AW calculated in this study, then the new value would be 30.89 mg N m^{-2} h^{-1} which is still three times lower than that reported from Hansell and Goering (1990).

Based on a 15-h photo period for 100 growing days (Hansell and Goering, 1990; Springer and McRoy, 1993), the mean annual total nitrogen production rates in this study were 13.9 g N m^{-2} (S.D. = ±16.2 g N m^{-2}) and 33.8 g N m^{-2} (S.D. = ±14.1 g N m^{-2}) for the entire and the central Chukchi Sea, respectively. In contrast, the mean annual production rates only for nitrate were 6.2 g N m^{-2} (S.D. = ±7.4 g N m^{-2}) in the entire Chukchi Sea and 14.6 g N m^{-2} (S.D. = ±6.3 g N m^{-2}) in the central Chukchi Sea in this study. If averaged assimilated C/N ratios of the entire (= 4.2) and central (= 5.6) Chukchi Sea are representative for those areas, then the estimated annual new production are 81.8 and 26.0 g C m^{-2}, respectively, for the central and entire Chukchi Sea. Hansell et al. (1993) estimated new production rate of 2.4 g C m^{-2} d^{-1} in AW north of Bering Strait. Based on their daily rates of new production and a 100-day growing season, the estimated annual new production is 240 g C m^{-2} for AW, which is about three-fold higher than in this study. This is consistent with lower values in the integrated chlorophyll-*a* concentration and total nitrogen uptake in this study.

4.5. Carbon uptake rates in Bering Strait and the Chukchi Sea

Carbon uptake rates in Bering Strait and the Chukchi Sea ranged from 0.1 to 3.6 g C m^{-2} d^{-1} with a mean of 0.7 g C m^{-2} d^{-1} (S.D. = ±0.9 g C m^{-2} d^{-1}) from 2002 to 2004 (in Table 2), based on a 15-h photo period in the Chukchi Sea (Hansell and Goering, 1990). Because of large differences among water masses in the Chukchi Sea, the production rates within the same water mass should be compared. In addition, the sampling season for the measurements should be considered since productivity has large seasonal variations in this region (Springer and McRoy, 1993; Wang et al., 2005). The average productivities in the southern part of the Chukchi Sea during late July to August from previous studies (Table 3) were 1.7 g C m^{-2} d^{-1} with a range from 0.4 to 4.7 g C m^{-2} d^{-1} (Korsak, 1992) and 1.6 g C m^{-2} d^{-1} with a range from 0.2 to 5.5 g C m^{-2} d^{-1} (Zeeman, 1992). The average rate from the stations (stations 10,

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Table 3
Comparison of daily primary productivity in Bering Strait and the Chukchi Sea

Source	Productivity ($g\,C\,m^{-2}\,d^{-1}$)	Method	Place or water mass	Season
McRoy et al. (1972)	4.1	^{14}C uptake	Western Being Strait	June
Hameedi (1978)	0.1–1.0	^{14}C uptake	Chukchi Sea	July
	>3.0		Central Chukchi Sea	
Sambrotto et al. (1984)	2.7	NO_3^- disappearance	Western Bering Strait	
Springer (1988)	1.5–16	^{14}C uptake	Central Chukchi Sea	11 July–2 August
Korsak (1992)	1.7	^{14}C uptake	Chukchi Sea	28 July–31 August
Zeeman (1992)	1.6	^{14}C uptake	Chukchi Sea	28 July–31 August
	0.8		Bering Strait	
Hansell et al. (1993)	4.8–6.0	NO_3^- disappearance	Anadyr Water in the north of Bering Strait	
Springer and McRoy (1993)	4.7	^{14}C uptake and chl-a concentration	Central Chukchi Sea	28 July–31 August
Hill et al. (2005)	0.8	^{14}C uptake	Northeastern Chukchi Sea	Summer
This study	0.6	^{13}C uptake	Chukchi Sea	10–22 August
	1.4		Central Chukchi Sea	

For comparison, the rate from this study is only 2004 RUSALCA data.

11, 14, 20, 24, and 27 in Table 2) in the southern Chukchi Sea from this study during 10–22 August 2004 was $0.6\,g\,C\,m^{-2}\,d^{-1}$ with the range from 0.1 to $1.5\,g\,C\,m^{-2}\,d^{-1}$ which is less than half of the values from the previous studies, although these values are not statistically different probably because of large geographical variations. The average daily productivity in the southern Chukchi sea from this study was somewhat lower than the rate ($0.8\,g\,C\,m^{-2}\,d^{-1}$) on the northeastern shelf region but higher than the value ($0.3\,g\,C\,m^{-2}\,d^{-1}$) on the edge of the Canada basin (Hill et al., 2005). The mean productivity ($1.4\,g\,C\,m^{-2}\,d^{-1}$) for stations 11 and 14 as representative for AW in the central Chukchi Sea during 10–22 August 2004 in this study was much lower than that from Springer and McRoy (1993) ($4.7\,g\,C\,m^{-2}\,d^{-1}$) based on the chlorophyll-*a* concentration from 1 to 28 July and the ^{14}C uptake from late July to August in 1988. However, the average productivity from this study is near the range (1.6–$1.9\,g\,C\,m^{-2}\,d^{-1}$) for the central Chukchi Sea during 12–25 July 1986 from Springer (1988), although his measurements were limited only to the US side of the Chukchi Sea and occurred at a different time in the year. Although the range for low to moderate levels of productivity (0.1–$1.0\,g\,C\,m^{-2}\,d^{-1}$) from Hameedi (1978) in Table 3 is similar to the range of this study, he measured productivity in the marginal ice zone of the northern Chukchi Sea during summer, and thus the comparison might be unreasonable since the physical and chemical structures could be different in the water columns of the two environments.

Based on 100 growing days (Springer and McRoy, 1993), the annual production of phytoplankton from the RUSALCA and HX cruises in this study was calculated to be between 10 and $360\,g\,C\,m^{-2}$ with a mean of $73\,g\,C\,m^{-2}$ for the southern Chukchi Sea, while the mean annual production for the whole Chukchi Sea including the northwestern part (stations 73B, 89, 106, and 107) was somewhat lower ($55\,g\,C\,m^{-2}$). In comparison, the estimated average annual rates of primary production for the whole Chukchi Sea were 148 and $170\,g\,C\,m^{-2}$ from Zeeman (1992) and Korsak (1992), respectively, based on their daily measurements. The production in this study was two- or three-fold lower than those from the previous studies. The difference between this and the previous studies might be caused by several factors. The lower production in this study could result from seasonal, annual, and/or geographical variations in primary productivity in the Chukchi Sea. Those variations are well known in this area and mostly attributed to different water masses and thus nutrient concentrations, i.e., the meandering nature of the flow field of AW (Springer and McRoy, 1993; Springer, 1988; Hansell and Goering, 1990). Most productivity data in this study were from the RUSALCA cruise during 10–22 August 2004. However, the daily production rates at stations 11

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and 14 from the 2004 RUSALCA cruise were very similar to the mean rates at stations A3 and CCL15 from the HX cruises (Table 2) as representative for the "plume" of AW (Springer and McRoy, 1993) based on their salinities, even though the rates at stations 11 and 14 were from the middle of August in 2004, while the rates at A3 and CCL15 were averaged from the different seasons and years from 2002 to 2004, although there was a large variation in CCL15 (in Table 2). The average annual production only for the central Chukchi Sea was 145 g C m^{-2} from this study, whereas the estimated value from Springer and McRoy (1993) was 470 g C m^{-2}, based on 100 growing days. In contrast, the production based on 120 days was 174 g C m^{-2} from this study which is still lower than those estimated by Hansell et al. (1993) (576–720 g C m^{-2}) and Sambrotto et al. (1984) (324 g C m^{-2}). When the annual primary production rates only for the plume of AW are compared, the production values from the previous studies were about two- four- fold higher than that from this study.

It should be noted that the large difference of productivity from the same water regime might result from the different methods to estimate the production. Springer and McRoy (1993) calculated the production from the relationship between chlorophyll-*a* biomass and estimated productivity of phytoplankton, and Sambrotto et al. (1984) and Hansell et al. (1993) estimated the annual production based on NO_3 utilization in Bering Strait. These measurements are likely to be indirect overestimates. For example, nitrate disappearance is controlled by not only phytoplankton but also denitrification. However, the mean production rates for AW estimated from Springer (1988), Korsak (1992), and Zeeman (1992) using a similar method (^{14}C uptake) are still two- or three-fold higher than the rate from this study. Their observed mean annual productions were 270, 263, and 327 g C m^{-2}, respectively, based on 100 growing days. The production estimates determined by Springer and McRoy (1993) were based on calculations using chlorophyll-*a* biomass and P/B ratios (production/biomass of phytoplankton). The mean chlorophyll-*a* concentration from four stations for the plume of AW in this study was much lower than their result. Moreover, the average P/B ratio from four stations in this study was 9.2, whereas their estimated ratio was 16.5, which indicates more production per unit of phytoplankton than in this study. Euphotic layer depths (100–1% light intensity depths) also were different between this and previous studies. The mean euphotic depths in this study were 23 m from the RUSALCA cruise in 2004 and 33 m from the HX cruises for 3 years from 2002 to 2004, whereas it was 45–50 m from Korsak (1992).

The lower production in the Chukchi Sea observed in this study is consistent with other recent studies (Grebmeier and Cooper, 2004; Gregg and Conkright, 2002; Abromaitis, 2000). Grebmeier and Cooper (2004) showed that the decline of benthic biomass related to a decrease in the carbon flux in the northern Bering Sea has continued into the late 1990s and early 2000s. Moreover, based on satellite data, Gregg and Conkright (2002) found that chlorophyll concentrations decreased in the North Pacific from 1979–1986 to 1997–2000 period. Retrospective assessment of primary productivity based on evidence from stable carbon isotopes in seabirds supports this hypothesis of a decline in the primary production on the Bering/Chukchi shelf (Abromaitis, 2000).

Four plausible hypotheses are suggested for the lower production in this study. The first hypothesis is that the composition of the water masses flowing through Bering Strait and their distributions in the Chukchi Sea might differ among years, since the production rates in the Chukchi Sea are highly dependent on the types of water masses (Hansell and Goering, 1990). For example, if ACW was displaced to the west in this study, then we might not able to sample the highest production areas because of the limitation in the HX cruises. ACW normally has low biomass and nutrients, whereas the Anadyr–Bering Shelf water masses, especially the AW, carry high biomass and nutrients (Robie et al., 1992; Springer and McRoy, 1993). Woodgate et al. (2005) found that the water column moving through Bering Strait was fresher and warmer during the summer/autumn period of 2000–2004 than previous years. The second hypothesis is related to temporal variability in transport through the strait especially during summer months. In years of strong summer transport through Bering Strait, the growing phytoplankton might be quickly moved through the system and might be distributed over a much larger area in the Chukchi Sea. In addition, the water column passing through Bering Strait might resuspend bottom sediments in this shallow shelf under strong transport. The third hypothesis is that the primary production has decreased in the Bering and Chukchi Seas (Schell, 2000). Therefore, the lower production observed in this study might

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be an indication of the long-term decline in primary production of the northern Bering and Chukchi Seas. The last hypothesis is that the apparent difference in the production might be spurious because of large annual and geochemical variations in the Chukchi Sea.

5. Conclusions

The highest nitrate concentrations in AW passing through the western side of Bering Strait from this study are consistent with those from previous studies. However, the integrated concentration of the high-nitrate pool in the central Chukchi Sea is somewhat higher in this study than those from previous studies. In contrast, the range of integrated chlorophyll-*a* in the area near the western Diomede Islands is somewhat lower in this study than in previous studies, whereas the highest range from the central Chukchi Sea is much lower than the lowest range from previous studies. Moreover, the highest chlorophyll-*a* concentrations in AW mass of the western Bering Strait is lower in 2004 than in previous decades.

The lower chlorophyll-*a* concentrations are consistent with the average annual carbon production from the stations in the southern Chukchi Sea from this study that are almost half the values from previous studies. Especially, the average value for the central Chukchi Sea is much lower in this study. The lower primary production from this study might be caused mainly by the lower phytoplankton biomass arriving in the southern Chukchi Sea to seed the area. Consistent with the lower carbon uptake rate, the total nitrogen uptake rate for the Chukchi Sea, especially the central area from this study, is lower than those from the previous studies (Hansell and Goering, 1990; Sambrotto et al., 1984; McRoy et al., 1972), which results in more unused nitrate in the regions. However, we do not know if the lower productivity rates from this study represent an overall trend or are related to interannual or shorter term variations because sampling covers limited spatial and temporal scales.

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