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Comparison of phytoplankton macromolecular compositions and zooplankton proximate compositions in the northern Chukchi Sea

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ABSTRACT

The macromolecular (proteins, lipids, and carbohydrates) composition of phytoplankton and the proximate (water, proteins, lipids, and ash) and elemental (carbon and nitrogen) compositions of mesozooplankton were determined in the northern Chukchi Sea to establish the relationship between zooplankton and their phytoplankton food source. Among the phytoplankton macromolecules examined in this study, lipids had the highest contents (58.4 ± 8.2%) and proteins had the lowest (16.1 ± 7.3%), which may be a consequence of a nitrogen deficiency in phytoplankton growth during the study period. In contrast, proteins (59.7 ± 10.6% DW) were the major proximate components in the mesozooplankton community, which was dominated by copepods up to 71% of total abundance. The low lipid contents (13.8 ± 12.4% DW) in the mesozooplankton community in this study might be due to the dominance of small species such as *Calanus glacialis*, which generally have relatively lower lipid contents than large copepods. Moreover, the spawning period of *C. glacialis* from April to June might be an additional reason for the low lipid contents, because copepods have normally very low lipid contents after spawning. The low lipid contents resulted in a low energy content in this mesozooplankton community in the northern Chukchi Sea. The different biochemical compositions of phytoplankton and zooplankton should be considered in order to understand the impacts of climate change on the quality of prey provided by lower trophic levels and subsequently on Arctic marine ecosystems.

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1. Introduction

Arctic environments are currently experiencing rapid change. Higher temperatures and the ice export to Baffin Bay and Greenland Sea through the Fram Strait have decreased the extent and thickness of the perennial sea ice in the Arctic Ocean over several decades, producing more open water (Rothrock et al., 2003; Nghiem et al., 2007). Recently, areas in the Western Arctic Ocean such as the northern Chukchi Sea have experienced the most rapid changes in sea ice cover (Perovich and Richter-Menge, 2009). Other sub-Arctic and Arctic waters are subject to the effects of global warming because even a small change in the heat content in the water column causes significant impacts on the spatial distribution and dynamics of sea ice (e.g., Meier et al., 2005; Overpeck et al., 2005; Sarmiento et al., 2004). These changes in climate and ice conditions alter the quantity, quality, and timing of phytoplankton production and subsequently the seasonal distributions, geographic ranges, and nutritional structure of their primary consumers. Those lower trophic level changes are projected to alter the functioning of higher trophic levels (Tynan and DeMaster, 1997). Because seasonal cycles are strongly coupled to the timing of ice-break up and phytoplankton blooms (Smith and Schnack-Schiel, 1990), recent and projected changes in the sea ice cover can affect the protist and metazoan zooplankton communities (Hopcroft et al., 2008). Changes in zooplankton communities lead to changes at higher trophic levels, such as those of fish, seabirds, and marine mammals, because the seasonal success of the zooplankton communities determines the resources available to many higher trophic levels (Hunt and Stabeno, 2002; Hopcroft et al., 2008). Therefore, the current physiological status of phytoplankton to indicate food quality and their primary production to indicate food quantity are needed in order to better understand the impacts of ongoing changes in climate and sea-ice conditions on the Arctic marine ecosystem.

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The biochemical composition and biosynthetic patterns of phytoplankton can provide important clues to their physiological status (Morris, 1981; Smith et al., 1997a; Lee et al., 2009) and about the cycling and trophic transfer of photosynthetically fixed carbon in the marine food web (Laws, 1991; Parrish et al., 1995). Consequently, these photosynthetically synthesized biochemicals (proteins, lipids, polysaccharides, and low-molecular-weight metabolites (LMWM)) could influence the nutritional status of higher trophic levels (Scott, 1980; Lindqvist and Lignell, 1997).

The 3rd Korean Arctic expedition was conducted in the northern Chukchi Sea around the Chukchi Borderland and Mendeleyev Ridge from August 1 to September 10, 2012, onboard the Korean research icebreaker *ARAON*. The primary objective of this study was to find spatial distribution of the macromolecular compositions of phytoplankton in the northern Chukchi Sea. The second objective was to evaluate the nutritional status of the zooplankton community based on their proximate compositions related to macromolecular compositions of phytoplankton.

2. Materials and methods

2.1. Sampling

The vertical profiles of water temperature, salinity, and density were obtained from downcast measurements using a Seabird SBE-911+CTD profiler mounted on a rosette. Oceanographic water samples were collected from a total of 50 stations with a rosette sampler equipped with 20-L Niskin bottles. Samples for the macromolecular composition of phytoplankton were obtained at 25 selected stations (Fig. 1 and Table 1). Mesozooplankton samples were collected within the upper 200 m with a Bongo net (mesh apertures 330 and 500 μm) at 22 stations (Fig. 1 and Table 1) and then distributed for identification and compositional analysis.

2.2. Nutrient and chlorophyll a concentration measurements

The discrete water samples for dissolved inorganic nutrient concentrations (nitrite+nitrate, ammonium, phosphate, and silicate) were analyzed onboard immediately after collection, using an automated nutrient analyzer (SEAL, QuAAtro, UK) according to the manufacturer's instruction. The water samples used for the measurement of total chlorophyll *a* concentration were filtered through Whatman GF/F filters (25 mm). The size-fractionated chlorophyll *a* concentration was determined for samples that were passed sequentially through 20- and 5-μm Nuclepore filters (47 mm) and 0.7-μm Whatman GF/F filters (47 mm). Chlorophyll *a* concentrations were measured using a Trilogy fluorometer (Turner Designs, USA) following the method outlined by Parsons et al. (1984).

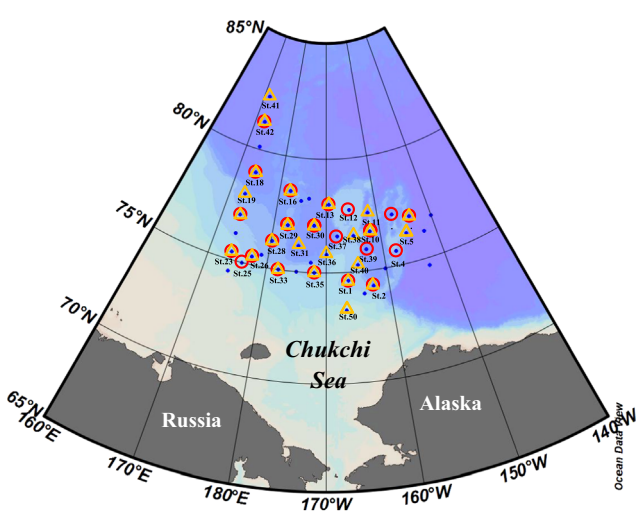

Fig. 1. Locations of sampling stations during the 2012 *ARAON* cruise in the northern Chukchi Sea. Red circles indicate mesozooplankton sampling stations. Yellow triangles indicate phytoplankton macromolecular stations.

Table 1
Location, the water depth (m), and the euphotic depth (Z_{eu}) for phytoplankton and mesozooplankton sampling stations in the northern Chukchi Sea, 2012.

Station	Location		Depth (m)	Z_{eu} (m)
	Latitude (°N)	Longitude (°W)		
1	74.6180	166.3970	374	76
2	74.3000	162.5000	1220	62
4	75.6560	157.7800	915	–
5	76.3249	155.3760	1010	68
6	76.9990	154.0000	1720	62
7	77.2520	157.1520	713	–
10	76.7120	161.8640	1061	76
11	77.5347	161.7760	2690	65
12	77.7500	165.3740	435	–
13	77.9970	169.4480	1232	65
16	78.5000	177.7500	1227	62
18	79.0000	186.0000	2452	41
19	77.9675	186.9585	1090	43
21	77.0350	186.6980	658	46
23	75.3450	186.2340	191	51
25	74.9930	184.1410	155	–
26	75.3710	182.7090	359	51
28	76.2180	179.8360	1193	57
29	77.0060	177.3630	1400	62
30	77.0760	172.3270	2013	65
31	76.1450	174.9480	2169	68
33	75.0000	177.9980	323	57
35	75.0000	171.9990	382	57
36	75.7970	169.9920	754	68
37	76.6000	168.0020	1783	–
38	76.5955	165.0040	567	62
39	75.9450	162.9400	2075	–
40	75.2819	164.6680	618	76
41	82.3237	188.3825	2758	41
42	81.2120	187.5970	2757	41
50	73.3137	165.0571	65	56

2.3. Macromolecular compositional analysis of phytoplankton

Water samples for macromolecular composition of phytoplankton were obtained from 3 light depths (100%, 30%, and 1%). One liter of each seawater sample was passed through a precombusted 47 mm GF/F filter (Whatman, 0.7 μm pore) and was then immediately stored at −80 °C until analysis. Quantitative protein analysis followed the method of Lowry et al. (1951), with absorbance measured at 750 nm using a spectrophotometer (Labomed, Germany). The concentration of proteins was calculated using calibration curves constructed using a protein standard solution (2 mg mL^{-1}, SIGMA). Carbohydrate analyses were performed following extraction using the phenol–sulfuric method of Dubois et al. (1956). The concentration of carbohydrates was determined by measuring the absorbance of samples at 490 nm with a glucose standard solution (1 mg mL^{-1}, SIGMA). Lipids were extracted with chloroform and methanol (1:2, v/v) according to Bligh and Dyer (1959) and Marsh and Weinstein (1966). Absorbance for lipids was measured at 360 nm. Tripalmitin solutions were used as the standards for lipid concentration. The calorific

content (kcal m^{-3}) as food material was calculated using the Winberg (1971a) equation.

2.4. Identification of mesozooplankton

Mesozooplankton samples were immediately fixed and preserved with buffered formaldehyde (pH 8, final concentration ~5%) for quantitative analyses. Mesozooplankton abundance and biomass were analyzed from samples obtained from the 330-μm mesh net at 12 selected stations (Table 3). Subsampling was carried out using a Folsom plankton splitter, and mesozooplankton were identified to the lowest taxonomic level possible under a dissecting microscope using a Bogorov tray. Abundance is expressed in terms of individual numbers per cubic meter (ind. m^{-3}) using the volume filtered by the net, as obtained from the revolution counts of a flow meter attached to the net.

2.5. Proximate analysis of mesozooplankton

Mesozooplankton samples for compositional analysis were stored in a −80 °C deep freezer after collection until analysis in the marine ecological laboratory of Pusan National University, Korea. Lipid, water, ash, and protein contents were determined from bulk mesozooplankton samples using proximate analysis following the procedures outlined in Foy (1996). The samples were combined with an amount of water equivalent to 49% of the sample weight and then homogenized using a T 10 basic ultra-turax homogenizer (IKA, China) for approximately 5 min. Finally, the homogenized sample was distributed for each analysis. Lipids were extracted using a mixture of chloroform:methanol:water (2:1:1 by volume) according to the modified method of Bligh and Dyer (1959). Water content was determined by drying the homogenate aliquots by placing them in a 65 °C oven for approximately 24 h. The ash content was determined by combusting the homogenate aliquots in a muffle furnace at 600 °C for four hours until a constant weight was attained. The protein content was determined by finely grinding a subsample of dried homogenate from the water content analysis. The dried samples (approximately 0.5 mg aliquot) were analyzed with a CHN elemental analyzer (Eurovector 3000 Series, Milan, Italy) coupled with a continuous-flow isotope ratio mass spectrometer (IsoPrime, GV Instruments, Manchester, UK) in the POSTEC Ocean Science and Technology Institute. Proteins were then estimated by multiplying percent nitrogen by a factor of 6.25, on the basis of a 16% nitrogen content in proteins (Winberg, 1971b; Dowgiallo, 1975). Although the nitrogen–protein conversion factor may vary somewhat according to amino acid compositions or the presence of non-protein nitrogenaceous such as chitin (Gnaiger and Bitterlich, 1984), the factor of 6.25 is commonly used to obtain the protein content from organic nitrogen (Winberg, 1971b; Dowgiallo, 1975). All proximate analysis results are expressed both as percent wet weight (%WW), and percent dry weight (%DW) and the elemental components (carbon and nitrogen) are expressed as percent dry weight (%DW) (Table 4). To assess the nutritional value of the mesozooplankton community, we roughly estimated their caloric contents. We assumed that carbohydrates were 0.5% of the dry weight (Raymont et al., 1969; Morris and Hopkins, 1983), though carbohydrates were not analyzed in this study. The caloric potential was calculated using the conversion factors of 5.7, 9.3, and 4.0 kcal g^{-1} for proteins, lipids, and carbohydrates, respectively (Elliot and Davison, 1975).

3. Results

3.1. Physical and chemical conditions

The water mass distribution in the Western Arctic Ocean was characterized by a layering of Pacific Water composed of Pacific Summer Water (PSW) and Pacific Winter Water (PWW) in the upper layers and Atlantic Water. The temperature and salinity of the upper 200 m are shown in Fig. 2. In the upper 200 m, temperature and salinity ranged from −1.8 to 1.4 °C and from 24 to 35 psu, respectively. Salinity was lowest at the surface due to summer sea ice melt, river runoff, and the low salinity PSW.

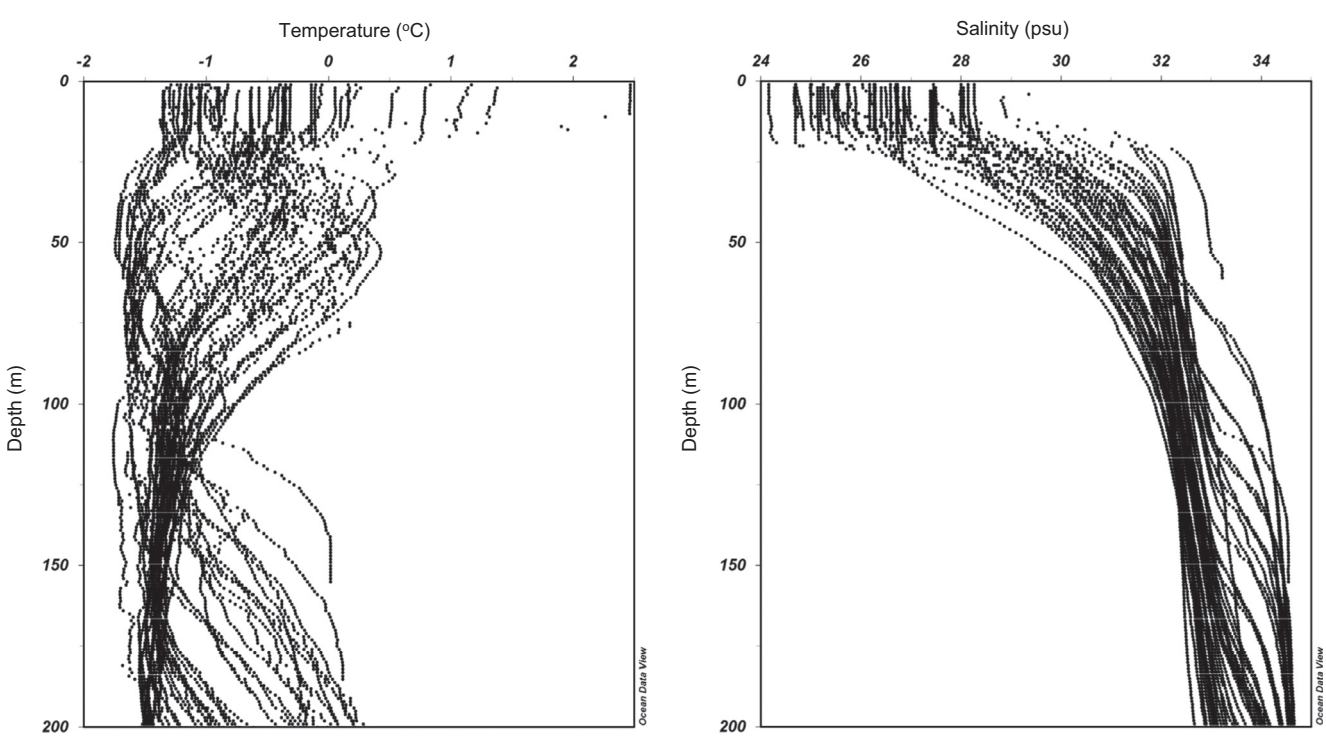

Fig. 2. The vertical structure of temperature (a) and salinity in the study area in 2012.

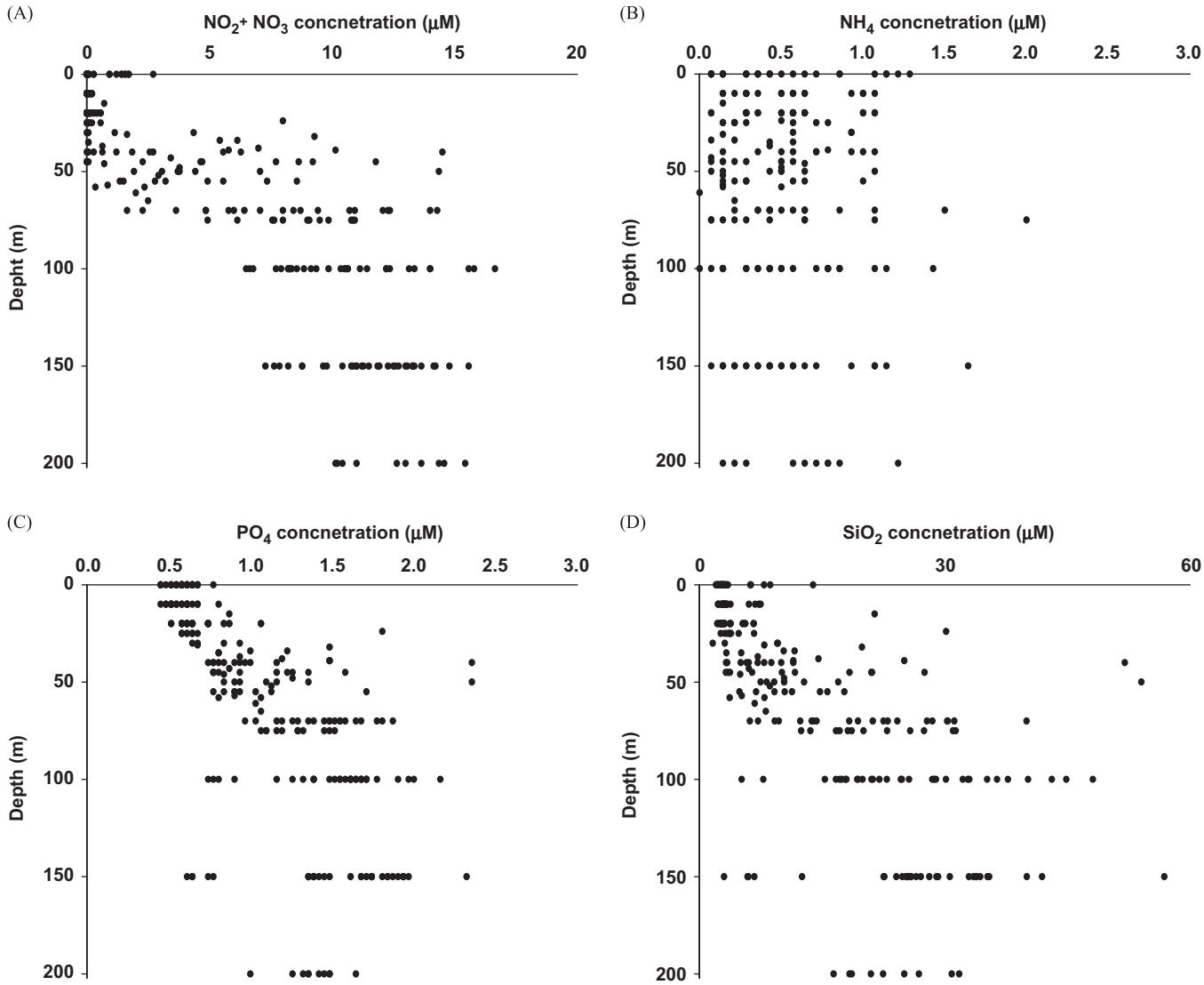

Fig. 3. The vertical structure of nitrite and nitrate (A), ammonium (B), phosphate (C), and silicate (D) concentrations in the study area in 2012.

The inorganic nutrient concentrations of the upper 200 m are shown in Fig. 3. The concentrations of nitrite and nitrate were largely depleted in the upper 20 m (Fig. 3A) but rapidly increased from near zero to 16 μM. The concentrations of ammonium and phosphate were generally low throughout the water column (<2 μM and <2.5 μM, respectively) (Figs. 3B and C). Silicate concentration ranged from <3 to 56.8 μM, and its vertical distribution was very similar to that of nitrate (Fig. 3D).

3.2. Phytoplankton biomass

The averaged chlorophyll *a* concentration integrated from the surface to euphotic depth was 30.5 mg m^{-2} (SD$=\pm 35.2$ mg m^{-2}) (Fig. 4). The highest concentration was 175.8 mg m^{-2} at station 23. High chlorophyll *a* concentrations of over 50 mg m^{-2} were observed at stations from 21 to 28 and at station 33.

The proportions of chlorophyll *a* fraction by size at each station are shown in Fig. 5. Generally, the phytoplankton community was dominated by small phytoplankton (0.7–5 μm), which contributed 55.1% (SD$=\pm 26.8$%) of the total chlorophyll *a* concentration, followed by large (>20 μm: 27.7 ± 25.2%) and medium-size phytoplankton (5–20 μm: 17.2 ± 8.5%). The contribution of large phytoplankton (>20 μm) was much higher (>75%) at stations 21, 23, and 26 (Fig. 5).

3.3. Macromolecular composition of phytoplankton

Because there was no substantial difference in the macromolecular concentration of phytoplankton among the three light depths ($p>0.05$), the concentrations were averaged from the three depths for each station (Fig. 6). The ranges of concentrations of carbohydrates, proteins, and lipids were from 15.9 to 88.0 μg L^{-1}, from 9.2 to 183.1 μg L^{-1}, and from 37.0 to 147.4 μg L^{-1}, respectively (Table 2). At each station, the lipid contents were higher than those of other macromolecular classes (Fig. 6). Overall, the content of lipids averaged from all stations was 58.4 ± 8.2%, followed by carbohydrates (25.5 ± 7.1%) and proteins (16.1 ± 7.3%). The average calorific content was 1.2 ± 0.2 kcal m^{-3} (Table 2).

3.4. Mesozooplankton community

A total of 20 mesozooplanktonic taxa was identified, including 12 copepod species (Table 3). Copepods accounted for 71% of the total mesozooplankton abundance, followed by *Oikopleura* spp.

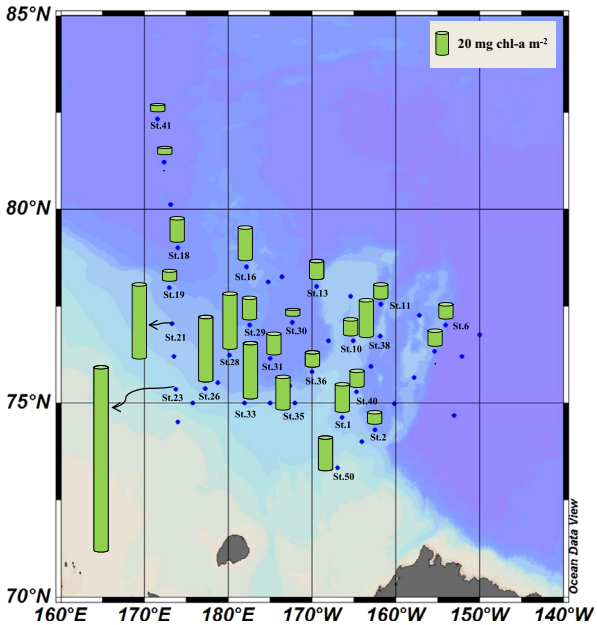

Fig. 4. Distribution of total chlorophyll *a* concentrations (mg chl-*a* m^{-2}). The chlorophyll *a* data were obtained by the integration of volumetric values from the surface to 1% light depth.

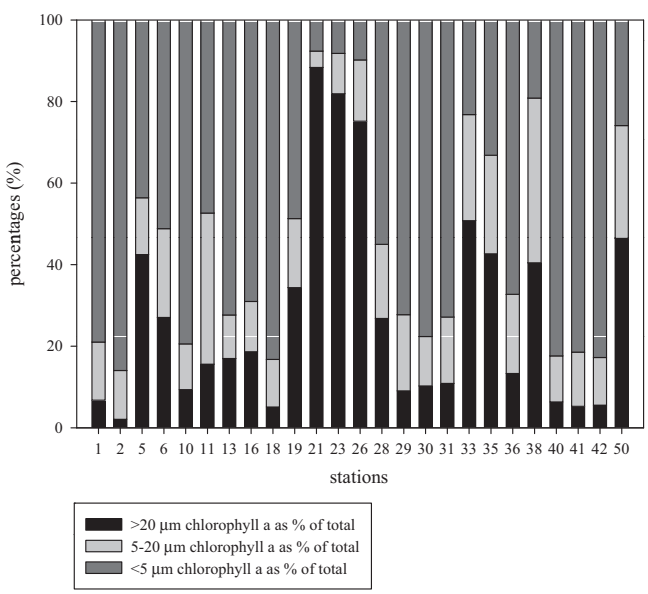

Fig. 5. Percentage of chlorophyll *a* in the different size fractions (>20 μm, 5–20 μm, and <5 μm) for each of the 25 selected stations.

(20%). Chaetognaths (*Sagitta* spp.) and the Mollusca (Gastropoda larvae) represented 4% and 2% of total mesozooplankton abundance, respectively. Among the copepod species, *Calanus glacialis* were dominated as 28% of total copepod species, whereas the abundance of *Calanus hyperboreus* was low and made up only 9% of the total copepod species.

3.5. Proximate and elemental composition of mesozooplankton

Values for all of the proximate and elemental compositional components as well as the estimated energy contents for each station are shown in Table 4. Water contents ranged from 85.0 to 93.6%WW, and the mean water content was 90.1 ± 2.6%. Ash ranged from 0.5 to 4.5%WW (mean ± S.D. = 2.2 ± 0.9%WW) and from 5.2 to 45.5%DW (mean ± S.D. = 26.4 ± 10.0%DW). Proteins

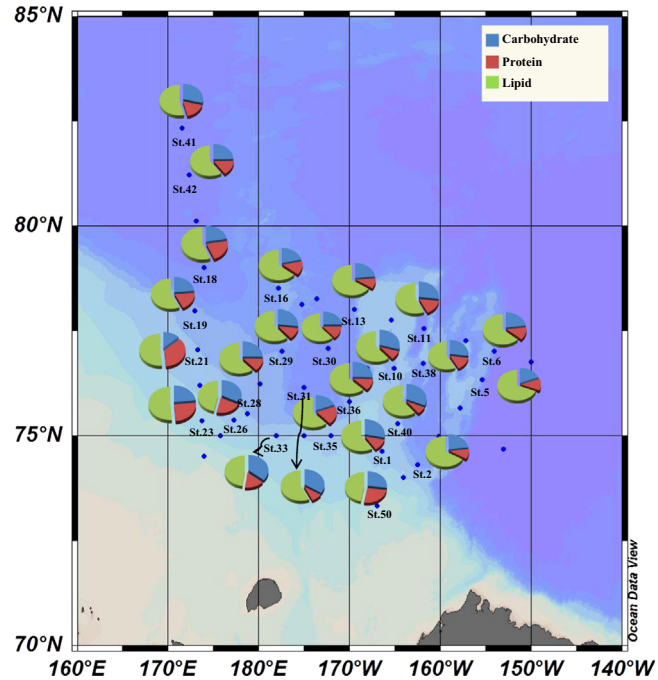

Fig. 6. Distribution of the macromolecular composition of phytoplankton in the study area in 2012.

Table 2
The phytoplankton macromolecule (carbohydrate, protein, and lipid) concentrations and associated caloric content at 25 selected stations in the northern Chukchi Sea, 2012.

Station	Carbohydrate con. (μg L^{-1})	Protein con. (μg L^{-1})	Lipid con. (μg L^{-1})	Calorific contents (kcal m^{-3})
1	46.2 (22.2–88.0)	20.7 (18.2–23.7)	96.4 (82.7–101.5)	1.2 (1.0–1.4)
2	31.5 (20.1–37.1)	14.9 (11.6–18.2)	91.4 (76.6–100.3)	1.1 (0.9–1.2)
5	22.3 (19.7–23.6)	14.9 (13.9–16.3)	81.4 (77.0–87.5)	0.9 (0.9–1.0)
6	28.7 (25.3–35.4)	16.9 (14.3–19.8)	79.0 (77.9–80.7)	1.0 (0.9–1.0)
10	44.4 (36.2–45.0)	13.9 (9.2–19.8)	90.9 (90.0–91.8)	1.1 (1.1–1.1)
11	40.4 (36.6–43.5)	23.4 (17.8–26.8)	84.9 (73.3–92.6)	1.1 (1.0–1.2)
13	30.6 (24.8–36.8)	20.1 (13.1–27.9)	75.3 (37.0–97.1)	1.0 (0.6–1.2)
16	31.8 (27.6–35.0)	22.1 (19.4–24.4)	95.5 (90.7–101.7)	1.2 (1.1–1.2)
18	36.0 (32.0–39.1)	35.7 (35.0–36.5)	91.2 (85.0–95.3)	1.2 (1.1–1.3)
19	37.7 (22.7–51.4)	30.9 (21.7–40.4)	90.5 (83.8–97.8)	1.2 (1.0–1.4)
21	29.7 (25.8–36.8)	82.8 (31.1–183.1)	118.2 (92.6–142.4)	1.7 (1.2–2.5)
23	40.6 (23.6–51.5)	44.5 (26.0–69.7)	89.2 (81.4–98.9)	1.3 (1.1–1.5)
26	62.7 (44.1–86.2)	40.0 (30.7–58.4)	90.0 (86.6–92.6)	1.3 (1.2–1.5)
28	43.7 (21.6–72.4)	23.5 (20.1–28.7)	106.3 (84.8–147.4)	1.3 (1.1–1.6)
29	36.3 (22.5–56.6)	16.8 (9.6–22.9)	82.0 (71.3–90.2)	1.0 (0.8–1.2)
30	37.4 (18.5–56.3)	20.1 (10.0–30.3)	89.3 (88.6–90.0)	1.1 (1.1–1.1)
31	49.9 (45.2–57.9)	12.7 (9.2–15.1)	82.7 (66.3–94.4)	1.1 (0.9–1.2)
33	58.2 (44.2–65.5)	25.2 (17.8–35.4)	77.3 (73.3–80.6)	1.1 (1.0–1.2)
35	29.2 (15.9–44.4)	30.0 (18.6–44.3)	94.0 (90.2–96.9)	1.2 (1.1–1.3)
36	35.1 (29.8–38.0)	17.0 (11.6–20.1)	85.9 (76.1–94.1)	1.1 (1.0–1.1)
38	40.1 (33.8–47.0)	22.5 (13.1–36.5)	85.1 (82.2–87.8)	1.1 (1.0–1.2)
40	46.0 (37.4–53.1)	11.6 (9.6–15.1)	87.4 (80.6–98.1)	1.1 (1.0–1.2)
41	47.8 (43.3–50.2)	28.1 (13.5–43.5)	88.2 (86.8–90.7)	1.2 (1.1–1.3)
42	40.1 (37.2–43.0)	21.4 (24.4–26.4)	92.8 (88.4–103.1)	1.2 (1.1–1.3)
50	53.8 (45.5–67.2)	51.3 (47.4–59.1)	94.0 (87.0–99.2)	1.4 (1.3–1.5)

ranged from 3.0 to 9.3%WW and from 35.1 to 76.0%DW. The mean protein content was 5.0 ± 1.6%WW and 59.7 ± 10.6%DW. Lipids ranged from 0.2 to 3.6%WW with a mean of 1.2 ± 1.1%WW and from 2.3 to 44.1%DW with a mean of 13.8 ± 12.4%DW. Overall, in the mesozooplankton, the protein content was the highest (59.7 ± 10.6%DW), followed by ash content (26.4 ± 10.0%DW) and lipid content (13.8 ± 12.4%DW).

Table 3
Abundance (ind. m^{-3}) and composition (Com, %) of mesozooplankton at 12 selected stations in the northern Chukchi Sea, 2012.

Taxon	Station												Com (%)
	1	2	4	6	10	12	16	18	21	25	33	35	
Calanus hyperboreus	7	65	4	4	5	2	5	6	3	2		7	6
Calanus glacialis	1	45	3	4	3	1	4	14	12	203	22	48	20
Metridia longa	2	11	4	3	1	< 1	3	14		79	33	28	10
Metridia pacifica		1							15	4			1
Oithona similis	2	10	< 1	1	1	< 1	1	3	12	10	8	4	3
Pseudocalanus spp.	< 1	48	< 1	< 1	< 1	< 1	< 1	3	2	78	18	31	10
Paraeuchaeta barbata	1	4	1	2	1	< 1	1	1	2	1		5	1
Scolecithricella minor	< 1		1	1	< 1	< 1	< 1	1	10	42	1	3	3
Heterohabdus austrinus	< 1		< 1			< 1	1	< 1	1			1	< 1
Aetideopsis rostrata	< 1		< 1	< 1			< 1	1	2				< 1
Microcalanus pygmaeus		5					< 1			4	1		1
Scaphocalanus magnus	< 1		< 1	< 1	< 1			< 1	< 1				< 1
Calanoid copepodite	< 1	58		< 1	< 1	1	6	2	16	113	36	40	15
Euphausiids						< 1					9	2	1
Amphipoda	1			< 1	< 1	< 1	< 1	< 1	1	1		1	< 1
Ostracoda	1		2	4	1	< 1	2	6	1			2	1
Sagitta spp.	1	4	2	2	2	< 1	2	16	12	18	10	9	4
Hydrozoa	< 1	1	< 1	1	< 1	< 1	1	2	1	4	3	2	1
Gastropoda larvae		2		1			3	3		2	15	5	2
Oikopleura spp.	1	11	< 1	4	3	< 1		1	8	131	93	107	20
Total	18	267	19	27	17	6	27	72	98	693	249	294	100

Table 4
Proximate, elemental composition and energy content of mesozooplankton at 22 selected stations in the northern Chukchi Sea, 2012.

Stations	Wet weight (g)	Water content (%)	Proximate composition							Elemental composition			Energy content kcal/ g DW
			Protein (%WW)	Protein (%DW)	Lipid (%WW)	Lipid (%DW)	Ash (%WW)	Ash (%DW)	Lipid/ protein	Carbon (%DW)	Nitrogen (%DW)	C/N ratio	
1	5.7	92.8	3.6	65.8	0.3	4.7	1.6	29.5	0.1	66.8	8.0	9.8	1.7
2	2.4	93.2	3.4	35.1	3.5	36.2	2.8	28.8	1.0	68.5	8.0	10.0	0.9
4	1.8	90.1	5.4	56.7	3.6	38.1	0.5	5.2	0.7	67.0	8.7	9.0	1.2
6	1.2	93.5	3.0	45.6	2.9	44.1	0.7	10.2	1.0	–	7.3	–	0.5
7	16.0	89.9	4.6	47.6	2.5	25.7	2.6	26.7	0.5	87.7	7.3	14.0	8.3
10	9.4	91.5	3.5	58.6	1.2	20.8	1.2	20.6	0.4	47.9	6.5	8.6	4.2
12	3.3	94.2	3.0	53.0	0.3	5.3	2.3	41.6	0.1	60.2	8.2	8.5	0.7
13	3.5	89.3	5.5	75.0	0.2	2.3	1.7	22.7	0.0	57.5	8.2	8.2	1.7
16	4.2	87.8	5.9	71.7	0.5	5.7	1.9	22.6	0.1	75.2	7.8	11.2	2.4
18	5.1	87.8	5.8	69.1	0.5	6.4	2.1	24.5	0.1	69.8	7.6	10.7	2.9
21	4.9	90.4	4.0	51.8	0.2	2.7	3.5	45.5	0.1	69.9	6.7	12.2	1.5
23	4.1	90.9	4.8	56.7	1.3	15.6	2.3	27.7	0.3	66.0	8.4	9.2	1.7
25	7.3	89.1	5.6	53.8	0.2	2.3	4.5	43.9	0.0	66.2	8.2	9.4	2.6
26	7.0	88.5	5.8	53.5	1.8	16.7	3.2	29.9	0.3	81.0	8.1	11.6	3.7
28	4.4	86.0	8.2	72.8	1.1	9.5	2.0	17.7	0.1	72.9	9.4	9.1	3.1
29	2.9	86.2	6.5	76.0	0.3	3.7	1.7	20.3	0.0	66.0	7.5	10.3	1.9
30	3.9	89.2	5.0	61.1	0.5	6.5	2.6	32.4	0.1	69.5	7.4	10.9	1.7
33	3.6	90.6	5.5	56.4	1.5	15.3	2.8	28.3	0.3	59.2	9.4	7.3	1.6
35	2.5	91.9	4.3	56.4	1.3	17.8	2.0	25.8	0.3	73.0	8.4	10.1	1.0
37	5.0	93.6	3.7	56.7	0.6	9.7	2.2	33.6	0.2	73.0	9.2	9.3	1.3
39	5.9	91.6	4.0	66.2	0.2	2.7	1.9	31.1	0.0	76.4	7.6	11.7	2.0
42	5.1	85.0	9.3	74.1	1.6	12.6	1.7	13.2	0.2	73.2	9.9	8.7	4.1

Total carbon contents ranged from 47.9 to 87.7%DW, with a mean of 68.9 ± 8.5%DW. The total nitrogen contents ranged from 6.5 to 9.9%DW, with a mean of 8.1 ± 0.9%. C:N values ranged from 7.3 to 14.0, with a mean of 10.0 ± 1.6. Caloric levels (energy content) ranged from 0.5 kcal g dry wt^{-1} to 8.3 kcal g dry wt^{-1}, with a mean of 2.3 ± 1.7 kcal g dry wt^{-1}.

4. Discussion

4.1. Macromolecular composition and energy content of phytoplankton

Overall, for the phytoplankton, the protein content was lowest (16.1 ± 7.3%) and the lipid content was highest (58.4 ± 8.2%) in this study (Fig. 6). The low protein composition of phytoplankton could be due to deficient nitrogen for phytoplankton growth (Mayzaud et al., 1989; Lizotte and Sullivan, 1992; Danovaro et al., 2000) because proteins are nitrogenous substrates, whereas lipids and carbohydrates are non-nitrogenous compounds (Lombardi and Wangersky, 1991; Smith et al., 1997b; Takagi et al., 2000). In fact, previous studies have reported that protein production is dominant under conditions of sufficient nitrogen (Fabiano et al., 1993; Lee et al., 2009), whereas phytoplankton produced more lipids and carbohydrates when nutrients are limited (Shifrin and Chisholm, 1981; Harrison et al., 1990). During this study, the N:P ratio (2.45 ± 2.07) in the euphotic zone was considerably lower than the Redfield ratio, and the proteins:carbohydrates ratio (0.7 ± 0.6) of phytoplankton was less than 1, both of which suggest nitrogen deficiency for phytoplankton growth (Mayzaud et al., 1989; Lizotte

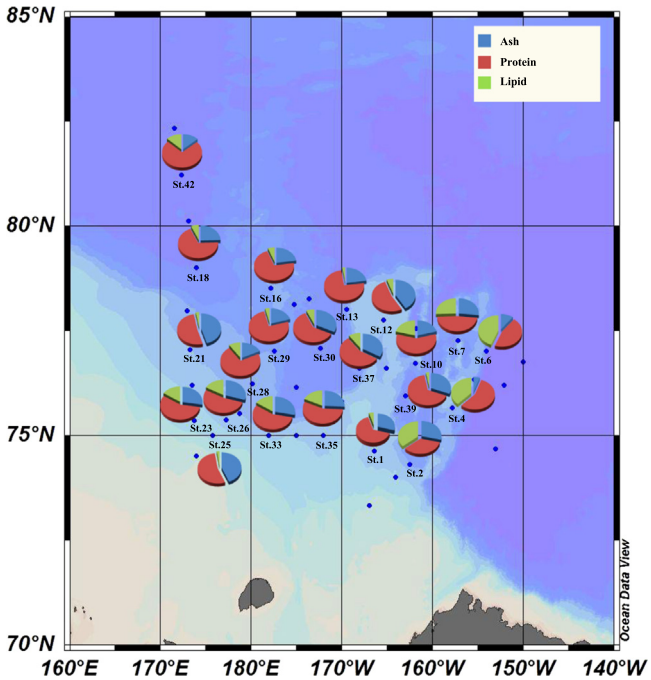

Fig. 7. Distribution of proximate composition of mesozooplankton community in the study area in 2012.

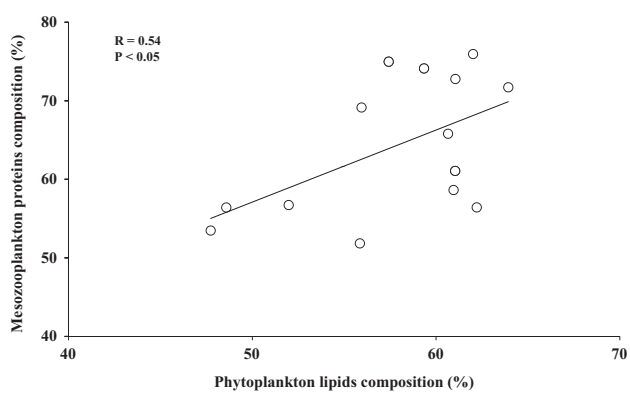

Fig. 8. Relationship between phytoplankton lipids composition (%) and mesozooplankton proteins composition (%).

and Sullivan, 1992; Danovaro et al., 2000). Thus, the low protein composition of phytoplankton in this study could be a result of nitrogen deficiency for phytoplankton growth in the northern Chukchi Sea (Fig. 6).

The average calorific content of phytoplankton was 1.2 ± 0.2 kcal m^{-3} in this study. This value is similar to that reported by Kim et al. (2015) in the northern Chukchi Sea during 2011 (1.0 ± 0.2 kcal m^{-3}). According to Kim et al. (2015), the calorific content of Arctic phytoplankton was not lower than that of the Antarctic phytoplankton (1.6 ± 1.3 kcal m^{-3}) (Fabiano et al., 1993, 1996). Although phytoplankton in the northern Chukchi Sea had very low productivity (Yun et al., 2015), they might maintain a high caloric content by having a higher lipid content.

4.2. Proximate and biochemical composition of mesozooplankton

In this study, proteins were the principle biochemical component in the mesozooplankton community dominated by copepods (Fig. 7). The mean protein content was 5.0 ± 1.6%WW and 59.7 ± 10.6%DW. This result is similar to those reported in previous studies (Ikeda, 1972; Morris and Hopkins, 1983; Donnelly et al., 1994). Ikeda (1972) found a mean of 60%DW protein for 10 zooplankton species examined in the Bering Sea. In the eastern Gulf, protein levels ranged from 30 to 70%DW and 4–14%WW for the copepod and euphausiid zooplankton fractions (Morris and Hopkins, 1983). Donnelly et al. (1994) reported a mean protein level of 4.2 ± 2.2% WW (ranged from 1.8 to 9.4%WW) in the Antarctic copepods. The water content in the mesozooplankton community varied from 85% to 94%, which generally agrees with values reported by previous studies for copepods (84.2–89.8%: Curl, 1962; 75.9–88.4%: Nakai, 1955; 74.0–91.0%: Donnelly et al., 1994). The mean ash content of mesozooplankton (26.4 ± 10.0% DW) in this study is somewhat higher than the values reported by Curl (1962) and Donnelly et al. (1994). Curl (1962) found ash contents of 17.6–22.8%DW for copepods, 18.6–22.4%DW for euphausiids, and 21.6%DW for sagitta. In the Antarctic, Donnelly et al. (1994) found relatively lower ash contents (15.2% and 11.0% for copepods in fall and winter). The lipid composition of the mesozooplankton in this study (1.2 ± 1.1%WW and 13.8 ± 12.4% DW) was lower than that of copepods reported by Donnelly et al. (1994) (2.9 ± 2.3%WW). According to Percy and Fife (1981), the lipid content in *Calanus* species reaches up to approximately 60%DW. In this study, a relatively high variation in lipid and ash contents was observed within stations (Table 4), which might result from the mixture of various mesozooplankton groups because ash and lipid contents vary with species (Ikeda, 1972; Morris and Hopkins, 1983).

The mean carbon content (68.9 ± 8.5%DW) of mesozooplankton was significantly higher than that of copepods of the Antarctic (43.1 ± 6.8%DW), but the mean nitrogen value (8.1 ± 0.9%DW) was almost identical to that of the Antarctic copepods (8.0 ± 1.2%DW) (Donnelly et al., 1994). The C/N ratio (10.0 ± 1.6) from this study is twice as high as that of the Antarctic copepods (5.5 ± 1.4) (Donnelly et al., 1994). In fact, the C/N ratio from zooplankton might reflect the C/N ratio from particulate organic matter. For example, the C/N ratio of particulate organic matter (10.6 ± 1.5) in the Arctic Ocean (e.g., northeast Chukchi Sea) was higher than that (7.3 ± 1.1) in the Antarctic Ocean (e.g., Amundsen Sea) (unpublished data from 2010 cruises). Thus, our high C/N ratio for mesozooplankton might have resulted from the high C/N ratio in the particulate organic matter that served as a food source. The mean caloric potential of the Arctic mesozooplankton (2.30 ± 1.60 kcal g dry wt^{-1}) is considerably lower than that of the zooplankton of other regions. For example, the zooplankton from the Tropical Pacific Ocean and Gulf of Mexico showed higher energy content than this study (4.83–5.85 kcal g dry wt^{-1} and 4.44 kcal g dry wt^{-1}, respectively) (Ostapenya and Shushkina, 1973). According to Donnelly et al. (1994), the caloric content of Antarctic copepods was 3.9 kcal g dry wt^{-1}. In addition, Percy and Fife (1981) reported a considerably higher energy content, ranging from 6.84 to 7.69 kcal g dry wt^{-1}, in *Calanus* species in Frobisher Bay of the Arctic. The low energy content in the mesozooplankton community in this study might be due to their compositional attributes (e.g., low lipid content). Some plausible explanations for the low lipid content of the mesozooplankton community are discussed in Section 4.3.

4.3. Relationship between the phytoplankton and zooplankton compositions

In this study, the lipid composition of phytoplankton was found to have a significantly positive relationship with the protein composition in mesozooplankton ($r = 0.54$, $p < 0.05$) (Fig. 8). Generally, macromolecular composition of phytoplankton can affect the biochemical components of the zooplankton predators of phytoplankton. For example, prey items with few lipids contribute to the low total lipid levels in predator species (Stickney and Torres, 1989),

whereas the incorporation of carbon into lipids can be higher in copepods that consume prey with high lipid contents (Parson et al., 1961). In contrast, the biochemical compositions of zooplankton could be different from those of phytoplankton (Scott, 1980). Scott (1980) reported that the transfer efficiencies between the prey organisms and the predators were different among major biochemical classes (such as proteins, lipids, and carbohydrates). Proteins have high transfer efficiency (approximately 56.5%), but lipids and carbohydrates have very low efficiency (11.1% and 5.5%, respectively) because they are mainly used for respiration (Scott, 1980). However, some portions of the algal carbohydrates and lipids can be used in animal protein synthesis (Droop and Scott, 1978). Another plausible explanation for the difference in the biochemical compositions of phytoplankton and mesozooplankton is that mesozooplankton may primarily consume protozoans rather than phytoplankton. Protozoans can constitute a substantial portion of the mesozooplankton diet in the Arctic Ocean (Thibault et al., 1999; Campbell et al., 2009; Sherr et al., 2009). According to Campbell et al. (2009), microzooplankton was preferred as prey by mesozooplankton, with the strength of the preference positively related to the proportion of microzooplankton available as prey in the western Arctic Ocean. Therefore, the substantial contribution of protozoans as food source for mesozooplankton might explain the difference in biochemical composition. Overall, the lipid contents in the mesozooplankton community were very low in this study (Fig. 7). Generally, lipids serve as the principle nutritional reserve of most zooplankton species (Percy and Fife, 1981). In addition, they contribute as the energy reserves to sustain the animals through starvation periods and supply energy for developing embryos (Morris and Hopkins, 1983). High lipids in some species are reported to be an accumulation of reserves for subsequent periods of low food availability and/or changes in feeding strategies during the winter and early spring months (Donnelly et al., 1990). However, the lipid content of zooplankton can vary significantly with factors such as body size, species, sex, depth of occurrence, and season. For example, lipid levels increase in females with eggs and also increase with depth (Morris and Hopkins, 1983; Clarke, 1980; Lee, 1974; Donnelly et al., 1993). According to Conover (1962), the lipid contents in *Calanus hyperboreas* from the Gulf of Maine ranged from 15 to 50%DW, with the highest values in the summer. Lee (1974) also reported that lipids of *C. hyperboreas* from the Arctic Ocean varied from 29% in June to 75% in August. Although many various factors generally affect the lipid content in the mesozooplankton community, a main reason for our low lipid contents might be the dominance of small zooplankton in this study. As the dominant species in the Arctic, *C. hyperboreas* have a large body size (body length; 7.2–8.0 mm) and contain very high lipid mass per individual (Lee, 1974; Lee et al., 2006), whereas relatively small *C. glacialis* (body length; 3.5–5.2 mm) have a lipid mass that is about five times lower (Scott et al., 2000; Lee et al., 2006). In this study, the abundance of *C. hyperboreas* was very low, 6% of the total mesozooplankton community, while small forms such as *C. glacialis* dominated (Table 3).

The spawning period of *C. glacialis* is from April to June in the high Arctic, whereas *Calanus hyperboreas* have an early spawning period from January to April in the high Arctic (Lee et al., 2006). The lipid contents are generally high in the mesozooplankton during the reproduction periods, whereas they are very low after spawning (Conover and Corner, 1968; Lee et al., 2006). In fact, the lipids of *Calanus hyperboreas* decreased from 50 to 25%DW during the winter/early spawning period (Conover and Corner, 1968).

5. Conclusions

This study is the first report of the relationship between the biochemical compositions of phytoplankton and zooplankton communities in the northern Chukchi Sea. However, the biochemical compositions of zooplankton are determined by complex ecological parameters (e.g., sex, food availability, reproduction, and diapause). Even identical species from different studies may exhibit notably different compositions in the Arctic and Antarctic regions, with strong seasonal nature or with a regional variability in production (Donnelly et al., 1994). Because our results represent the average biochemical compositions of phytoplankton and zooplankton communities at the time of collection, additional measurements of biochemical composition of phytoplankton and zooplankton would be needed to better understand the impacts of ongoing changes in climate and sea-ice conditions on lower trophic levels and subsequently Arctic marine ecosystems.

Recently, the dominant phytoplankton community has changed under the freshening and warming surface layer in the Canada Basin: small phytoplanktons (<2 μm diameter) have increased, whereas larger cells have decreased (Li et al., 2009). Consistently, Hopcroft et al. (2005) found that smaller zooplankton were numerically dominant in the upper 100 m of the water column in Arctic oceanic waters, although they may contribute relatively little to the total biomass. These changes in the community structures of phytoplankton and zooplankton under the rapidly changing environmental conditions of the Arctic could result in different biochemical compositions. In fact, Lee et al. (2009) reported a large difference in macromolecular production between small and large phytoplankton cells in the Chukchi Sea. Because the biochemical composition of phytoplankton is directly related to food quality for higher trophic levels, which could lead a change in the nutritional status, reproduction periods, and survival strategy of higher trophic levels, the measurement of the biochemical compositions of phytoplankton and zooplankton should be considered for the long-term monitoring of the marine ecosystem in the Arctic Ocean.

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