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High lipid composition of particulate organic matter in the northern Chukchi Sea, 2011

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ABSTRACT

We investigated the biochemical compositions (lipids, proteins, and carbohydrates) of particulate organic matter (POM) as a potential food source in the northern Chukchi Sea. We aimed to understand physiological status of phytoplankton, determine important controlling factors, and estimate the energetic contents of POM. The major inorganic nutrients were generally depleted at upper mixed-layer depth (>20 m). The average chlorophyll a (chl-*a*) concentration was 31.9 mg m^{-2} (S.D.= ±31.3 mg m^{-2}) in this study, significantly higher than that reported previously in the northern Chukchi Sea. Small phytoplankton (0.7–5 μm) accounted for 65.9% of total chl-*a* concentration. The overall average compositions of lipids, carbohydrates, and proteins were 50% (S.D.= ±10.7%), 35% (S.D.= ±11.0%), and 15% (S.D.= ±11.2%) for POM, respectively. Along with other evidence (e.g., low N:P and protein–carbohydrate ratios), the high lipid and low protein compositions of POM in this study suggests that phytoplankton might have had a nitrogen limitation and/or stationary growth phase in the northern Chukchi Sea during the cruise period, 2011. The overall average calorific content of food material (FM) was 149.2 μg L^{-1} (S.D.= ±36.5 μg L^{-1}) or 1.0 Kcal m^{-3} (S.D.= ±0.2 Kcal m^{-3}). The relatively higher calorific contents in the northern Chukchi Sea were due to high lipid contributions and the considerably high calorific content of FM per POC.

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1. Introduction

Phytoplankton are basic primary producers in marine food webs. They obtain energy through photosynthesis, chemical synthesis of organic compounds from carbon dioxide using sunlight. Their carbon is divided into three macromolecular classes: proteins, lipids, and carbohydrates. Earlier studies have reported how phytoplankton responds to changes in such environmental conditions as light, nutrients, salinity and temperature. Such changes determine phytoplankton's nutritional value (food quality) to herbivorous animals, which can affect secondary production as well as the higher trophic levels in marine ecosystems. Research has investigated phytoplankton incorporation of ^{14}C or ^{13}C into protein, lipid, polysaccharide, and low molecular weight metabolites (LMWM) during short or long incubation in regions including the Antarctic and Arctic Oceans (Smith and Morris, 1980; Morris, 1981; Priscu and Priscu, 1984; Rivkin and Voytek, 1987; Lindqvist and Lignell, 1997; Suárez and Marañón, 2003; Lee et al., 2007, 2009). Unfortunately, these studies have focused on either the physiologies of several species of phytoplankton from cultivated conditions, or patterns of short-term photosynthetic allocations. Although isotope-labeled carbon patterns in phytoplankton can reflect their physiological and nutritional status (Lee et al., 2009) at their exact growth moment, this is just a snapshot. Actually, phytoplankton continuously reallocate macromolecular compositions at night (Lancelot and Mathot, 1985). Instead, we are going to analyze composition patterns of proteins, lipids, and carbohydrates to reflect phytoplankton's longer-term responses to their environment (Marañón et al., 1995).

The Arctic Ocean shows most substantial alterations due to climate change worldwide. Increasing temperature has led to thinning, melting sea ice, affecting its marine ecosystem over the past several decades (Pabi et al., 2008; Matrai et al., 2013). These changes have altered the timing of phytoplankton spring blooms, the overall primary production, and the individual size and composition of benthic invertebrates, and the life histories of zooplankton (Arrigo et al., 2008; Li et al., 2009; Søreide et al., 2010; Grebmeier, 2012). In addition to the quantity of phytoplankton

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biomass, the quality of phytoplankton as a major food source could be changed. This study aims first to analyze compositions of macromolecular pools (proteins, lipids, and carbohydrates) of biopolymeric particulate organic matters (POM) in the northern Chukchi Sea. Its second goal is to find important environmental controlling factors for changes in these compositions, such as light and nutrients. The third goal is to estimate the energetic contents of biopolymeric particulate organic matter (POM), determining their food values to higher trophic organisms. This is the first work to analyze POM in the Arctic Ocean for potential food quality.

2. Materials and methods

2.1. Study area

We investigated fourteen stations in the northern Chukchi Sea between July and August 2011 (Fig. 1). At each station, we used the CTD system to obtain physical properties such as water temperature and salinity. Niskin were used for bottles collecting water samples using a CTD rosette sampler. Table 1 summarizes the characteristics of each station's location.

2.2. Phytoplankton chlorophyll a and nutrient analysis

Water samples for nutrient and chlorophyll a (chl-*a*) concentrations were collected using a CTD rosette sampler in the photic zone. A QuAAtro auto analyzer (SEAL Analytical, UK), used according to the manufacturer's manual, was used for determing the major dissolved inorganic nutrient concentrations (nitrite + nitrate, ammonium, silicate, and phosphate). We filtered water samples for measurements of total chl-*a* concentration through 25 mm GF/F (Whatman, 0.7 μm pore) and filtered them further by size with 20 and 5 μm membrane filters and 47 mm GF/F (Whatman, 0.7 μm pore). A Trilogy fluorometer determined concentrations of chl-*a* (Turner Designs, USA), after 24 h extraction in 90% acetone at 4 °C.

2.3. Particulate organic carbon and nitrogen analysis

We filtered seawater onto 25 mm GF/F (Whatman, 0.7 μm pore) for particulate organic carbon (POC) and particulate organic nitrogen (PON) measurements, immediately freezing the filters at −80 °C until analysis. We determined total POC and PON using a Finnigan Delta+XL mass spectrometer, after overnight HCl fuming to remove carbonate, at the stable isotope laboratory of University of Alaska Fairbanks.

2.4. Macromolecular compositions of POM

Water samples of POM were obtained from 3 light depths (100, 30, and 1%) during the second Korean Arctic cruise, 2011. Each one-liter seawater sample of proteins, lipids, and carbohydrates was filtered through a pre-combusted 47 mm GF/F filter (Whatman, 0.7 μm pore) and was then immediately stored at −80 °C

Table 1
Description of stations in the northern Chukchi Sea in 2011 (Water temperature, salinity, and integrated chl-*a* concentrations were averaged from surface to 100 m).

Station	Latitude (°N)	Longitude (°E)	Photic zone (m)	Water temperature (°C)	Salinity (‰)	Integrated chl-*a* (mg chl-*a* m^{-2})
St. 1	73.61	193.49	38	−1.21	32.01	93.29
St. 2	74.28	192.35	54	−1.24	30.89	183.52
St. 3	75.1	193.67	92	−1.25	30.58	7.38
St. 4	76.4	195.34	100	−0.71	30.19	3.91
St. 5	77.73	198.09	95	−0.65	30.26	4.8
St.6	78	191.69	84	−1.05	30.67	4.73
St. 7	78	188.04	87	−1.17	31.06	7.24
St. 9	77.98	180.69	79	−1.11	31.24	6.67
St. 11	77.98	173.98	60	−1.17	31.35	14.98
St. 13	76.4	174	57	−1.44	31.27	14.16
St. 15	76.4	180.66	81	−1.31	30.87	12.4
St. 16	76.4	183.97	81	−0.96	30.5	6.05
St. 17	77	188	98	−0.7	30.19	5.37
St. 18	76.29	192.84	98	−0.87	30.04	7.87

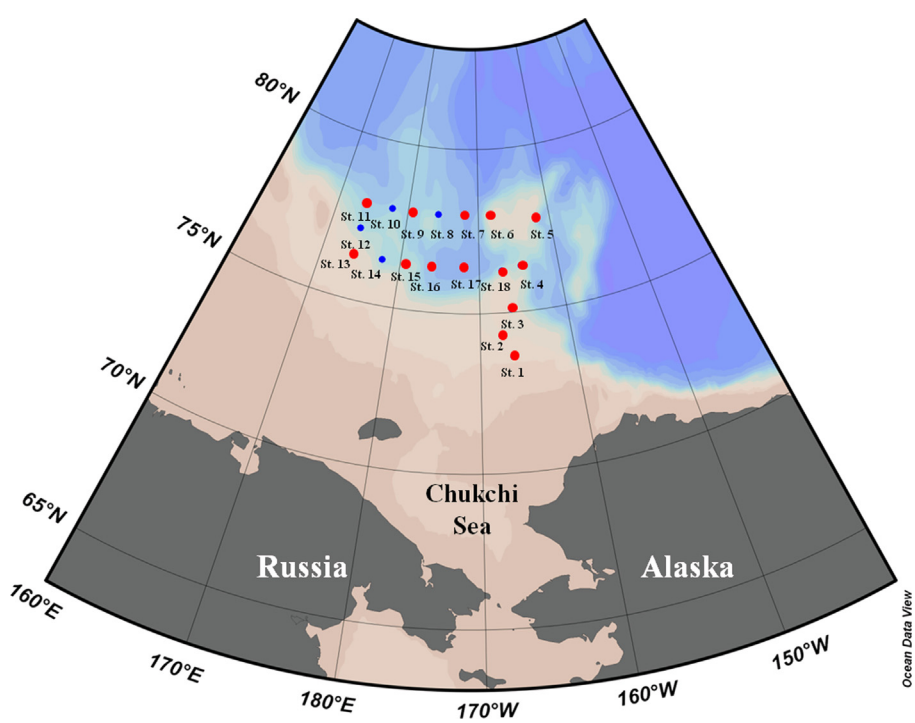

Fig. 1. Location of sampling area in the northern Chukchi Sea in 2011 (large closed circles: macromolecular stations).

until analysis. A modified method of Lowry et al. (1951) determined protein concentration, the phenol–sulfuric method from Dubois et al. (1956) extracted the carbohydrates and a column method modified from Bligh and Dyer (1959) and Marsh and Weinstein (1966) separated the lipids.

2.4.1. Protein extraction

For total protein extraction, a filter was ground (using a glass rod for each sample) in a 15 mL glass tube, after additions of 1 mL distilled water (DH_2O) and 5 mL Alkaline Copper solution. After 10 min, we added 5 mL reagent (0.5% Folin–Ciocalteu phenol) to the glass tube, and set the sample for 1 h 30 min at room temperature with occasional shaking with a vortex. We centrifuged the mixture at 3000 rpm for 10 min. After transferring the supernatant, we measured absorbance at 750 nm using a spectrophotometer (Labomed, Germany). For determing protein concentrations, we prepared calibration curves with the protein standard solution (2 mg mL^{-1}, SIGMA).

2.4.2. Lipid extraction

We extracted lipids in a 3 mL mixture of chloroform and methanol (1:2, v/v). After that, we centrifuged the mixture at 2500 rpm for 10 min and stored it at 4 °C for 1 h, then transferred the supernatant into another tube. We repeated this twice to extract all lipids from the filters, combining the later supernatants with the first. After adding 4 mL of DH_2O to the solution and centrifuging it at 2000 rpm for 2 min, we removed the top part of soluble mixture (methanol + DH_2O) from the tube. The remaining mixture of chloroform + lipids was dried at 40 °C for 48 h in an oven. After drying, we added 2 mL of H_2SO_4 and heated the mixture to 200 °C for 15 min, then quickly cooled it to room temperature in a water bath. Finally, the spectrophotometer measured absorbance for lipids at 360 nm, after we added 3 mL of DH_2O and mixed. Tripalmitin solutions were used as a standard for lipid concentration.

2.4.3. Carbohydrate extraction

To extract carbohydrates, a filter was put into a 13 mL polypropylene tube and added with 1 mL DH_2O and 1 mL 5% phenol solution. Keeping it at room temperature 40 min, we then added 5 mL H_2SO_4 and set the sample for 10 min to measure carbohydrates, then centrifuged at 3500 rpm for 10 min. After we transferred the supernatant, the spectrophotometer was used for determining the absorbance of samples at 490 nm. A calibration curve with the glucose standard solution (1 mg mL^{-1}, SIGMA) determined carbohydrate concentration.

2.5. Caloric value calculation and statistical analyses

The WinBerg (1971) equation (Fabiano et al., 1993, 1996) was used for calculating caloric value (Kcal g FM^{-1}) and calorific content (Kcal m^{-3}) of FM (carbohydrate + lipid + protein concentrations). We used the statistical software SPSS to perform *t*-tests and Pearson's Correlation Coefficient at level of significance $p < 0.05$.

3. Results

3.1. General physical characteristics (salinity and temperature) of the study area

Fig. 2 shows the distributions of salinity and water temperature from surface to 100 m depth. The salinity ranged from 25.2 to 32.9‰ and the temperature only ranged from −1.4 to 1.5 °C. Except St. 1 and St. 5, all stations were below 0 °C. Melting sea ice left at the upper mixed layer (> 20 m) relatively diluted surface waters during the sampling period (Fig. 2A). Below that layer, salinity increased with depth, but temperature did not drop consistently. Water was relatively warm between 30 and 80 m at some stations (Fig. 2B).

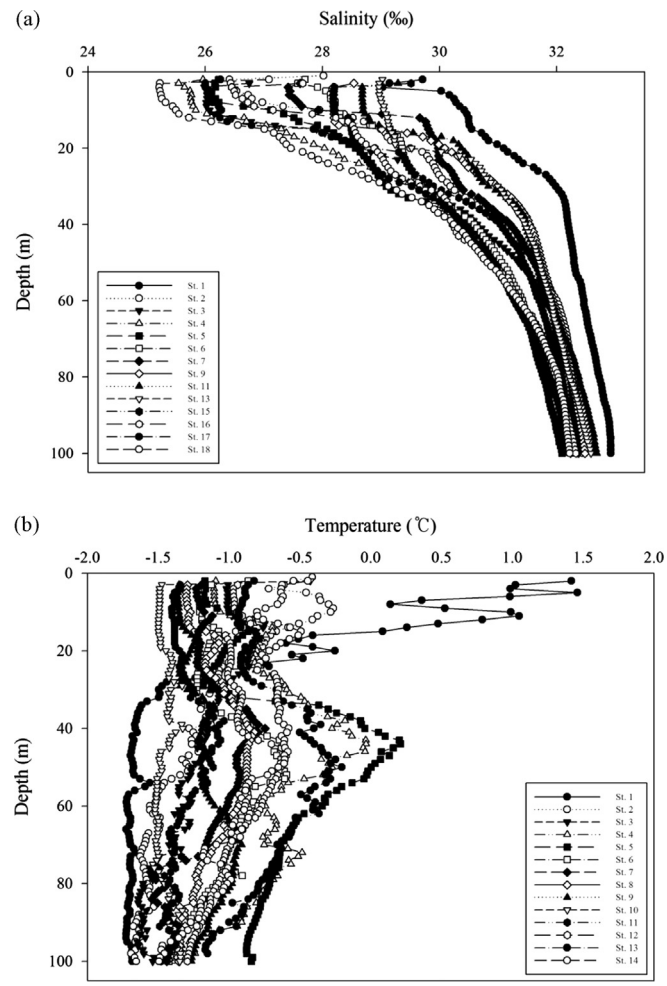

Fig. 2. The vertical pattern in salinity (A) and temperature (B) from surface to 100 m water depths at macromolecular stations.

3.2. Chlorophyll a concentration and nutrient distribution

Fig. 3 shows distributions for major nutrients (PO_4, NO_2+NO_3, NH_4, and SiO_2). All inorganic nutrients except NH_4 increased with depth from surface to 100 m depth. The concentration of NO_2+NO_3 ranging from 0 to 14.5 μM was mostly depleted at upper mixed layer (> 20 m). We found relatively high concentrations of SiO_2 (1.4–34.7 μM). The concentrations of NH_4 and PO_4 ranged from 0.2 to 1.0 μM and 0.5 to 1.8 μM, respectively.

The lowest total chlorophyll a (chl-*a*) concentration integrated from six light depths (100, 50, 30, 12, 5 and 1%) was 12.5 mg m^{-2} at St. 6, whereas the highest concentration was 120.6 mg m^{-2} at St. 2 (Fig. 4). The overall average chl-*a* concentration was 31.9 mg m^{-2} (S.D. = ± 31.3 mg m^{-2}) (Fig. 4). The size-fractionated chl-*a* concentrations from 3 light depths (100, 30, and 1%) show a phytoplankton community dominated by small phytoplankton (0.7–5 μm) accounting for 65.9 ± 11.2% of the total chl-*a* concentration, followed by middle-sized (5–20 μm; 17.5 ± 4.8%) and large cells (> 20 μm; 16.6 ± 13.8%) (Fig. 5).

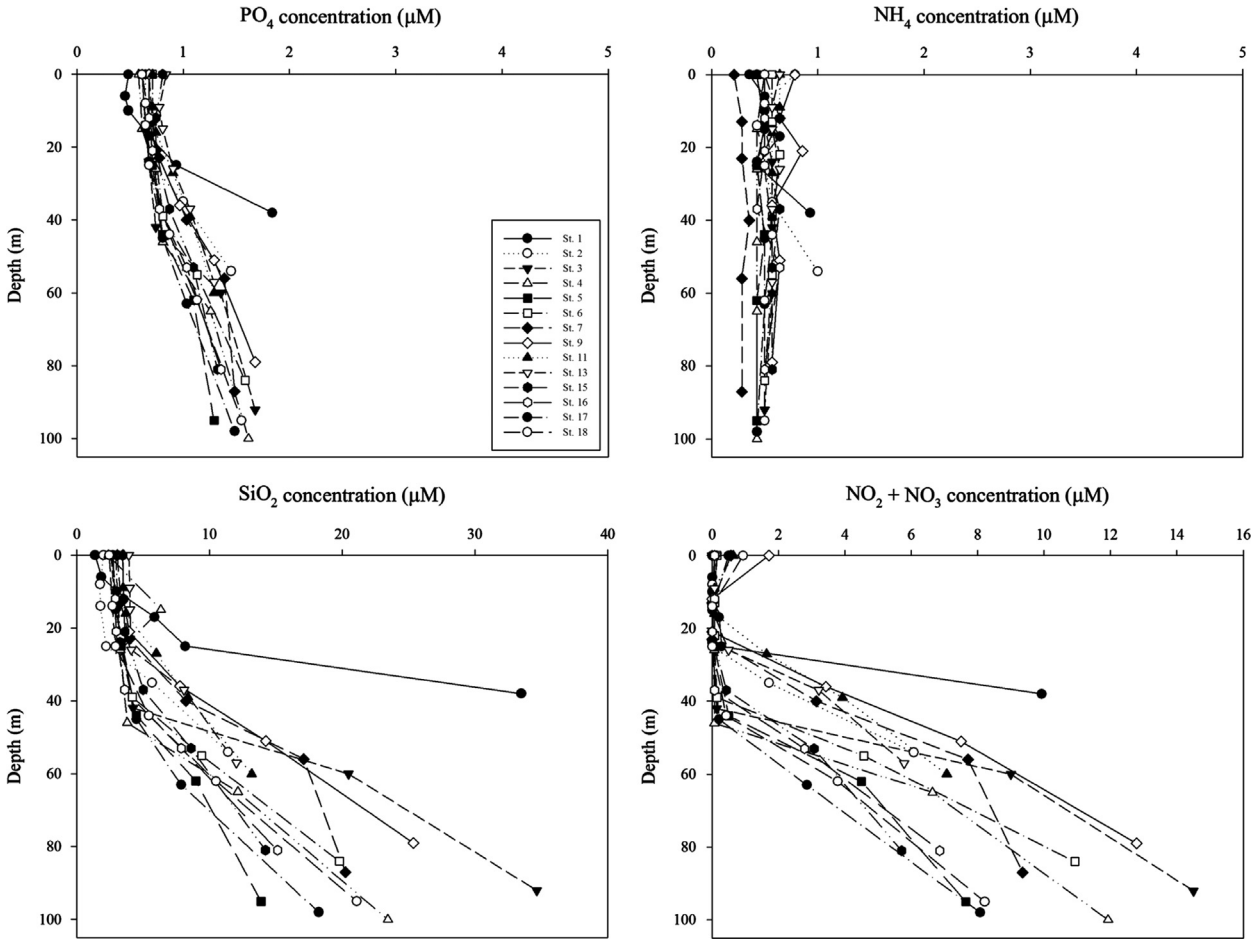

Fig. 3. The vertical distributions of inorganic major nutrient concentrations from surface to 100 m in the northern Chukchi Sea.

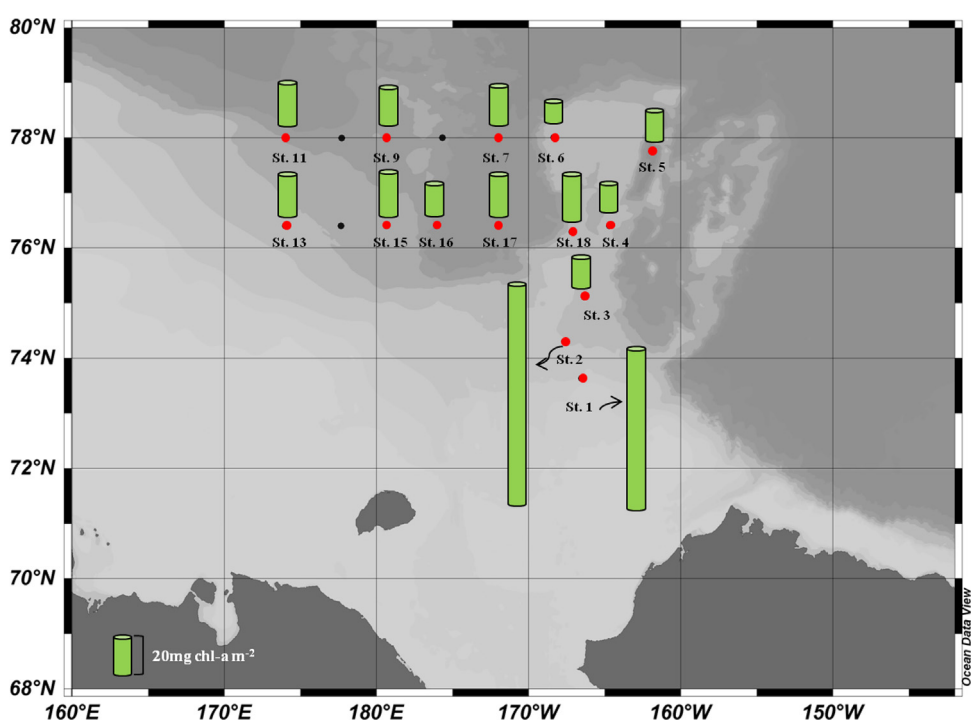

Fig. 4. Distribution of chlorophyll-a concentrations (mg chl-*a* m^{-2}) integrated from surface to 1% light depth at macromolecular stations.

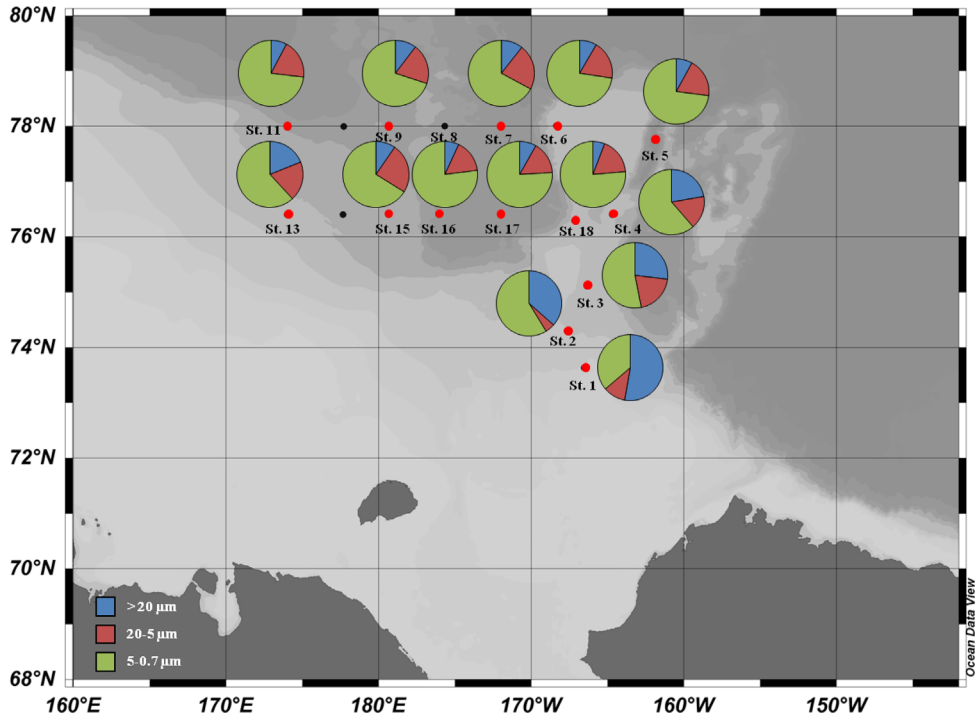

Fig. 5. Compositions of different size-fractionated chlorophyll-a concentration in the northern Chukchi Sea.

3.3. Particulate organic carbon and nitrogen

Mean concentrations of POC and PON from surface to 1% light depth were $50.2 \pm 45.4\ \mu g\ L^{-1}$ and $7.9 \pm 6.7\ \mu g\ L^{-1}$, respectively (Table 2). The ratio of carbon to nitrogen (C:N) of organic matter ranged from 4.2 to 10.5 (7.4 ± 1.3). POC and PON showed a strong linear trend (POC = 6.7484 × PON − 3.264, $r^2 = 0.98$, $p < 0.001$, *t*-test), as indicated by the high and significant determination coefficient in the whole data set.

3.4. Macromolecular compositions of POM

Since there was no substantial difference among the three light depths, we averaged macromolecule concentrations of phytoplankton for each station (Fig. 6). The ranges of concentrations of proteins, lipids, and carbohydrates were 0.7–86.3 $\mu g\ L^{-1}$, 50.2–105.0 $\mu g\ L^{-1}$, and 21.8–146.7 $\mu g\ L^{-1}$, respectively (Table 2). The highest and lowest compositions of lipids were at St. 4 (62%) and St. 1 (37%), respectively. Although carbohydrate compositions accounted for half of all macromolecular compositions at some stations (St. 5 and St. 18), they were generally less than those of lipids (Fig. 7). Overall, the average concentration of lipids ($50 \pm 10.7\%$) was higher than other classes, followed by carbohydrates ($35 \pm 11.0\%$), and proteins ($15 \pm 11.2\%$) (Fig. 7).

3.5. Relationship between macromolecular compositions and environmental factors

We used a Pearson's correlation matrix to test for relationships between macromolecular classes and environmental factors (Table 3). We found no significant correlations except the relationships between proteins and lipids and NH_4 concentration ($r = 0.34$ and 0.35, respectively, $p < 0.05$, $n = 42$). The calorific content of food was positively correlated with biomolecules ($r = 0.52$, 0.71, 0.61 for carbohydrates, proteins, and lipids, respectively, $p < 0.01$, $n = 42$).

4. Discussion and conclusions

4.1. Chl-a concentration in the northern Chukchi sea

The average chl-*a* concentration was 31.9 mg chl-*a* m^{-2} (SD = ± 31.3 mg chl-*a* m^{-2}) with a large variation from 12.5 to 120.6 mg chl-*a* m^{-2} (Fig. 4), significantly higher (*t*-test, $p < 0.05$) than that of the ice-free deep region in the northern Chukchi Sea during summer 2008 (13.8 mg chl-*a* m^{-2}) (Lee et al., 2012). Using satellite data, Pabi et al. (2008) and Arrigo et al. (2008) reported an increase in the Arctic Ocean's annual primary production. The decreased minimum summer ice extent has lengthened phytoplankton growing season. Especially in the Chukchi Sea, which has shown recent extreme reductions in area and thickness of sea ice (Perovich and Richter-Menge, 2009), Arrigo et al. (2008) found substantially higher annual production in 2007 than in 1998–2002. The higher chl-*a* concentration in this study might be resulted from this increase.

However, we should also consider seasonal variations in phytoplankton productivity and biomass, common in the Arctic Ocean (English, 1961; Pautzke, 1979; Yun et al., 2012). Our field cruise period was from late July to middle of August, 2011, whereas the period of field cruise in Lee et al. (2012) was from middle August to early September, 2008. Previously, English (1961) and Pautzke (1979) reported that phytoplankton biomass was significantly higher (5–10 times) in July and August than in September and October, and that productivity also decreased sharply after mid-August in the Arctic Ocean. During the sea ice cover period from late June to late July, 2005, the average chl-*a* concentrations integrated from the surface to about 50 m depth, under sea ice 1.2–2.5 m thick, was 10.4 mg chl-*a* m^{-2} (Lee et al., 2010). It is similar to the chl-*a* concentration (9.7 ± 3.7 mg m^{-2}) in the northeast Chukchi Sea from middle July to early August, 2010 with heavy ice conditions (Yun et al., 2015-a). To make a regional comparison, the southwestern Chukchi Sea normally have high levels (> 200 mg chl-*a* m^{-2}) of chlorophyll-a whereas low values (< 50 mg chl-*a* m^{-2}) exist in the southeast, reflecting different

Table 2
The macromolecules (proteins, lipids, and carbohydrates), POC, PON concentrations, and associated caloric value of FM from three light depths (100%, 30%, and 1%).

Station	Light (%)	Depth (m)	Carbohydrates ($\mu g\ L^{-1}$)	Proteins ($\mu g\ L^{-1}$)	Lipids ($\mu g\ L^{-1}$)	FM ($\mu g\ L^{-1}$)	POC ($\mu g\ L^{-1}$)	PON ($\mu g\ L^{-1}$)	Caloric value of FM (Kcal g^{-1})	Calorific content of FM (Kcal m^{-3})
St. 1	100	0	55.37	48.06	59.59	163.02	66.68	10.01	6.49	1.06
	30	10	88.2	58.13	78.76	225.09	98.14	15.71	6.35	1.43
	1	38	75.72	70.8	88.54	235.05	217.16	33.63	6.56	1.54
St. 2	100	0	46.31	53.53	71.72	171.55	65.52	8.78	6.79	1.17
	30	14	39.48	51.23	67.22	157.93	60.11	9.14	6.85	1.08
	1	54	65.72	43.17	84.04	192.93	263.07	37.68	6.77	1.31
St. 3	100	0	53.72	6.04	67.03	126.79	53.93	7.23	7.02	0.89
	30	24	46.78	16.12	57.64	120.53	45.04	7.82	6.87	0.83
	1	92	57.37	15.54	58.62	131.52	41.17	6.78	6.67	0.88
St. 4	100	0	29.83	5.47	70.35	105.65	38.71	4.31	7.77	0.82
	30	26	35.24	1.73	74.07	111.04	36.39	4.37	7.72	0.86
	1	100	39.48	11.22	64.48	115.19	30.3	4.09	7.26	0.84
St. 5	100	0	36.07	9.21	66.24	111.52	38.27	6.78	7.42	0.83
	30	25	92.78	12.37	69.76	174.92	39.43	6.64	6.35	1.11
	1	95	127.38	11.8	57.44	196.62	25.51	5.31	5.76	1.13
St.6	100	0	29.57	24.3	65.46	119.33	40.01	5.7	7.35	0.88
	30	22	38.37	15.83	78.76	132.96	37.11	5.86	7.47	0.99
	1	84	36.95	0.74	73.09	110.77	22.61	4.98	7.67	0.85
St. 7	100	0	33.02	19.14	67.42	119.58	43.06	5.92	7.37	0.88
	30	23	41.47	32.39	69.76	143.62	46.39	6.75	7.04	1.01
	1	87	57.05	7	63.7	127.74	40.59	4.98	6.87	0.88
St. 9	100	0	49.08	19.14	63.31	131.53	39.33	4.8	6.9	0.91
	30	21	31.95	15.46	66.63	114.05	35.92	4.44	7.44	0.85
	1	79	30.52	1.11	61.94	93.57	24.21	3.95	7.69	0.72
St. 11	100	0	27.79	70.68	73.28	171.75	36.24	5.05	6.98	1.2
	30	16	35.99	64.42	67.03	167.44	41.12	6.45	6.8	1.14
	1	60	39.21	10.68	82.67	132.55	32.67	4.62	7.58	1
St. 13	100	0	50.86	32.03	77.59	160.47	57.37	9.61	6.99	1.12
	30	15	61.33	30.92	72.31	164.56	48.43	8.76	6.74	1.11
	1	57	36.59	6.26	90.1	132.95	23.4	4.56	7.83	1.04
St. 15	100	0	79.13	19.57	74.85	173.55	35.59	6.57	6.59	1.14
	30	21	36.89	86.34	79.34	202.57	42.74	6.57	6.81	1.38
	1	81	55.6	19.86	104.96	180.42	26.82	4.56	7.4	1.33
St. 16	100	0	63.6	6.04	64.29	133.93	45.67	8.09	6.76	0.9
	30	21	40.42	14.39	86.38	141.2	38.84	6.87	7.55	1.07
	1	81	21.83	20.43	74.65	116.91	28.28	4.07	7.79	0.91
St. 17	100	0	72.43	10.65	65.07	148.15	40.3	7.66	6.57	0.97
	30	24	74.31	9.5	50.21	134.02	29.9	5.53	6.22	0.83
	1	98	38.54	7.77	67.42	113.73	25.03	6.87	7.4	0.84
St. 18	100	0	85.25	18.99	76.41	180.66	43.39	8.21	6.53	1.18
	30	25	146.68	23.02	76.22	245.92	37.7	7.12	5.9	1.45
	1	95	56.9	5.47	72.31	134.67	26.98	6.02	7.06	0.95

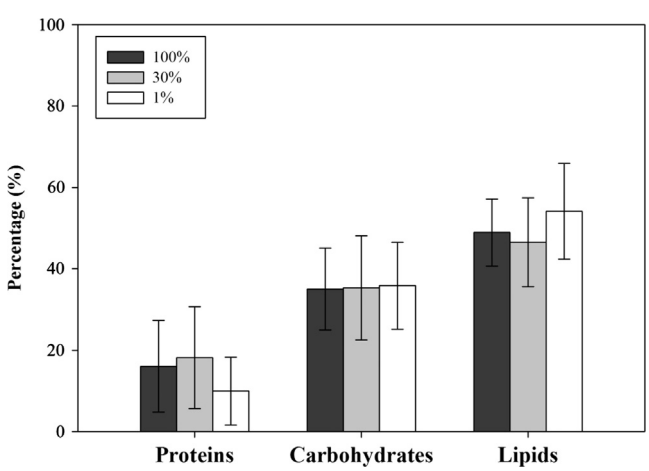

Fig. 6. The macromolecular (proteins, carbohydrates, and lipids) compositions from three light depths (100%, 30%, and 1%).

nutrient concentrations in the different water masses (Lee et al., 2007). In Herald Canyon, a part of the northern Chukchi Sea where high chl-*a* concentrations exist below the surface layer (~30 m), the chl-*a* ranged from 200 to 300 mg chl-*a* m^{-2} in 2004. Despite this variation in the southern Chukchi Sea, large cells (>5 μm) generally dominated (>60%) (Lee et al., 2007), while small cells dominated in the northern Chukchi Sea during our 2011 study (Fig. 5). Lee et al. (2012) reported the average contribution of small phytoplankton to the total carbon uptake rate as 62.8% (S.D.= ±8.5%) in ice-free deep waters in the northern Chukchi Sea during summer 2008.

4.2. Environmental factors and macromolecular pools

Environmental factors, such as nutrients, light, salinity, and temperature are expected to directly affect phytoplankton growth and their macromolecular pool composition. A large number of studies have tried to confirm this (Morris et al., 1974; Smith and Morris, 1980; Rivkin and Voytek, 1987; Boëchat and Giani, 2008).

Although this study found no strong relationships between macromolecular compositions and major nutrients except NH_4 (Table 3), availability of major inorganic nutrients is an important determining factor for end products of photosynthesis. Protein productions are dominant under sufficient nitrogen conditions (Fabiano et al., 1993; Lee et al., 2009), whereas phytoplankton produce more lipids and carbohydrates if their nutrients are limited (Shifrin and Chisholm, 1981; Harrison et al., 1990).

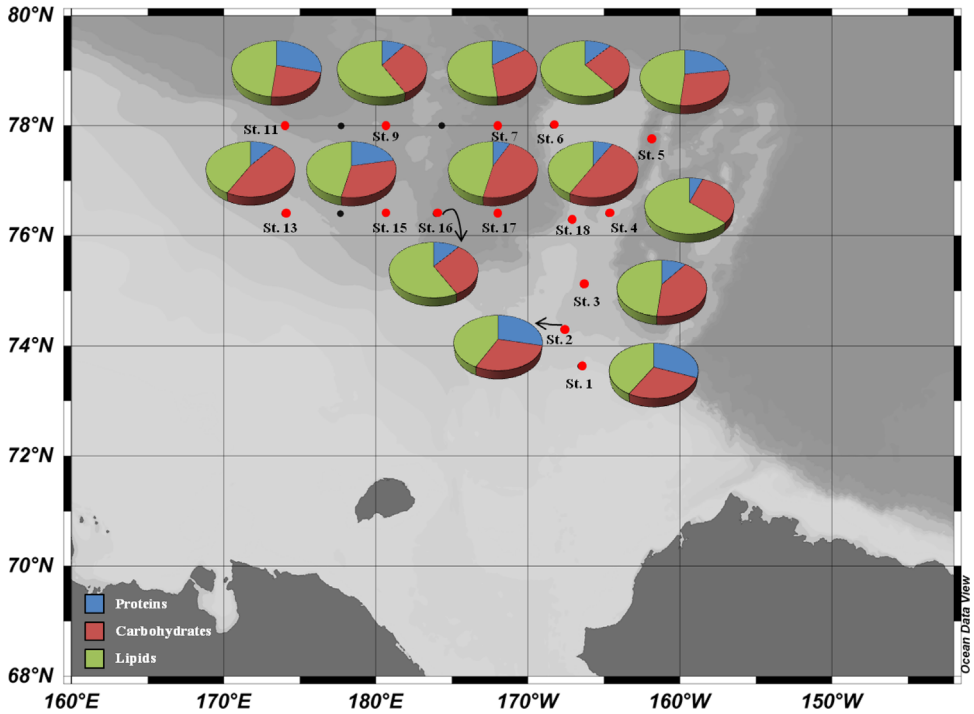

Fig. 7. Macromolecular compositions of POM in the northern Chukchi Sea.

Table 3
Pearson's correlation matrix of macromolecular compositions and environmental factors. DIN: total dissolved inorganic nitrogen.

	Carbohydrates	Proteins	Lipids	Calorific of FM	PO_4	NO_2+NO_3	NH_4	SiO_2	DIN	Total chl-*a*
Carbohydrates	1									
Proteins	–	1								
Lipids	–	–	1							
Calorific of FM	0.52**	0.71**	0.61**	1						
PO_4	–	–	–	–	1					
NO_2+NO_3	–	–	–	–	0.96**	1				
NH_4	–	0.34*	0.35*	0.35*	–	–	1			
SiO_2	–	–	–	–	0.95**	0.96**	–	1		
DIN	–	–	–	–	0.96**	0.99**	–	0.96**	1	
Total chl-*a*	–	0.37*	0.33*	0.46**	0.35*	–	0.63**	–	–	1

"-" indicate that *r* values are not significant.
* $p<0.01$ indicate that *r* values are not significant.
** $p<0.05$ indicate that *r* values are not significant.

Triglyceride content (energy storage) increases and shifts from protein to lipid metabolism if nitrogen or phosphorous is limited, because lipids and carbohydrates are non-nitrogenous compounds, whereas proteins are nitrogenous substrates (Lombardi and Wangersky, 1991; Smith et al., 1997; Takagi et al., 2000).

In particular, a nitrogen limitation explains low ratios of N:P, proteins–carbohydrates, and proteins–lipids (Kilham et al., 1997; Hecky and Kilham, 1988; Danovaro et al., 2000). The average value of total nitrogen ($NO_2+NO_3+NH_4$)/PO_4 ratio (N:P) was very low in this study: 2.50 ($\pm$2.29) compared with the Redfield ratio of 16:1 (Redfiled et al., 1963). In fact, the concentration of NO_2+NO_3 was generally low at upper mixed layer (0–20 m) and NH_4 concentration was low (<1 μM) throughout the photic layer (Fig. 3 and Table 3). The results were low protein–carbohydrate and protein–lipid ratios (0.53 $\pm$ 0.58 and 0.33 $\pm$ 0.29, respectively). In other studies, protein–carbohydrate ratios less than 1 suggest nitrogen deficiency in phytoplankton growth (Mayzaud et al., 1989; Lizotte and Sullivan, 1992; Danovaro et al., 2000). By contrast, high protein–carbohydrate ratios (>1) are generally found in productive areas or phytoplankton bloom periods (during logarithmic growth phases) (Fabiano et al., 1984, 1992, 1993).

Light is also important in limiting protein synthesis or promoting lipid synthesis (Smith and Morris, 1980; Lee et al., 2008). In the Chukchi Sea, Lee et al. (2008) reported that the protein productions increased whereas the lipid productions decreased as light decreased, which is consistent with previous studies (Smith et al., 1987, 1997; Suárez and Marañón, 2003). No difference in macromolecular compositions at different light depths in this study might indicate that overall light conditions were similar for phytoplankton at each light depth throughout some well mixed mechanism within the eutrophic layer in the Arctic Ocean during summer.

4.3. Macromolecular compositions of POM

In general, the proportions of carbon incorporation into lipids reported in the Arctic Ocean ranged from 5 to 30% (Li and Platt, 1982; Tillmann et al., 1989; Lindqvist and Lignell, 1997; Smith et al., 1997). In the Chukchi Sea, Lee et al. (2009) had reported a relatively low carbon allocation into lipids (<4%). In our study, overall lipid composition was highest (50 $\pm$ 11%) and protein composition was lowest (15 $\pm$ 11%) (Fig. 7). This large difference

in lipid proportions could be resulted from different methods of lipid analysis. We analyzed macromolecular composition, not production, of POM, mainly phytoplankton. Lee et al. (2009) measured relative macromolecular productions of phytoplankton after 4–7 h of daytime incubation. In fact, previous studies had reported that phytoplankton's biochemical composition could be changed diurnally with the availability of light (Lancelot and Mathot, 1985; Boëchat and Giani, 2008). However, Boëchat and Giani (2008) observed more lipids and carbohydrates than proteins during the day, and more proteins than other classes at night, which is somewhat inconsistent with our study.

Natural samples for POM are generally composed of organic detritus and autochthonous organisms such as phytoplankton (Volkman and Tanoue, 2002), which might result in different chemical compositions of only phytoplankton populations. However, detritus is rare in polar waters (Liebezeit, 1984). The C:N ratio is useful to determine a source of POM (Lobbes et al., 2000; Lee and Whitledge, 2005). It generally ranges between 6 and 10 for fresh living phytoplankton, between 3 and 5 for bacteria, and over 15 for terrestrial organisms (Redfiled et al., 1963; Goldman et al., 1987; Zweifel, et al., 1993; Montagnes et al., 1994; Fagerbakke et al., 1996; Ríos et al., 1998; Lobbes et al., 2000). Our mean C:N ratio of POM of 7.4 ($\pm$ 1.3) was slightly higher than the Redfield ratio (6.6). Thus, we believe that this POM is autochthonous and mainly phytoplankton, based on the C:N ratio in this study. Therefore, no substantial detritus or terrestrial organic matter composed of POM led to different macromolecular compositions in this study compared to those mentioned by Lee et al. (2009). A more likely cause for the differences between these studies is the time lapse between production and measurement of macromolecules.

4.4. Total FM and energy content of Arctic phytoplankton

Food material (FM) is the sum of carbohydrate, protein, and lipid concentrations (Danovaro et al., 2000). The overall average of FM was 149.2 $\mu g\,L^{-1}$ (S.D.= $\pm$ 36.5 $\mu g\,L^{-1}$) in this study (Fig. 8). There was no clear increasing or decreasing trend in total FM concentration with depth (Table 3). Since there were no comparable FM data available in the Arctic Ocean, we compared our data with FM concentrations in Antarctic regions. Fabiano et al. (1993) reported FM concentrations ranging from 80.5 to 698.8 $\mu g\,L^{-1}$ with an average of 294.4 $\mu g\,L^{-1}$ (S.D.= $\pm$ 228.1 $\mu g\,L^{-1}$) in photic layers in the Ross Sea (Antarctica), about twice as high as ours. Fabiano et al. (1996) also found a somewhat greater concentration of FM in Terra Nova Bay, Antarctica, ranging from 142.5 to 1140.6 $\mu g\,L^{-1}$ with an average of 374.3 $\mu g\,L^{-1}$ in mixed layer ($>$ 48 m) during the austral summer. The Antarctic studies found

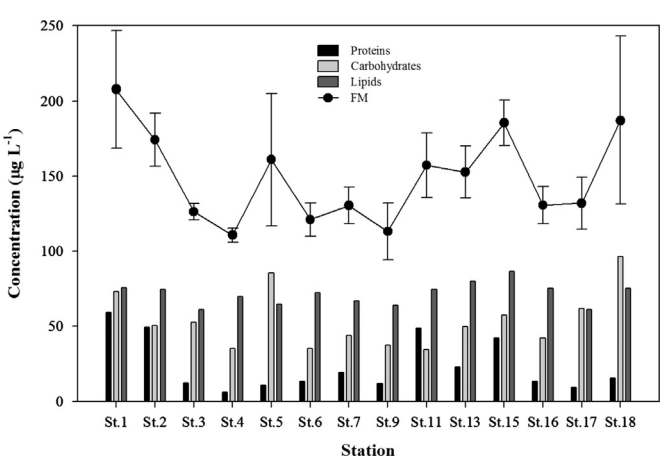

Fig. 8. Protein, carbohydrate, lipid, and FM concentrations of POM averaged from three different light depths (100%, 30%, and 1%) at each station.

large contributions of proteins (50%) to the FM compared to this Arctic study (mainly large contribution of lipids=50%).

We calculated the caloric value of the FM using the Winberg (1971) equation (Kcal g^{-1} dry weight=0.055 proteins%+0.041 carbohydrates%+0.095 lipids%). The average calorific value and calorific content of FM were 7.0 $\pm$ 0.5 Kcal g FM^{-1} and 1.0 $\pm$ 0.2 Kcal m^{-3}, respectively (Table 3). The calorific content of FM in this study was somewhat lower than that in the photic layer of the Ross Sea (1.6 $\pm$ 1.3 Kcal m^{-3}) (Fabiano et al., 1993; Fabiano et al., 1996). This is very interesting, in regards to very different ambient biomasses and productivities of phytoplankton between the two study regions. Generally, they are significantly lower in the northern Chukchi Sea than in the Ross Sea (Smith and Dunbar, 1998; Smith et al., 2000). Our average chl-*a* concentration was 31.9 $\pm$ 31.3 mg chl-*a* m^{-2} compared to 185.8 $\pm$ 93.2 mg chl-*a* m^{-2} in the Ross Sea (Smith et al., 2000). The concentration in the Ross Sea ranged from 76.5 to 377 mg chl-*a* m^{-2} in late summer and from 17.2 to 256 mg chl-*a* m^{-2} (average 102.1 $\pm$ 66.0) during the austral spring and early summer (Smith and Dunbar, 1998). Primary productivity ranged from 0.33 to 2.8 g C m^{-2} d^{-1} in the Ross Sea, one of the most productive regions in the Southern Ocean, although the productivity varied greatly with location and time (El-Sayed et al., 1983; Smith et al., 1996; Arrigo et al., 1998; Smith et al., 2000). The Chukchi Sea is a very productive region in the Arctic Ocean (Sambrotto et al., 1984; Springer and McRoy, 1993; Gosselin et al., 1997; Lee et al., 2007). However, the northern Chukchi Sea does not appear that productive compared with its southern part. The daily productivity in the northern Chukchi Sea was 0.16–0.18 g C m^{-2} d^{-1} (Lee et al., 2007 and 2013a) and was very low (about 0.02 g C m^{-2} d^{-1}) in 2010 (Yun et al., 2015-a), which was approximately one order lower than that in the Antarctic Ross Sea.

Despite the northern Chukchi Sea has lower biomass and lower primary productivity, calorific contents in this study were not substantially lower than those of the Ross Sea. It could be resulted from the different FM compositions between the two study regions. The Arctic had large lipid contributions (50 $\pm$ 11%) to its total FM, whereas the Antarctic had large protein contributions ($>$ 50%) (Fabiano et al., 1993, 1996). The caloric value of lipids is about 1.7 times higher than that of proteins, when converted using the Winberg (1971) equation above. Calorific content of FM to POC ratio in this study (35.0 $\pm$ 41.3 Kcal mg^{-1}) was substantially higher than that in the Ross Sea (6.7 $\pm$ 1.3 Kcal mg^{-1}) (Fabiano et al., 1993), which indicate high calorific contents of FM per unit of POC amount in this study. The regional difference in calorific content of FM per POC between the Arctic and Antarctic Oceans should be further tested for other regions and times since seasonal and regional variations in biomass, production, and compositions of phytoplankton are very large in polar oceans (Smith et al., 1996; Smith et al., 2000; Arrigo et al., 1998; Lee et al., 2007; Yun et al., 2012).

In conclusion, this study showed no direct relationships between absolute concentration of each macromolecular compound and environmental factors (except for NH_4), which made it difficult for us to determine major controlling factors on different macromolecular compositions of phytoplankton in the Arctic Ocean. Based on previous results, high lipid contributions to total FM might suggest that the phytoplankton in our study was a stationary phase, which is indicated by large storage of lipids under severe nutrient stress (Shifrin and Chisholm, 1981; Harrison et al., 1990) and low protein–carbohydrate ratio ($<$ 1) in POM (Mayzaud et al., 1989; Lizotte and Sullivan, 1992; Danovaro et al., 2000). However, its high lipid contents could be important for its nutritional value for zooplankton and other consumers, since lipids are the most calorific biomolecules and thus a critical energy source (Smith et al. 1987; Wainman and Lean, 1992). In fact, there

appears to be a strong relationship between lipid concentrations of phytoplankton and protein concentrations of zooplankton in the Arctic (Yun et al., 2015-b). More measurements for macromolecular compositions of phytoplankton, especially for different sampling seasons, under a variety of environmental conditions throughout the Arctic Ocean would improve our understanding of changes to phytoplankton physiology and how phytoplankton responds to the rapid environmental changes affecting sea ice in the Arctic Ocean. In addition, more data for macromolecular compositions of different cell-sized POM are also needed. Recent increases in Ekman convergence and freshening surface waters result in deepening nutricline and stronger stratification and consequently lower nutrient supply in the upper water column in the Canada Basin (McLaughlin and Carmack, 2010; Li et al., 2009). Consequently, small phytoplankton ($<2\,\mu$m diameter) have increased, whereas larger cells have declined there (Li et al., 2009). The increase in contributions of small phytoplankton to overall phytoplankton production will probably change quality as well as quantity (e.g., primary production) of a food source for higher trophic levels because different size phytoplankton communities have different macromolecular compositions (Lee et al., 2009; Lee et al., 2013b).

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