Continental Shelf Research 29 (2009) 1689–1696

Contents lists available at ScienceDirect

Continental Shelf Research

journal homepage: www.elsevier.com/locate/csr

High incorporation of carbon into proteins by the phytoplankton of the Bering Strait and Chukchi Sea

Sang H. Lee [a,*], Hak-Jun Kim [a], Terry E. Whitledge [b]

[a] Korea Polar Research Institute, KORDI, Songdo Techno Park, 7-50, Songdo-dong, Yeonsu-gu, Incheon 406-840, Republic of Korea
[b] Institute of Marine Science, University of Alaska, Fairbanks, AK 99775-7220, USA

ARTICLE INFO

Article history:
Received 19 November 2008
Received in revised form
19 May 2009
Accepted 26 May 2009
Available online 21 June 2009

Keywords:
Photosynthetic allocations
Phytoplankton
Lipids
Proteins
Chukchi Sea

ABSTRACT

High incorporation of carbon into proteins and low incorporation into lipids were a characteristic pattern of the photosynthetic allocations of phytoplankton throughout the euphotic zone in the Bering Strait and Chukchi Sea in 2004. According to earlier studies, this indicates that phytoplankton had no nitrogen limitation and a physiologically healthy condition, at least during the cruise period from mid-August to early September in 2004. This is an interesting result, especially for the phytoplankton in the Alaskan coastal water mass-dominated region in the Chukchi Sea which has been thought to be potentially nitrogen limited. The relatively high ammonium concentration is believed to have supported the nitrogen demand of the phytoplankton in the region where small cells ($<5\,\mu m$) composed of about 50% of the community, since they prefer to use regenerated nitrogen such as ammonium. In fact, a small cell-size community of phytoplankton incorporated much more carbon into proteins in nitrate-depleted water suggesting that small phytoplankton had less nitrogen stress than large phytoplankton. If the high carbon incorporation into proteins by the phytoplankton in 2004 is a general pattern of the photosynthetic allocations in the Chukchi Sea, they could provide nitrogen-sufficient food for the highest benthic faunal biomass in the Arctic Ocean, sustaining large populations of benthic-feeding marine mammals and seabirds.

1. Introduction

Currently, the environments in the Arctic are rapidly changing. Higher temperatures and ice export to Baffin Bay and Greenland Sea through Fram Strait have decreased the extent and thickness of perennial sea ice in the Arctic Ocean over several decades and have produced more open water (Rothrock et al., 2003; Nghiem et al., 2007). These changes of climate and ice conditions may alter the quantity, quality, and timing of carbon production of phytoplankton and, thus, consequently the seasonal distributions, geographic ranges, and nutritional structure of higher trophic levels have been projected to be altered (Tynan and DeMaster, 1997). Therefore, more studies of current status of phytoplankton production and their physiological condition are needed for better understanding of the impact of ongoing changes in climate and sea-ice conditions on the Arctic marine ecosystems.

The Bering Strait/Chukchi Sea (Fig. 1) is the sole gateway of water masses and organic matter from the North Pacific to the Arctic Ocean. The transport through the strait has a strong seasonal variability with a summer maximum and a winter minimum, as well as large interannual variations (Coachman and Aagaard, 1988; Woodgate et al., 2005), which are caused mainly by the regional wind conditions (Coachman et al., 1975). Three different water masses pass northward through Bering Strait into the Chukchi Sea. These are Anadyr water (AW), Bering shelf water (BSW), and Alaska coastal water (ACW) which are distinguished primarily by their salinity differences (Coachman et al., 1975; Aagaard, 1987). ACW has a low salinity (< approximately 31.8) owing to fresh water input from rivers combined with Alaskan coastal water from the Gulf of Alaska (Coachman et al., 1975). The BSW originating primarily in the middle shelf south of St. Lawrence Island is more saline (31.8–32.5) than ACW and AW has the highest salinity (32.5–33.0) which is a northern branch of the Bering Slope Current (Coachman et al., 1975; Coachman and Shigaev, 1992). Of these water masses, AW through the western Bering Strait supplies the Chukchi continental shelf with high nutrients that promote abundant phytoplankton growth throughout the summer (Springer and McRoy, 1993). Usually, the ratio of the three different water masses is 6:3:1 for AW, BSW, and ACW, respectively, although the ratio varies seasonally and interannually, 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 communities observed in this important gateway to the Arctic Ocean (Springer and

* Corresponding author. Tel.: +82 32 260 6181; fax: +82 32 260 6109.
E-mail address: sanglee@kopri.re.kr (S.H. Lee).

0278-4343/$ - see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.csr.2009.05.012

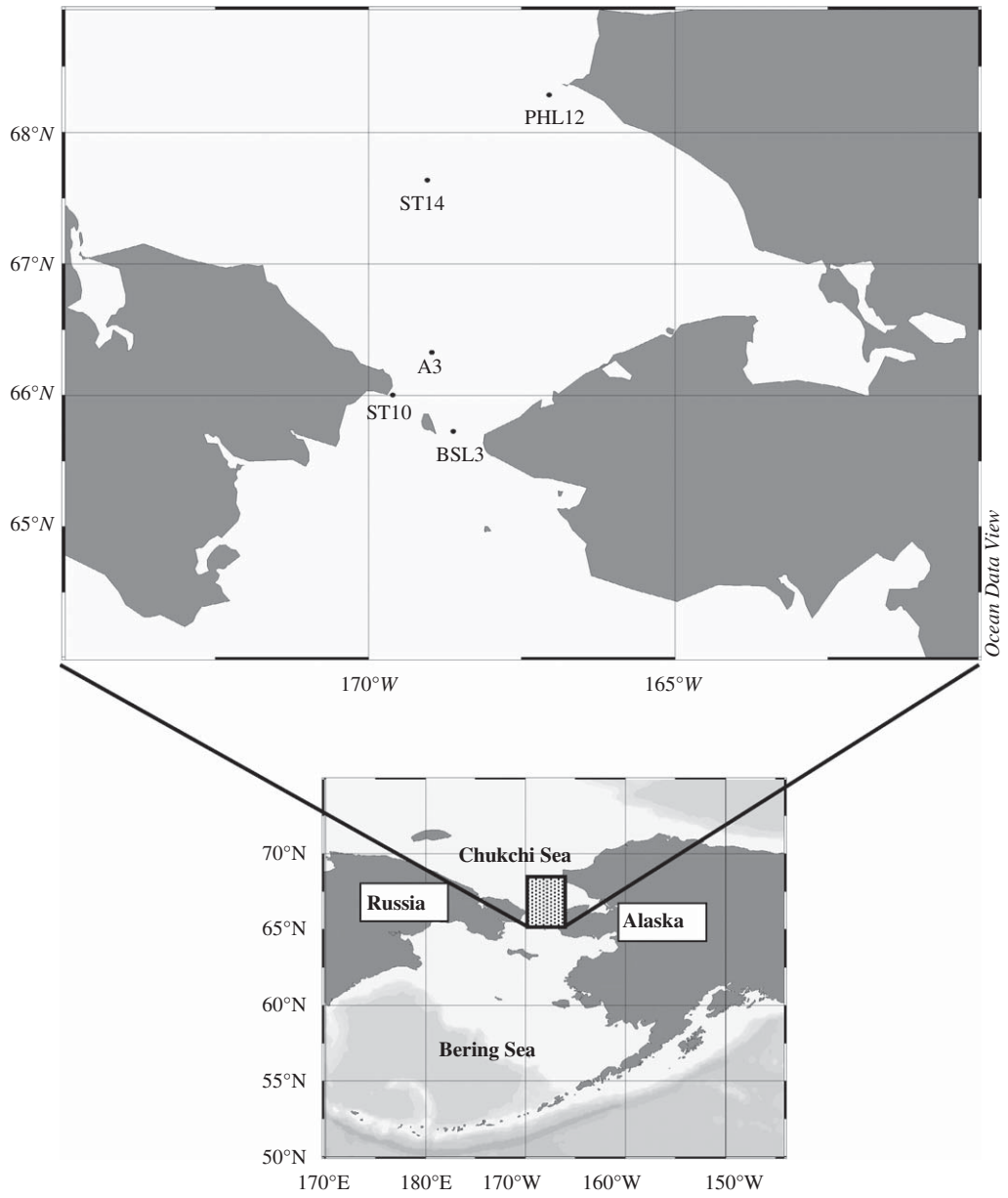

Fig. 1. Locations of five productivity stations for macromolecular composition analysis in the Chukchi Sea in 2004. ST10 and ST14 were from the RUSALCA cruise and BSL3, A3, and PHL12 were from the *Alpha Helix* (HX) cruise in 2004.

McRoy, 1993; Lee et al., 2007). Recently, Lee et al. (2007) found there are two distinctly different size compositions of phytoplankton communities in the two different water masses (determined by bottom salinities at 40 m depth) in the Strait and Chukchi Sea. Phytoplankton >20 μm contributed about 42% and 94% of total biomass in the water columns of ACW and AW, respectively (Lee et al., 2007).

The photosynthetic carbon allocations into different macromolecular classes (proteins, lipids, polysaccharides, and low-molecular-weight metabolites (LMWM)) of primary producers can provide important clues to the environmental factors that control their physiological conditions and thus productions (Morris, 1981; Smith et al., 1989, 1997). Moreover, their biochemical composition could affect the nutritional status of higher trophic levels (Scott, 1980; Lindqvist and Lignell, 1997). The primary objective in this study was to compare physiological conditions of phytoplankton in different water masses with different nutrient concentrations. The second objective was to evaluate their importance in the Bering Strait and Chukchi Sea ecosystem – one of the highly productive regions in the Arctic Ocean (Gosselin et al., 1997) – by determining carbon allocations into different macromolecules as photosynthetic end-products.

2. Materials and methods

2.1. Samplings

The samples for the determination of the photosynthetic carbon allocation at five stations in the Bering Strait and Chukchi Sea were collected from two consecutive cruises (Fig. 1). The first was the Russian–American Long-term Census of the Arctic (RUSALCA), a joint US–Russian research program, provided the ideal sampling across all major water masses including territorial waters of the Russian Federation in the Bering Strait and Chukchi Sea from mid to late August in 2004. Two (ST10 and ST14) of the five stations were from the RUSALCA cruise. The second was the

Alpha Helix (HX) cruise as a part of the long-term monitoring of the effect of inflow into the Arctic Ocean via Bering Strait, which covered mainly US waters from late August to early September in 2004. The samples from BSL3, A3, and PHL12 were obtained from the HX cruise.

2.2. Inorganic nutrient analysis and size fractionation of chlorophyll-a

Six light depths (100%, 50%, 30%, 12%, 5%, and 1% penetration of the surface irradiance, PAR) were determined from an underwater PAR sensor lowered with CTD/rosette samplers on the HX cruise, while a LICOR 4π light sensor (LI-193SB model) was used for the light depth determinations on the RUSALCA cruise. Water samples for inorganic nutrients (nitrate, ammonium, silicate, and phosphate) at each light depth were obtained from Niskin bottles mounted on CTD/rosette sampler 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 within $\pm 0.1\,\mu M$.

Size-fractionated chlorophyll-a was determined on samples passed sequentially through 20 and 5 μm Nuclepore filters (47 mm) and 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 dimethyl sulfoxide (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.

2.3. Productivity experiments for photosynthetic carbon allocation

Productivity experiments were conducted at the same six light depths for hourly carbon uptake rates and three light depths (100%, 30%, and 1%) for photosynthetic carbon allocations at five different stations, using a ^{13}C isotope tracer technique. Seawater samples of each light depth were transferred from the Niskin bottles to 8.8 L polycarbonate incubation bottles which were covered with screens appropriate for each light depth. To measure the uptake rates of carbon, isotope-enriched (99%) solutions of $NaH^{13}CO_3$, was added to the bottles at concentrations of ~0.2 mM ($^{13}CO_2$) (Hama et al., 1983). Bottles were incubated in a deck incubator cooled with surface seawater. The 4–7 h incubations were terminated by filtration through pre-combusted (450 °C) GF/F glass fiber filters (47 mm). For size-fractionated macromolecular compositions, incubated waters were well mixed and distributed into two filtration sets for total phytoplankton and small-size cells ($<5\,\mu m$). Then, samples were passed sequentially through 5 μm Nuclepore filters and GF/F for the small-size cell separations. The filters were immediately frozen at −20 °C and preserved for photosynthetic carbon allocation analysis at the stable isotope laboratory of the University of Alaska Fairbanks (UAF), US.

2.4. Photosynthetic carbon allocation analysis

The differential extractions of macromolecular classes (low-molecular-weight metabolites, lipids, proteins, and polysaccharides) were performed based on the method of Li et al. (1980). The filters with particulate material were cut into small pieces and transferred individually into test tubes. To the test tubes, 3 ml of chloroform-methanol (2:1 v/v) was added and ultrasonified for 20–30 min to extract lipids and low-molecular-weight metabolites from phytoplankton on the filters. After the extraction, the suspension was collected by a Pasteur pipette and stored in a new test tube. This extraction procedure was repeated three times to completely extract all lipids and LMWM from the filters. When the extractions were completed, 1.5 ml distilled water was added to the solution in the tube. The mixture was shaken vigorously for 2–3 min each time and set up for separation of the chloroform phase for lipids and the methanol–water phase for LMWM. The filters were resuspended in 4 ml of 5% trichloroacetic acid (TCA) and heated at 95 °C for 20–30 min. The suspension was collected for polysaccharides (TCA-soluble) with a Pasteur pipette. The filters were extracted with an additional further 4 ml of 5% TCA, washed with 5% TCA solution, and saved for protein analysis (TCA-insoluble). Abundances of ^{13}C in different macromolecular classes were determined in the Finnigan Delta+XL mass spectrometer laboratory. Carbon production rates for each class were calculated according to Hama et al. (1983). A separate measure of total carbon assimilation per each class was not obtained for this study, because the total carbon abundance was too high for the mass spectrometer to measure. So, the data from the results do not indicate absolute rates of carbon production, but show relative carbon assimilations for comparison.

3. Results

3.1. Water mass distributions

Based on the salinities in the productivity stations (Fig. 2), three different water masses flowing through Bering Strait into the Chukchi Sea were determined for comparison. The locations and environmental conditions of the five stations are summarized in Table 1. The water column from surface to bottom of PHL12 was the ACW mass whose salinity is normally lower than 31.8. In contrast, station BSL3 had characteristics of BSW. The water columns of ST10, A3, and ST14 stations had a typical water mass composition of AW (>32.5).

3.2. Vertical nutrient concentrations

In general, the nutrient concentrations were low in the upper water column from 100% to 30% light depths and increased from 12% to 1% light depths at all stations except PHL12, where the nutrients were constant in the water column from the 100% to 1% light depths (Fig. 3). Phosphate was usually found to be at low concentrations, whereas silicate was relatively high at all the stations except BSL3 which contained very low concentrations (~0.1 μM) from 100% to 12% light depths. Nitrate was depleted at all light depths at PHL12 but other stations had somewhat higher concentrations at 5% and 1% light depths. In contrast, relatively high concentrations of ammonium existed in the water columns from 100% to 1% light depths at BSL3, A3, and PHL12.

3.3. Size fractionation of chlorophyll-a and carbon uptake rates of phytoplankton

The large-size cells (>5 μm) were predominant (>85%) at all stations except PHL12 where large-size cells contributed about 50% of biomass, as estimated by chlorophyll-a concentrations, in the water column (Fig. 4). The carbon uptake rate integrated over the euphotic zone at ST14 was the highest ($84.6\,mg\,C\,m^{-2}\,h^{-1}$) followed by A3 ($51.0\,mg\,C\,m^{-2}\,h^{-1}$), whereas the uptake rate at ST10 was the lowest ($25.8\,mg\,C\,m^{-2}\,h^{-1}$) among the five productivity stations (Fig. 5). The rates in stations BSL3 and PHL12 were 29.0 and $37.7\,mg\,C\,m^{-2}\,h^{-1}$, respectively. However, the biomass-specific rates of production were highest (1.67 mg C

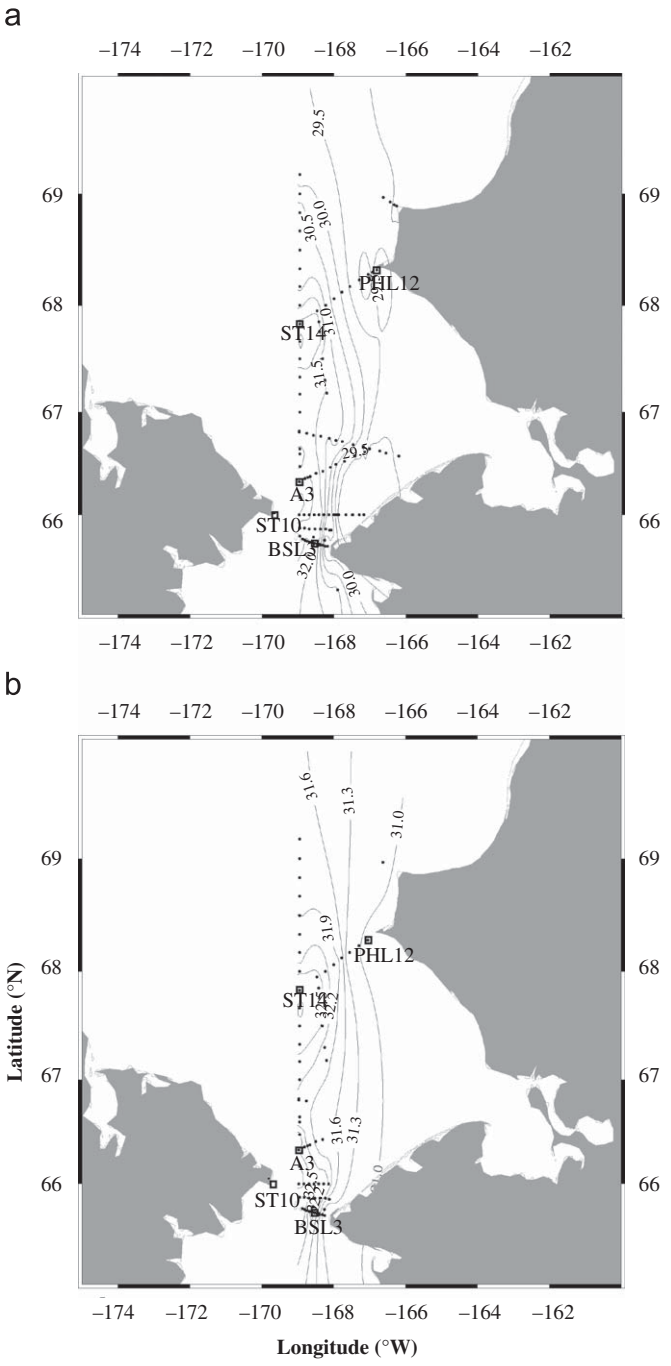

Fig. 2. Salinity distributions at surface (0 m) (a) and bottom (40 m) (b) sampling depths of the productivity stations in the Chukchi Sea during the HX cruise in 2004. The figure was adapted from Fig. 5 in Lee et al. (2007).

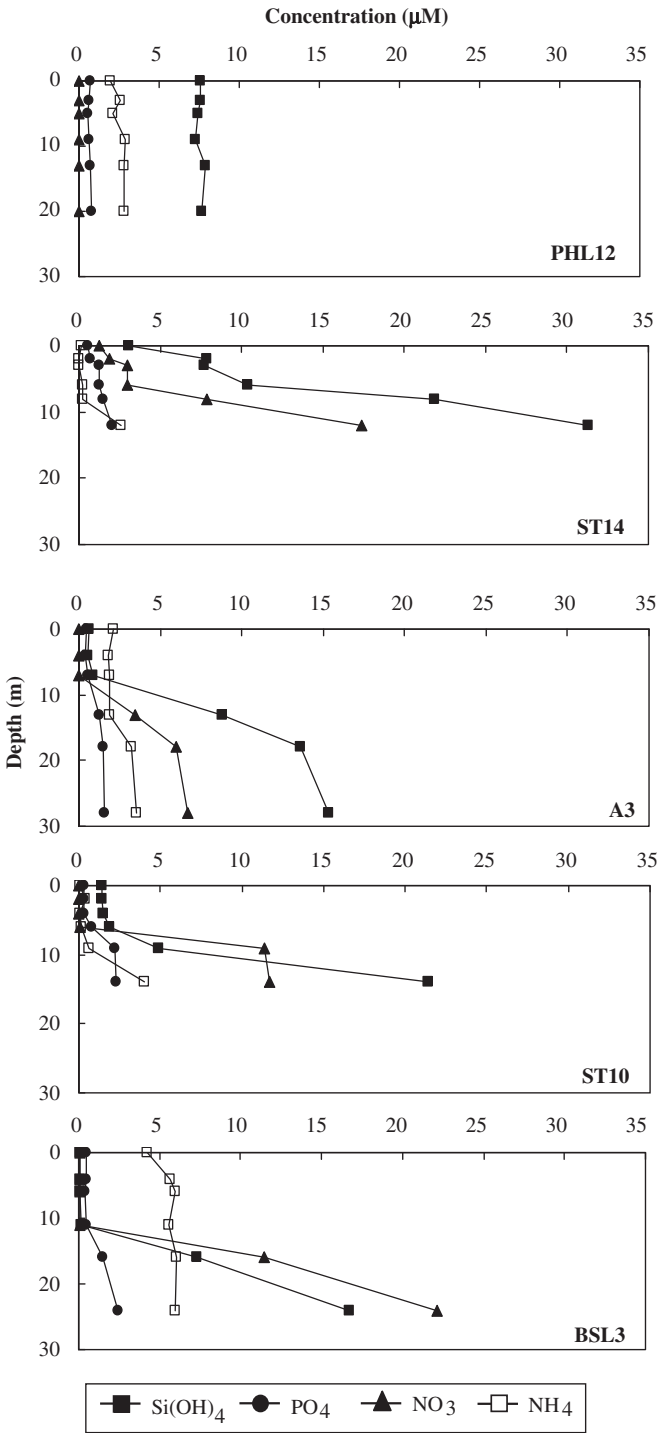

Fig. 3. Vertical nutrient concentrations from 100% to 1% light depths at the five productivity stations in the Chukchi Sea in 2004.

Table 1
Locations and environmental conditions at the five productivity stations in the Bering Strait and Chukchi Sea in 2004.

Station	Location		Water depth (m)	Water temperature (°C)	Salinity	Surface mixed layer depth (m)	Total Chl-a concentration (mg chl-a m^{-2})
	Latitude (°N)	Longitude (°W)					
BSL3	65 43. 59	168 36. 93	49	5.1	32.3	18	17.4
ST10	66	169 36. 60	52	4.7	33.0	5	134.3
A3	66 19. 52	168 58. 06	55	5.3	32.6	5	184.6
ST14	67 38. 40	169 02. 40	50	4.2	32.7	7	160.9
PHL12	68 17. 01	167 03. 08	37	11.1	29.4	10	26.2

Water temperature, salinity, surface mixed layer depth, and total Chl-a concentration were averaged throughout the euphotic zone from 100% to 1% light depths.

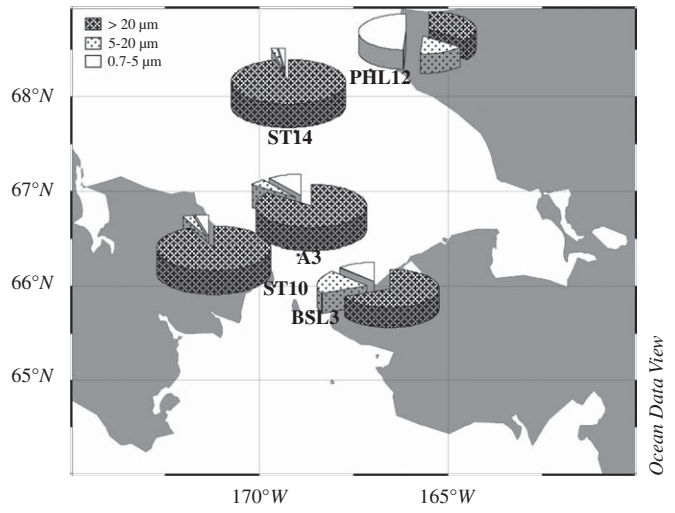

Fig. 4. Compositions of different size-fractionated phytoplankton averaged from three different light depths (100%, 30%, and 1%) at the productivity stations.

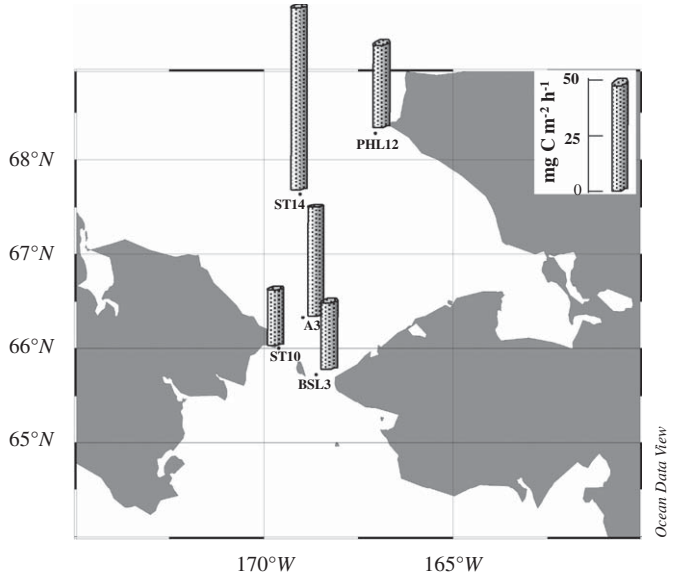

Fig. 5. The carbon uptake rates of phytoplankton at the productivity stations in the Chukchi Sea.

(mg Chl-a)$^{-1}$ h^{-1}) at ST10 followed by PHL12 (1.44 mg C (mg Chl-a)$^{-1}$ h^{-1}) and was lowest (0.19 mg C (mg Chl-a)$^{-1}$ h^{-1}) at ST10.

3.4. Photosynthetic carbon allocations of phytoplankton in the Chukchi Sea

Protein allocations at the three optical depths (100%, 30%, and 1%), especially 1% light depths, were most dominant among different products except 100% and 30% light depths at ST14 in the central Chukchi Sea, where LMWM productions were predominant (>70%) (Fig. 6). The carbon allocation patterns of small cell-size communities (<5 μm) were compared with those of large phytoplankton communities (>5 μm) in BSL3 (Fig. 7). Proteins and LMWM productions in large-size communities were highly active at three optical depths. The production rates of proteins ranged from 30.9% to 58.3%, whereas the LMWM rates were between 28.1% and 57.9%. In contrast, the protein production rates of small cells were much larger (78.4–83.7%). For comparison of euphotic zone at each station, allocation was averaged from the

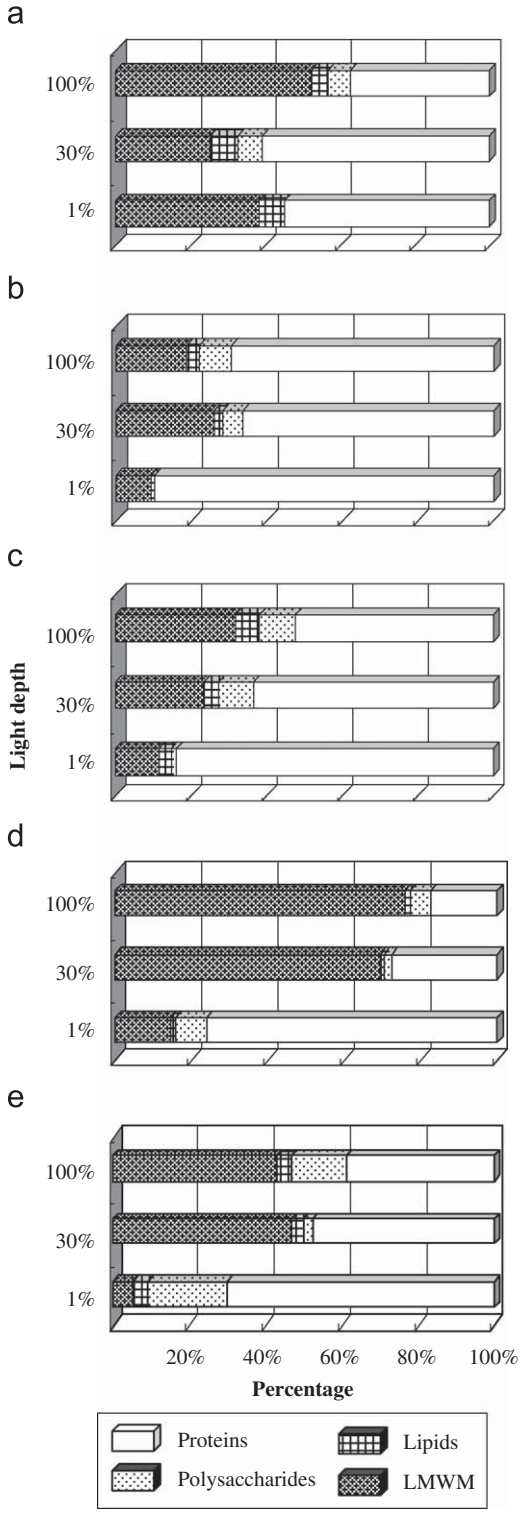

Fig. 6. Photosynthetic carbon allocations of macromolecules in phytoplankton in the Chukchi Sea. (a) BSL3 (b) ST10 (c) A3 (d) ST14 (e) PHL12.

three light depths (Fig. 8). In general, the allocations of proteins and LMWM were very high (57.1% and 32.7%, respectively) whereas those of polysaccharides and lipids were relatively low (6.7% and 3.5%, respectively). The highest allocation of proteins was in the water column of ST10 (75.3%) followed by A3 (66.6%). In contrast, the lowest allocation was at ST14 (40.0%). The allocations of PHL12 and BSL3 were 52.2% and 51.0%, respectively.

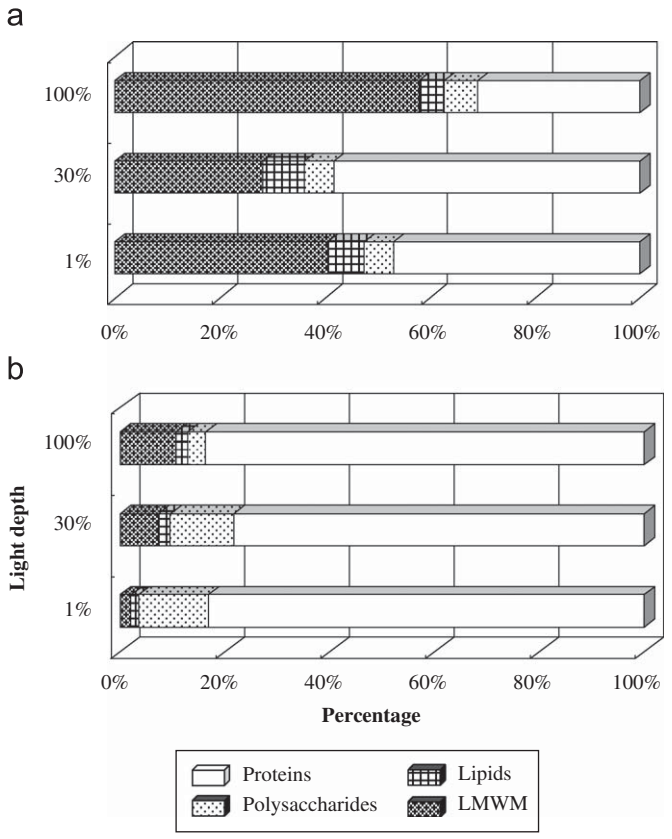

Fig. 7. Comparison of macromolecular compositions between different phytoplankton communities in BSL3, based on their cell sizes. (a) large cells (>5 μm) (b) small cells (<5 μm).

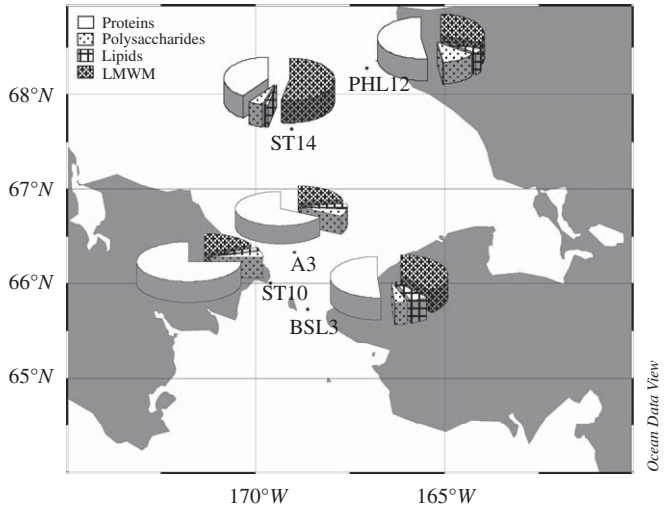

Fig. 8. Carbon allocations of macromolecules in phytoplankton averaged from three different light depths at the productivity stations.

3.5. Macromolecular allocations in relation to environmental factors

Pearson's correlation matrix was used to test for relationships between biosynthetic patterns and environmental factors using the data from all five stations (Table 2). No significant correlation for any macromolecular synthesis and physicochemical factors were found except the relationships between lipids and NH_4 concentration and polysaccharides and temperature. LMWM synthesis was positively correlated with total chlorophyll-a (r-values = 0.68, $n = 15$, $p<0.01$), whereas lipids and proteins were negatively correlated with total chlorophyll-a (r-values = −0.53 and −0.60, respectively). The inverse relationship between LMWM and proteins was highly significant (r-value = −0.96, $n = 15$, $p<0.01$).

4. Discussion

Earlier studies in the Chukchi Sea have shown different rates of primary production depending on different water masses which have different nutrient concentrations and phytoplankton biomass (Hansell et al., 1993; Springer and McRoy, 1993; Lee et al., 2007). However, there have been no data for their carbon allocations with regard to macromolecular compositions of phytoplankton in different water masses in this region. This is the first work to analyze the photosynthetic allocations of phytoplankton in different water masses passing through Bering Strait into the Chukchi Sea.

In general, the phytoplankton in the Chukchi Sea allocated more photosynthate to proteins and much less to lipids throughout the euphotic zones at all stations in the Chukchi Sea in 2004 (Fig. 8). However, there were some differences in photosynthetic carbon allocations between the different water masses in the region. Phytoplankton at ST10 and A3 which were largely affected by AW based on their salinities incorporated relatively more carbon into proteins than those in BSW (BSL3) and ACW (PHL12) (Fig. 8). Although ST14 had characteristics of the AW mass in the central Chukchi Sea, its protein production was lowest among the five stations. Under sufficient nutrient conditions, the dominant pathway is the production of LMWM, which are the precursors of macromolecules such as free amino acids and carbohydrates as storage forms (Smith et al., 1989; Lindqvist and Lignell, 1997; Mock and Gradinger, 2000). Conover (1975) and Dortch et al. (1984) described the storage of free amino acids in diatom cells. The predominant phytoplankton community at ST14 in the central Chukchi Sea is believed to be large, chain-forming diatoms (Springer and McRoy, 1993; Joo, personal communication).

For general vertical patterns of macromolecular allocations in the Bering Strait and Chukchi Sea, each allocation at optical depths of 100%, 30%, and 1% was averaged over all the five stations in Table 3 although they were variable among stations (Fig. 6). The percentage of the protein production increased with depth, whereas the fractions of LMWM and lipids decreased with depth in this study (Table 3). The vertical patterns in this study were consistent with the results from the earlier studies of allocation under different light depths (Suárez and Marañón, 2003; Smith et al., 1987, 1997). These trends of carbon allocations appear to be related to the light intensity, since irradiance is an important factor affecting carbon allocations into different macromolecules of phytoplankton (Suárez and Marañón, 2003). However, these might have also resulted from major nutrient concentrations with depth, although the proportions of carbon allocations at 100% and 30% light depths were still different (Table 3) under similar nutrient concentrations at the two depths except at ST14 (Fig. 3).

The averaged protein production over all the euphotic zones in the Chukchi Sea in 2004 was 57.1% (S.D. ±13.8%). In other studies, the maximal proportions of algal protein production range generally from 40% to 55% in nutrient-sufficient conditions (Morris, 1981; Ditullio and Laws, 1986). In contrast, the carbon incorporation into lipids was very low (<4%) in the water columns. The proportion of lipids reported in the Arctic Ocean is 5–30% (Lindqvist and Lignell, 1997; Smith et al., 1997; Li and Platt, 1982). According to earlier studies, high incorporation into

Table 2
Pearson's correlation matrix of macromolecular compositions and environmental parameters.

	LMWM	Lipids	Poly	Proteins	PO4	SIO4	NO3	NH4	DIN	SAL	TEMP	TCHL	A
LMWM	1												
Lipids	*	1											
Poly	*	*	1										
Proteins	−0.96	*	*	1									
PO4	*	*	*	*	1								
SIO4	*	*	*	*	0.89	1							
NO3	*	*	*	*	0.93	0.84	1						
NH4	*	0.62	*	*	*	*	*	1					
DIN	*	*	*	*	0.92	0.80	0.98	0.64	1				
SAL	*	*	*	*	*	*	*	*	*	1			
TEMP	*	*	0.58	*	−0.60	*	−0.64	*	−0.60	−0.91	1		
TCHL	0.68	−0.53	*	−0.60	*	*	*	*	*	*	*	1	
A	*	*	*	*	*	*	*	*	*	0.89	−0.85	*	1

The *r*-values shown in this table indicate statistical significance when *p*-values are <0.05. Asterisks indicate that *r*-values are not significant. Poly: polysaccharides, DIN: total dissolved inorganic nitrogen, SAL: salinity, TEMP: water temperature, TCHL: total chlorophyll-a, A: large cell size of phytoplankton (>20 mM).

Table 3
Incorporation of carbon into different macromolecular products in phytoplankton at three different light depths averaged from five productivity stations in the Chukchi Sea in 2004.

	Light Depths		
	100%	30%	1%
LMWM	44.3±21.7	38.2±19.8	15.7±13.1
Lipids	3.9±1.8	3.5±2.4	3.3±2.3
Polysaccharides	8.8±3.6	5.1±2.9	6.0±8.9
Proteins	43.0±19.3	53.2±16.1	75.0±13.6

±: S.D.

proteins generally reflects physiologically healthy phytoplankton with high relative growth rates (DiTullio and Laws, 1986; Palmisano et al., 1988), whereas high incorporation into lipids is to be expected under physiologically nitrogen-deficient phytoplankton or during stationary growth phases (Morris, 1981; Parrish, 1987). If applied to our results, low incorporation into lipids and relatively high incorporation into proteins would suggest that the phytoplankton had no nitrogen limitation in any water mass of the Chukchi Sea at that time in 2004. This is an interesting result since the phytoplankton in ACW has been thought to be nitrogen limited (Hansell and Goering, 1990; Hansell et al., 1993; Springer and McRoy, 1993). Although nitrate was nearly depleted, ammonium was relatively high (2.0–2.9 μM) throughout the water column at PHL12. The high ammonium concentration is believed to have provided a nitrogen source for phytoplankton demand at PHL12 where small cells (<5 μm) comprised about 50% of the community. In fact, a small-size community of phytoplankton (<5 μm) incorporated much more carbon into proteins than large cells (>5 μm) at three optical depths (100%, 30%, and 1%) at BSL3, where there was substantially high NH_4 concentration (~5 μM) throughout the euphotic depth (Fig. 7), which suggests that small phytoplankton have less nitrogen stress than large phytoplankton. Some studies have shown that photosynthesis by small plankton depends on regenerated nitrogen such as ammonium, whereas large plankton depends largely on nitrate (Probyn, 1985; Koike et al., 1986; Lee et al., 2008). However, more size fractionation data will be needed to validate the result of more carbon incorporation into proteins in small cells than lager cells in nitrate-depleted waters, since this was based on a single station. It is interesting to also note that shallow inner shelf waters of the Bering Sea have been observed to maintain a relative high production rate through the utilization of rapidly regenerated ammonium (Rho and Whitledge, 2007).

In conclusion, the high incorporation carbon into proteins suggest that phytoplankton is not physiologically nitrogen limited in water masses of the Chukchi Sea, at least at the time of this study in 2004. The phytoplankton with high protein allocations could provide nitrogen-sufficient food for higher trophic levels, since protein carbon is incorporated with much higher efficiency into herbivores than those of the other macromolecular products (Scott, 1980; Lindqvist and Lignell, 1997). In fact, the high pelagic primary productivity provides enhanced local secondary production in the Chukchi Sea. A strong pelagic–benthic coupling of biological processes sustains some of the highest benthic faunal biomass in the Arctic Ocean, and consequently supports large populations of benthic-feeding marine mammals, the Western Arctic Bowhead whales, and seabirds at higher trophic levels in the food chain (Grebmeier and McRoy, 1989; Highsmith and Coyle, 1992; Springer and McRoy, 1993; Lee et al., 2005).

Since *in situ* measurements for the allocations were conducted at only five stations in the Bering Strait and Chukchi Sea in 2004, more *in situ* measurements for macromolecular compositions, especially for the compositions of different cell-size phytoplankton, under a variety of environmental conditions in the Chukchi Sea should be obtained to improve the understanding of arctic primary production processes and marine ecosystem responses to ongoing changes in the region.

Acknowledgments

We would like to thank the crew members of the R/V *Alpha Helix* and R/V *Professor Khromov*. We are also grateful to Dr. Rebecca Woodgate and Sarah Thornton for help with sampling and the CTD data. This research was supported by grants from KOPRI (PM08030 and PE009070) for sample analysis. For the field works, this study was supported by the NOAA Ocean Exploration and Arctic Research Offices through CIFAR grants (11-061a). We very much appreciate the constructive comments by anonymous reviewers that greatly improved an earlier version of the manuscript.

References

Aagaard, K., 1987. Physical oceanography of the Chukchi Sea: An overview. In: Chukchi Sea nformation Update, June 1987. Outer Continental Shelf Environmental Assessment Program US Department of the interior Minerals Management Service Alaska OCS Region OCS Study, MMS 86–0097.

Coachman, L.K., Aagaard, K., 1988. Transport through Bering Strait: annual and interannual variability. Journal of Geophysical Research 93, 15535–15540.

Coachman, L.K., Aagaard, K., Tripp, R.B., 1975. Bering Strait: The Regional Physical Oceanography. Univ. of Washington Press, Seattle, p.172.
Coachman, L.K., Shigaev, V.V., 1992. Northern Bering-Chukchi Sea ecosystem: the physical basis. In: Nagel, P.A. (Ed.), Results of the Third Joint US-USSR Bering and Chukchi Seas Expedition (BERPAC), Summer 1988. US Fish and Wildlife Service, Washington, DC, pp. 17–27.
Conover, S.A.M., 1975. Partitioning of nitrogen and carbon in cultures of the marine diatom *Thalassiosira fluviatilis* supplied with nitrate, ammonium or urea. Marine Biology 32, 231–246.
DiTullio, G.R., Laws, E.A., 1986. Estimates of phytoplankton N uptake based on $^{14}CO_2$ incorporation into protein. Limnology and Oceanography 28, 177–185.
Dortch, Q., Clayton Jr., J.R., Thoresen, S.S., Ahmed, S.I., 1984. Species differences in accumulation of nitrogen pools in phytoplankton. Marine Biology 81, 237–250.
Gosselin, M., Levasseur, M., Wheeler, P.A., Horner, R.A., Booth, B.C., 1997. New measurements of phytoplankton and ice algal production in the Arctic Ocean. Deep-Sea Research 44, 1623–1644.
Grebmeier, J.M., McRoy, C.P., 1989. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. III Benthic food supply and carbon cycling. Marine Ecology Progress Series 53, 79–91.
Hansell, D.A., Goering, J.J., 1990. Pelagic nitrogen flux in the northern Bering Sea. Continental Shelf Research 10, 501–519.
Hansell, D.A., Whitledge, T.E., Goering, J.J., 1993. Patterns of nitrate utilization and new production over the Bering-Chukchi shelf. Continental Shelf Research 13, 601–627.
Hama, T., Miyazaki, T., Ogawa, Y., Iwakuma, T., Takahashi, M., Otsuki, A., Ichimura, S., 1983. Measurement of photosynthetic production of a marine phytoplankton population using a stable ^{13}C Isotope. Marine Biology 73, 31–36.
Highsmith, R.C., Coyle, K.O., 1992. Productivity of arctic amphipods relative to gray whale energy requirements. Marine Ecology Progress Series 83, 141–150.
Koike, I., Holm-Hansen, O., Biggs, D.C., 1986. Inorganic nitrogen metabolism by Antarctic phytoplankton with special reference to ammonium cycling. Marine Ecology Progress Series 30, 105–116.
Lee, S.H., Schell, D.M., McDonald, T.L., Richardson, W.J., 2005. Regional and seasonal feeding by bowhead whales *Balaena mysticetus* as indicated by stable isotope ratios. Marine Ecology Progress Series 285, 271–287.
Lee, S.H., Whitledge, T.E., Kang, S.H., 2007. Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. Continental Shelf Research 27, 2231–2249.
Lee, S.H., Whitledge, T.E., Kang, S-H., 2008. Carbon uptake rates of sea ice algae and phytoplankton under different light intensities in a Landfast Sea ice zone, Barrow, Alaska. Arctic 61, 281–291.
Li, W.K.W., Glover, H.E., Morris, I., 1980. Physiology of carbon photoassimilation by Oscillatoria thiebautii in the Caribbean Sea. Limnology and Oceanography 25 (3), 447–456.
Li, W.K.W., Platt, T., 1982. Distribution of carbon and among photosynthetic end-products in phytoplankton of the Eastern Canadian Arctic. Journal of Phycology 18, 466–471.
Lindqvist, K., Lignell, R., 1997. Intracellular partitioning of $^{14}CO_2$ in phytoplankton during a growth season in the northern Baltic. Marine Ecology Progress Series 152, 41–50.
Mock, T., Gradinger, R., 2000. Changes in photosynthetic carbon allocation in algal assemblages of Arctic sea ice with decreasing nutrient concentrations and irradiance. Marine Ecology Progress Series 202, 1–11.
Morris, I., 1981. Photosynthetic products, physiological state, and phytoplankton growth. Canadian Bulletin Fisheries Aquatic Science 210, 83–102.
Nghiem, S.V., Rigor, I.G., Perovich, D.K., Clemente-Colón, Weatherly, J.W., 2007. Rapid reduction of Arctic perennial sea ice. Geophysical Research Letters 34, L19504.
Palmisano, A.C., Lizotte, M.P., Smith, G.A., Nichols, P.D., White, D.C., Sullivan, C.W., 1988. Changes in photosynthetic carbon assimilation in Antarctic sea-ice diatoms during spring bloom: variation in synthesis of lipid classes. Journal of Experimental Marine Biology and Ecology 116, 1–13.
Parrish, C.C., 1987. Separation of aquatic lipids classes by chromarod thin-layer chromatography with measurement by Iatroscan flame inonization detection. Canadian Journal of Fisheries and Aquatic Science 44, 722–731.
Probyn, T.A., 1985. Nitrogen uptake by size-fractionated phytoplankton populations in the southern Benguela upwelling system. Marine Ecology Progress Series 22, 249–258.
Rho, T.K., Whitledge, T.E., 2007. Characteristics of seasonal and spatial variations of primary production over the southeastern Bering Sea shelf. Continental Shelf Research 27, 2556–2569.
Rothrock, D.A., Zhang, J., Yu, Y., 2003. The arctic ice thickness anomaly of the 1990s: a consistent view from observations and models. Journal of Geophysical Research 108 (C3), 3083.
Scott, J.M., 1980. Effect growth rate of the food alga on the growth/ingestion efficiency of a marine herbivore. Journal of the Marine Biological Association, UK 60, 681–702.
Shoaf, W.T., Lium, B.W., 1976. Improved extraction of chlorophyll-a and -b from algae using dimethyl sulfoxide. Limnology and Oceanography 21, 926–928.
Smith, R.E.H., Clement, P., Cota, G.F., Li, W.K.W., 1987. Intracellular photosynthate allocation and the control of arctic marine ice-algal production. Journal of Phycology 23, 124–132.
Smith, R.E.H., Clement, P., Head, E., 1989. Biosynthesis and photosynthate allocation patterns of high arctic ice algae. Limnology and Oceanography 34, 591–605.
Smith, R.E.H., Gosselin, M., Kattner, G., Legendre, L., Pesant, S., 1997. Biosynthesis of macromolecular and lipid classes by phytoplankton in the Northeast Water Polynya. Marine Ecology Progress Series 147, 231–242.
Springer, A.M., McRoy, C.P., 1993. The paradox of pelagic food webs in the northern Bering Sea-III. Patterns of primary production. Continental Shelf Research 13, 575–599.
Suárez, I., Marañón, E., 2003. Photosynthate allocation in a temperate sea over an annual cycle: the relationship between protein synthesis and phytoplankton physiological state. Journal of Sea Research 20, 285–299.
Tynan, C.T., DeMaster, D.P., 1997. Observations and predictions of Arctic climatic change: potential effects on marine mammals. Arctic 50, 308–322.
Whitledge, T.E., Malloy, S.C., Patton, C.J., Wirick, C.D., 1981. Automated nutrient analysis in seawater. Brookhaven National Laboratory Technical Report BNL 51398.
Woodgate, R.A., Aagaard, K., Weingartner, T.J., 2005. Monthly temperature, salinity and transport variability of the Bering Strait throughflow. Geophysical Research Letters 32.