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Abstract: The northern Bering and Chukchi seas are biologically productive regions but, recently, unprecedented environmental changes have been reported. For investigating the dominant phytoplankton communities and relative contribution of small phytoplankton (<2 µm) to the total primary production in the regions, field measurements mainly for high-performance liquid chromatography (HPLC) and size-specific primary productivity were conducted in the northern Bering and Chukchi seas during summer 2016 (ARA07B) and 2017 (OS040). Diatoms and phaeocystis were dominant phytoplankton communities in 2016 whereas diatoms and Prasinophytes (Type 2) were dominant in 2017 and diatoms were found as major contributors for the small phytoplankton groups. For size-specific primary production, small phytoplankton contributed 38.0% (SD =  $\pm 19.9\%$ ) in 2016 whereas 25.0% (SD =  $\pm 12.8\%$ ) in 2017 to the total primary productivity. The small phytoplankton contribution observed in 2016 is comparable to those reported previously in the Chukchi Sea whereas the contribution in 2017 mainly in the northern Bering Sea is considerably lower than those in other arctic regions. Different biochemical compositions were distinct between small and large phytoplankton in this study, which is consistent with previous results. Significantly higher carbon (C) and nitrogen (N) contents per unit of chlorophyll-a, whereas lower C:N ratios were characteristics in small phytoplankton in comparison to large phytoplankton. Given these results, we could conclude that small phytoplankton synthesize nitrogen-rich particulate organic carbon which could be easily regenerated.

Keywords: Bering Sea; Chukchi Sea; HPLC; small phytoplankton; primary productivity

## 1. Introduction

The biologically productive northern Bering Sea and the Chukchi Sea are important conduit of water masses and organic matters from the North Pacific Ocean transported into the Arctic Ocean and biologically productive regions [1–5]. Over the past few decades, many environmental changes have been reported in the regions [4,6–8]. Unprecedented high sea surface temperature was reported in the Bering Sea in 2014 and persisted in 2018 and 2019 [8; refs therein]. The Pacific origin freshwater flux with increasing northward volume transport into the Arctic Ocean had been increased over the 1991–2015 period [9]. Moreover, seasonal sea ice cover has been retreating earlier and forming later in the Pacific Arctic region over the last decade [10]. These current and ongoing changes in environmental conditions could subsequently cause changes in biogeochemical processes and consequently alter marine ecosystem structure in the northern Bering and Chukchi



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**Copyright:** © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). seas [11,12]. Indeed, the prior studies indicate that the variation in primary productivity of phytoplankton is mainly governed by freshwater content variability in the Pacific Arctic region [13,14]. Moreover, the seasonal sea ice cover could largely influence phytoplankton community composition [15], phytoplankton bloom period [16] and primary productivity [17].

Refs. [13,18–20] reported that pico-phytoplankton increased whereas larger cells declined in the Arctic Ocean because of stronger stratification and consequently lower nutrient supply into the upper water column caused by freshening surface waters. Based on the phytoplankton size classes derived from satellite ocean color data in the northern Bering and southern Chukchi seas [21], observed increasing trends in pico-phytoplankton in the Chirikov and St. Lawrence Island Polynya regions whereas an increasing trend in micro-phytoplankton in the southeastern Chukchi Sea from 1998 to 2016. The physiological conditions and subsequently photosynthetic end-products of phytoplankton affected by the recent environmental conditions were also previously reported in the northern Bering and southern Chukchi seas [21–23]. Phytoplankton as important primary producers in marine ecosystems can be a good indicator of environmental changes. These long-term changes in the functional phytoplankton group are strongly related to increasing annual sea surface temperature [13]. Therefore, monitoring the phytoplankton community responses such as shifts in dominant phytoplankton species and biomass to the current environmental changes is crucial to observe marine ecosystem alterations in the northern Bering and Chukchi seas [12,18–20].

Especially, the contribution of small phytoplankton could be necessary to understand potential impacts on the total primary production and, thus, whole marine ecosystems [12,20,21]. Moreover, the biochemical characteristics of phytoplankton such as C:N ratio are critical for understanding marine biogeochemical processes responding to environmental conditions. Ref. [24] reported higher C:N ratio related with low chlorophyll-*a* concentration and lower C:N ratio to high chlorophyll-*a* concentration in the Arctic Ocean. The C:N ratio could differ in various environmental conditions related to nutrients. However, little information on the small phytoplankton contribution to the total primary production and their biochemical traits such as C:N ratio is currently available in the northern Bering and Chukchi seas.

In this study, our objectives are to investigate the dominant phytoplankton communities and to assess the relative contribution of small phytoplankton (0.7–2.0  $\mu$ m; picophytoplankton) to the total primary production and their biochemical characteristics (e.g., C:N ratio) in the northern Bering and Chukchi seas.

### 2. Materials and Methods

## 2.1. Study Area and Water Sampling

The ARA07B cruise was conducted in the northern Bering Sea and the Chukchi Sea during 5–19 August, 2016 onboard the Icebreaker R/V *Araon* (Figure 1; Table 1). As a total of 16 stations during the ARA07B cruises, only one station (st. 1) was located in the northern Bering Sea and 15 stations were in the Chukchi Sea. Water was sampled by Niskin bottles on conductivity-temperature-depth (CTD)/rosette sampler for the total chlorophyll-*a* and size-fractionated chlorophyll-*a* concentration. Euphotic depths were measured by a Secchi disk [25]. The OS040 cruise was executed mostly in the northern Bering Sea (8 stations) and partly in the southern Chukchi Sea (2 stations) during 9–21 July, 2017 onboard T/S *Oshoro-Maru* (Figure 1; Table 1). Physical properties and water samples were collected by CTD/rosette with Niskin bottles. The euphotic depths were calculated by comparing downward irradiance and surface irradiance measured by compact optical profiling system (C-OPS; Biospherical instrument Inc., San Diego, CA, USA).



Figure 1. Sampling locations of (a) ARA07B and (b) OS040 cruises.

	Station	Date	Latitude (°N)	Longitude (°E)	Bottom depth (m)
	st. 1	5 Aug 2016	65.17	-168.69	49
	st. 3	6 Aug 2016	67.67	-168.96	50
	st. 6	6 Aug 2016	68.01	-167.87	52.3
	st. 12	8 Aug 2016	72.36	-168.67	55
	st. 14	9 Aug 2016	74.80	-167.90	223
	st. 15	17 Aug 2016	75.24	-171.98	512
	st. 16	10 Aug 2016	75.15	-176.00	331.57
	st. 18	11 Aug 2016	75.77	177.07	486
AKAU7D	st. 19	12 Aug 2016	76.00	173.60	282
	st. 20	12 Aug 2016	77.00	176.57	1232
	st. 21	13 Aug 2016	78.00	177.28	1693
	st. 23	15 Aug 2016	77.87	-175.91	1564
	st. 24	16 Aug 2016	77.00	-175.00	2008
	st. 28	18 Aug 2016	77.70	-169.50	1756
	st. 29	18 Aug 2016	77.47	-164.12	280
	st. 30	19 Aug 2016	76.58	-165.38	987
	1	9 Jul 2017	66.28	-168.90	57
	5	11 Jul 2017	65.66	-168.26	45
	7	12 Jul 2017	65.06	-169.64	51
	9	14 Jul 2017	65.07	-168.19	42
OS040	U-3	16 Jul 2017	64.44	-166.52	27
	13	17 Jul 2017	64.50	-169.52	42
	15	18 Jul 2017	64.50	-170.89	46
	19	19 Jul 2017	63.50	-173.02	66
	23	21 Jul 2017	62.17	-170.50	46

Table 1. Sampling locations in the Northern Bering and Chukchi Seas.

## 2.2. Chlorophyll-a Analysis

The water samples were obtained from 6 different light depths (100%, 50%, 30%, 12%, 5% and 1% of the surface photosynthetically active radiation (PAR) for measuring the chlorophyll-*a* concentration. For the total chlorophyll-*a* concentration, 300 mL of seawater was filtered through 25 mm glass fiber filter (GF/F; Whatman). To obtain size-fractionated

chlorophyll-*a* concentration, 500 mL seawater was filtered through 20  $\mu$ m and 2  $\mu$ m pore size membrane filters and then 47 mm GF/F sequentially. After the filtration was done, the filters were wrapped with aluminum foil and stored at  $-80^{\circ}$ C freezer until analysis at the home laboratory. Chlorophyll-*a* extractions were followed by [26] and the concentrations were measured with a fluorometer (Turner Designs 10AU).

## 2.3. High-Performance Liquid Chromatography Analysis for Accessory Pigment Concentration

For high-performance liquid chromatography (HPLC) analysis, the water from 3 light depths (100%, 30% and 1%) were sampled during the ARA07B and OS040 cruises. Seawater (0.8-2.5 L) was passed through 2  $\mu$ m membrane filter and 47 mm diameter GF/F filters to measure pigments concentration of small size phytoplankton (<2 µm) under gentle vacuum pressure (<100 mmHg). Seawater (0.5–1.5 L) was filtered onto GF/F for pigments of total phytoplankton during the ARA07B. For the OS040, samples were obtained only for total phytoplankton. For avoiding degradation, the filters for HPLC analysis were immediately frozen and stored in liquid nitrogen at  $-80^{\circ}$ C freezer until analysis at home laboratory. In the laboratory, the filter samples were broken into small pieces and then soaked in 3 mL of N'N-dimethylformamide (DMF) with canthaxanthin served as an internal standard. After 20 min of sonication, the filters were extracted at 4°C in dark for 24 h and then extracts were filtered through a 0.45 µm pore membrane filter to remove GF/F particles. For minimizing photo-degradation of pigments, all the procedures were conducted under a low light condition. Pigments were analyzed using HPLC (Agilent Infinite 1260 in operation by JAMSTEC, Mutsu, Japan) with a ternary linear gradient system to separate each pigment. The pigment concentrations were calculated by the function of peak area, standard response factors and peak area of the internal standard following [27]. All the standards for each pigment were purchased from DHI in Denmark.

The CHEMTAX software based on a factorization program was used for estimating the relative contributions of different phytoplankton communities to the total chlorophyll-*a* concentration [28]. The ratios of accessory pigments to chlorophyll-*a* for each phytoplankton taxon for the CHEMTAX program were based on marker pigment concentrations of algal groups present in the Arctic Ocean [13,29] (Table 2). Since our two research cruises were in different periods and years, the final ratio matrix was separated for phytoplankton communities (Table 2). The contributions of Diatoms. Dinoflagellates, Cryptophytes, Pelagophytes, Prasinophytes (Type 2 and 3), Chlorophytes, Haptophytes and Phaeosystis were estimated by the CHEMTAX program. Small phytoplankton community was estimated from HPLC results by the equations described in the literature [28,29]. The relative proportions of the three size classes are derived from the concentrations of phytoplankton diagnostic pigments for the Chukchi and Bering seas using the equations described in [30,31].

Class	chl-b	chl-c3	fucox	perid	allox	19butfu	19hexfu	chl-c	neox	prasinox	lut
Initial ratio matrix											
Diatoms	0	0	0.425	0	0	0	0	0.171	0	0	0
Dinoflagellates	0	0	0	0.6	0	0	0	0	0	0	0
Cryptophytes	0	0	0	0	0.673	0	0	0	0	0	0
Chryso-Pelago	0	0.114	0.285	0	0	0.831	0	0.285	0	0	0
Prasino-2	0.812	0	0	0	0	0	0	0	0.033	0	0.096
Prasino-3	0.764	0	0	0	0	0	0	0	0.078	0.248	0.009
Chlorophytes	0.339	0	0	0	0	0	0	0	0.036	0	0.187
Phaeocystis	0	0.208	0.35	0	0	0	0	0	0	0	0
Hapto-7	0	0.171	0.259	0	0	0.013	0.491	0.276	0	0	0

**Table 2.** Pigment:chlorophyll-*a* ratios for nine algal groups referred to [32]. CHEMTAX initial ratio matrix and final pigment ratios obtained by CHEMTAX on the pigment data.

Class	chl-b	chl-c3	fucox	perid	allox	19butfu	19hexfu	chl-c	neox	prasinox	lut
ARA07B Final ratio matrix											
Diatoms	0	0	0.785	0	0	0	0	0.395	0	0	0
Dinoflagellates	0	0	0	0.6	0	0	0	0	0	0	0
Cryptophytes	0	0	0	0	0.673	0	0	0	0	0	0
Chryso-Pelago	0	0.114	0.285	0	0	0.831	0	0.285	0	0	0
Prasino-2	0.593	0	0	0	0	0	0	0	0.007	0	0.007
Prasino-3	4.006	0	0	0	0	0	0	0	0.166	0.803	0.027
Chlorophytes	0.339	0	0	0	0	0	0	0	0.036	0	0.187
Phaeocystis	0	0.1791	0.301	0	0	0	0	0	0	0	0
Hapto-7	0	0.171	0.259	0	0	0.013	0.508	0.276	0	0	0
				OS040	Final ratio	matrix					
Diatoms	0	0	0.722	0	0	0	0	0.328	0	0	0
Dinoflagellates	0	0	0	1.409	0	0	0	0	0	0	0
Cryptophytes	0	0	0	0	0.673	0	0	0	0	0	0
Chryso-Pelago	0	0.114	0.285	0	0	0.831	0	0.285	0	0	0
Prasino-2	0.812	0	0	0	0	0	0	0	0.033	0	0.096
Prasino-3	0.280	0	0	0	0	0	0	0	0.107	0.471	0.011
Chlorophytes	0.643	0	0	0	0	0	0	0	0.029	0	0.969
Phaeocystis	0	0.558	1.457	0	0	0	0	0	0	0	0
Hapto-7	0	0.171	0.259	0	0	0.013	0.617	0.276	0	0	0

Table 2. Cont.

Abbreviations: chlorophyll-*b* (chl-b), chlorophyll-*c*3 (chl-c3), fucoxanthin (fucox), peridinin (period), alloxanthin (allox), 19'-butanoyloxyfucoxanthin (19butfu), 19'-hexanoyloxyfucoxanthin(19hexfu), chlorophyll-*c*1+*c*2 (chl-c), neoxanthin (neox), prasinoxanthin (prasinox), lutein (lut). Chrysophytes and Pelagophytes (Cryso-pelago). Prasinophytes type 2 (Prasino-2), Prasinophytes type 3 (Prasino-3), Haptophytes (Hapto-7).

#### 2.4. Particulate Organic Carbon and Primary Productivity

The water samples for particulate organic carbon (POC) and primary productivity were obtained from 6 light depths (100, 50, 30, 12, 5 and 1% of PAR). 300 mL of seawater was filtered through 0.7 µm GF/F (pre-combusted at 450 °C for 4 h) for total POC and 500 mL was passed through 2 µm pore size membrane filter and then filtered onto GF/F filter for small POC (0.7-2 µm). Carbon and nitrogen uptake experiments were conducted using a <sup>13</sup>C-<sup>15</sup>N dual isotope tracer technique previously reported from the Chukchi Sea [3,33]. After a 4 h incubation on deck, 300 mL water was filtered onto pre-combusted GF/F for total primary productivity and 500 mL water was filtered through 2 µm pore size membrane filter and sequentially onto GF/F filter for small phytoplankton productivity (0.7–2  $\mu$ m). The filters were immediately preserved and stored in a freezer  $(-20 \,^{\circ}\text{C})$  until further mass spectrometric analysis using a Delta V+ Isotope Ratio Mass Spectrometers of Alaska Stable Isotope Facility at the University of Alaska Fairbanks, USA for ARA07B samples and using a 20-22 Isotope Ratio Mass Spectrometer (SERCON) at Japan Agency for Marine-Earth Science and Technology (JAMSTEC, Mutsu, Japan) for OS040 samples after HCl fuming overnight to remove carbonate. The carbon and nitrogen uptake rates were calculated based on [34].

### 2.5. Statistical Analysis

Student's t-test was applied to verify correlations among factors and differences between the mean values of POC:chlorophyll-*a* ratio, PON:chlorophyll-*a* ratio, C:N ratio of each cruise and size group. The agglomerative hierarchical clustering (AHC) with Ward's method (XLSTAT software, Addinsoft, Boston, MA, USA) was performed to calculate the dissimilarity in observed 20 variables; temperature and salinity), size-fractionated primary productivity, particulate organic carbon of each size, size-fractionated chlorophyll-*a* and accessory pigments, among stations.

## 3. Results and Discussion

## 3.1. Spatial Distribution of Temperature and Salinity

The temperature and salinity ranged from -1.5 °C to 9.2 °C (mean ± standard deviation (SD) = 0 ± 2.7 °C) and from 26.5 to 32.3 (mean ± SD = 29.9 ± 1.6) during the ARA07B cruise (Figure 2). The temperature during the OS040 were from -1.1 to 13.3 °C (mean ± SD =  $6.2 \pm 3.6$  °C) and the salinity ranged from 28.9 to 32.9 (mean ± SD =  $31.7 \pm 0.9$ ). Water mass at the most stations in the northern Chukchi corresponded to melting glacier water, which called Ice melt water (IMW; temperature < 2.0 °C and salinity < 30.0) and Bering Chukchi winter water (BCWW; -2-0 °C and <30-33.5 for temperature and salinity; [35]) during the ARA07B cruise. Other stations during the ARA07B were influenced by Bering shelf water (BSW; 0.0-10.0 °C and 31.8-33.0 for temperature and salinity). During the OS040 cruise, the relatively warm and low salinity Alaskan coastal water (ACW; 2.0-13.0 °C and 31.8-33.0 for temperature (BSAW; -1.0-2.0 °C and 31.8-33.0 for temperature (BSAW; -1.0-2.0 °C and 31.8-33.0 for temperature (BSAW; -1.0-2.0 °C and 31.8-33.0 for temperature and salinity) were predominant (Figure 2). The Bering shelf Anadyr water (BSAW; -1.0-2.0 °C and 31.8-33.0 for temperature and salinity), which is a mixed BSW with cold/saline Anadyr water (AW; [36,37]), was observed at some stations for the OS040 cruise.



**Figure 2.** T–S diagram in the ARA07B (Red) and OS040 (Green). Alaskan coastal water (ACW), Bering Shelf water (BSW), ice melt water (IMW), Bering–Chukchi winter water (BCWW), Bering Sea Anadyr water (BSAW).

# 3.2. Chlorophyll-a Concentration and Different Size Chlorophyll-a Compositions in the Northern Bering and Chukchi Seas

The average euphotic depths were 45.6 m (SD =  $\pm 22.2$  m) for the ARA07B cruise and 23.8 m (SD =  $\pm 9.1$  m) for the OS040 cruise, respectively. In ARA07B, Chlorophyll-*a* concentrations were 0.02–1.3 mg chl-*a* m<sup>-3</sup> (mean  $\pm$  SD = 0.2  $\pm$  0.3 mg chl-*a* m<sup>-3</sup>) at surface, 0.02–15.0 mg chl-*a* m<sup>-3</sup> (mean  $\pm$  SD = 1.0  $\pm$  2.5 mg chl-*a* m<sup>-3</sup>) for euphotic layer. In OS040, Chlorophyll-*e* concentrations were 0.002–5.5 mg chl-*a* m<sup>-3</sup> (mean  $\pm$  SD = 0.7  $\pm$  1.4 mg chl-*a* m<sup>-3</sup>) at surface, 0.002–5.5 mg chl-*a* m<sup>-3</sup> (mean  $\pm$  SD = 1.6  $\pm$  2.2 mg chl-*a* m<sup>-3</sup>) for euphotic layer. Within the euphotic zone, integral chlorophyll-*a* concentrations were 3.2–172.1 mg chl-*a* m<sup>-2</sup> (mean  $\pm$  SD = 34.2  $\pm$  48.0 mg chl-*a* m<sup>-2</sup>) during the ARA07B and 12.3–107.8 mg chl-*a* m<sup>-2</sup> (mean  $\pm$  SD = 45.4  $\pm$  34.1 mg chl-*a* m<sup>-2</sup>) for the OS040, respectively (Figure 3). The average euphotic-depth integral chlorophyll-*a* concentrations in this study are within the range reported previously in the northern Bering Sea and the Chukchi Sea [3,14,21].



**Figure 3.** Spatial distributions of column-integrated chlorophyll-*a* concentration of (**a**) ARA07B and (**b**) OS040.

The chlorophyll-*a* contributions of each size phytoplankton (pico-, nano- and microphytoplankton) to the total phytoplankton were plotted in Figure 4 for the three different depths (100, 30 and 1% of light depths) at every station of the ARA07B and only surface for the OS040. The contributions of small phytoplankton to the total chlorophyll-*a* concentrations were found largely variable among the stations during both cruises.

The contributions of small phytoplankton to the total chlorophyll-a concentrations ranged from 2.9% to 71.1% with a depth-integrated average of 32.2% (SD =  $\pm 23.1\%$ ) during the ARA07B. In the ARA07B, the dominant size group of phytoplankton was microphytoplankton (mean  $\pm$  SD = 43.5  $\pm$  29.7% of chlorophyll-*a* concentration) followed by pico-phytoplankton (32.1  $\pm$  23.1%) and nano-phytoplankton (24.3  $\pm$  9.1%) during the observation period. In the Chukchi Sea, large phytoplankton are generally dominant although the areal distribution of their contribution mostly depends on local water masses in different nutrient conditions [3,21]. Normally, large phytoplankton growing under nutrient-enriched conditions are predominant in AW or BSW, whereas small phytoplankton are dominant in nutrient-depleted ACW [3,21]. Our average contribution of small phytoplankton is relatively higher than that  $(24.8 \pm 23.0\%)$  previously reported by [21] in the Chukchi Sea during the middle of August to early September, 2004. By contrast, our average contribution of small phytoplankton is relatively lower than that (55.1  $\pm$  26.8%) from the study by [38] that was conducted in the northern Chukchi Sea during mid-July–mid-August, 2012. This difference among the studies could be caused by different regions with non-homogeneous nutrient conditions and different observation periods with a seasonal phytoplankton succession. The relative contribution of small phytoplankton could be caused by freshwater content in the Chukchi Sea since the nutrient concentrations and primary production rates of phytoplankton are largely governed by the nutrient-depleted freshwater content in the Chukchi Sea [14,39].

In comparison to the Chukchi Sea, the contributions of small phytoplankton were 0.7–80% (mean  $\pm$  SD = 37.2  $\pm$  31.0%) to the total chlorophyll-*a* concentration in the northern Bering Sea for the OS040 in this study. The proportions of different size chlorophyll-*a* were 40.2% ( $\pm$ 35.4%), 22.5% ( $\pm$ 10.5%) and 37.2% ( $\pm$ 31.3%) for micro-, nano- and picophytoplankton, respectively, during our observation period in 2017. In the northern Bering Sea, the dominant size groups of phytoplankton are generally nano- and microphytoplankton based on phytoplankton size class results derived from satellite ocean color data from 1998 to 2016 [12]. The overall dominant size of phytoplankton is composed of nano-phytoplankton (49.0  $\pm$  9.6%), followed by micro-phytoplankton (34.9  $\pm$  8.0%) and pico-phytoplankton (16.1  $\pm$  7.3%) in the Chirikov Basin of the northern Chukchi Sea [12]. However, the chlorophyll-*a* contributions of small phytoplankton are largely variable

among different seasons [40]. The average contribution of small phytoplankton was 14.8% in late May to early June during the phytoplankton bloom period and largely increased up to 50.0% in middle June after the bloom [41]. Consistently, [13] found a seasonal increasing contribution of small phytoplankton in the northern Bering Sea (around Chirikov Basin) from May (5.2%) to July (31.8%). In addition to the seasonal variation, spatially the biochemical environmental conditions in the northern Bering Sea are also generally influenced by northward advection of AW, BSW and ACW [3,5]. Over recent decades, several environmental changes have been reported in the northern Bering Sea [4,5]. A steady increasing trend in the annual contribution of small phytoplankton is distinct in the Chirikov Basin from 1998 to 2016, although no significantly strong relationship was observed between the annual contribution of small phytoplankton and sea surface temperature [12]. Long-term changes in dominant phytoplankton communities should be monitored for Arctic marine ecosystems under ongoing environmental changes. Especially, the contribution of small phytoplankton communities should be monitored for Arctic marine ecosystems under ongoing environmental changes. Especially, the contribution of small phytoplankton communities for changing marine ecosystems.

![](_page_7_Figure_2.jpeg)

Figure 4. Total chlorophyll-a concentration of (a) ARA07B and (b) OS040.

### 3.3. Pigment Composition and Major Dominant Phytoplankton Groups

The euphotic depth-integral concentrations of marker pigments from the two cruises are shown in Figure 5. Fucoxanthin (a marker pigment of diatoms), chlorophyll-c1+c2 and chlorophyll-b (a marker pigment of chlorophytes) were major accessory pigments during the ARA07B, although the pigment compositions spatially varied significantly across the

stations. Among the pigments, fucoxanthin was the most dominant pigment with an average value of  $12.58 \pm 21.8$  mg m<sup>-2</sup> and the second and third predominant pigments were chlorophyll-c1+c2 ( $4.04 \pm 4.83 \text{ mg m}^{-2}$ ) and chlorophyll-b ( $2.64 \pm 2.53 \text{ mg m}^{-2}$ ). Previous studies reported that fucoxanthin dominating the Chukchi shelf is a typical characteristic during fall [13,31]. For the small phytoplankton group for the ARA07B (data not shown), major predominant pigments were chlorophyll-b ( $1.59 \pm 1.83$  mg m<sup>-2</sup>), fucoxanthin  $(1.46 \pm 1.47 \text{ mg m}^{-2})$  and chlorophyll-c1+c2  $(0.65 \pm 0.62 \text{ mg m}^{-2})$ . In comparison, fucoxanthin, chlorophyll-c1+c2 and peridinin (a marker pigment of dinoflagellates) were major accessory pigments for the OS040. Fucoxanthin was the most dominant pigment with an average value of  $23.03 \pm 19.89$  mg m<sup>-2</sup>, followed by chlorophyll-c1+c2  $(9.35 \pm 7.23 \text{ mg m}^{-2})$  and peridinin  $(7.54 \pm 9.89 \text{ mg m}^{-2})$  for the OS040. High proportions of diatom-related pigments (fucoxanthin, chlorophyll-c1+c2) were observed in both cruise periods. Small diatoms appeared to be major phytoplankton communities for the small phytoplankton group during the ARA07B, based on the high proportions of chlorophyll-b and fucoxanthin. No pigment data were available for the small phytoplankton during the OS040 cruises.

![](_page_8_Figure_2.jpeg)

Figure 5. Pigment compositions of total phytoplankton in the (a) ARA07B (b) OSO040.

Based on the CHEMTAX results, eight major phytoplankton communities were identified in the study area (Figure 6). Diatoms ( $43.1\% \pm 31.5\%$ ) and Phaeocystis ( $33.2\% \pm 14.9\%$ ) were co-dominated during the ARA07B. In comparison, Diatoms were the most dominant community ( $46.1 \pm 17.3\%$ ) and the second dominant community was Prasinophyte (Type 2) ( $11.8\% \pm 5.3\%$ ) for the OS040. Micro-phytoplankton communities were most dominant ( $59.7 \pm 30.5\%$ ), followed by nano-phytoplankton ( $11.5 \pm 9.7\%$ ) and pico-phytoplankton ( $28.9 \pm 23.5\%$ ) during the ARA07B. For the OS040, micro-phytoplankton contributed 51.5% ( $\pm 18.2\%$ ) of the total chlorophyll a concentration. In comparison, nano-phytoplankton and pico-phytoplankton contributed 11.0% ( $\pm 10.5\%$ ) and 37.5% ( $\pm 15.7\%$ ), respectively. The relative proportions of the three size classes based on the diagnostic pigments from HPLC are different from those of the size-fractionated chlorophyll-*a* concentrations (Figure 4). This is probably due to a simple assumption that diatom-related pigments belong to the micro-phytoplankton although small diatoms (<2 µm) could contribute to the phytoplankton group.

### 3.4. Primary Production Contribution of Small Phytoplankton and Their Ecological Roles

The daily primary productivities of total phytoplankton which were integrated over the euphotic zone at each station were 33.9–811.8 mg C m<sup>-2</sup> d<sup>-1</sup> (mean  $\pm$  SD = 142.6  $\pm$  205.7 mg C m<sup>-2</sup> d<sup>-1</sup>) for the ARA07B and 202.1–3100.1 mg C m<sup>-2</sup> d<sup>-1</sup> (mean  $\pm$  SD = 942.1  $\pm$  969.9 mg C m<sup>-2</sup> d<sup>-1</sup>) for the OS040 (Figure 7). In comparison, the daily primary productivities of small phytoplankton ranged from 4.9 to 227.7 (mean  $\pm$  SD = 42.3  $\pm$  53.1 mg C m<sup>-2</sup> d<sup>-1</sup>) and 56.1 to 322.2 mg C m<sup>-2</sup> d<sup>-1</sup> (mean  $\pm$  SD = 152.8  $\pm$  85.2 mg C

 $m^{-2} d^{-1}$ ) for the ARA07B and the OS040, respectively (Figure 8). The contribution of small phytoplankton to the total primary productivity ranged from 8.1 to 71.7% (mean  $\pm$  SD = 38.0  $\pm$  19.9%) for the ARA07B and from 6.0 to 40.3% (mean  $\pm$  SD = 25.0  $\pm$  12.8%) for the OS040 (Figure 9).

![](_page_9_Figure_2.jpeg)

Figure 6. Phytoplankton community compositions of (a) ARA07B and (b) OS040.

![](_page_9_Figure_4.jpeg)

Figure 7. Primary production of total phytoplankton during the (a) ARA07B and (b) OS040.

![](_page_9_Figure_6.jpeg)

Figure 8. Primary production of small phytoplankton during the (a) ARA07B and (b) OS040.

![](_page_10_Figure_2.jpeg)

Figure 9. Primary production of small phytoplankton of (a) ARA07B and (b) OS040.

Overall, the primary productions of total and small phytoplankton communities during the study period were different depending on the sea area. Indeed, agglomerative hierarchical clustering (AHC) analysis based on 25 stations and phytoplankton size-related variables sorted stations into four distinct groups (Figure 10; Table 3). Cluster 1 include station 1 of OS040 that was high primary productive region (1992.9 mg C m<sup>-2</sup> d<sup>-1</sup>) near Bering strait. Cluster 1 had a relative low contribution of small phytoplankton in primary productivity (5.9%) and surface chlorophyll-a (2.9%). Cluster 2 was station 7 of OS040 that was an extremely high productive station (3100.0 mg C m<sup>-2</sup> d<sup>-1</sup>) and represented the lowest contribution of small phytoplankton among clusters. Small phytoplankton contribution to primary production was 6.9% and the contribution to surface chlorophyll-a concentration was only 0.7% for clusters 2. The physical properties of Cluster 1 (3.5  $^{\circ}$ C and 32.7 psu) and 2 (5.5 °C and 32.7 psu) were similar. These two clusters are influence by BSW [3,21]. Cluster 3 contains all the stations of the northern Chukchi Sea and two stations of the Bering Sea. The stations form Cluster 3 had a lower productivity and lower concentration of surface chlorophyll-a. In Cluster 3, small phytoplankton contribution was the highest among the clusters. 40.5% of primary production, 39.1% of surface chlorophyll-a and 40.9% of POC were contributed by small phytoplankton. Dominant water mass, IMW can explain the high contribution of small phytoplankton in Cluster 3 because IMW has nutrient-depleted water from sea ice melting [34]. Cluster 4 includes most of the stations in the Bering Sea and 3 stations of the southern Chukchi sea in ARA07B. Cluster 4 had a lower productivity (559.2 mg C m<sup>-2</sup> d<sup>-1</sup>) than cluster 1 and 2 but higher than cluster 3. Cluster 4 seems to be affected by nutrient-depleted ACW but not too low productivity for Cluster 4. This suggests that water masses that had an effect on Cluster 4 were not only ACW but also other source such as mixed water of AW, ACW and BSW.

<b>Table 3.</b> Mean values of properties for the 4 clusters classified by the A	HC.
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Cluster	Т (°С)	S (psu)	Small Contribution to PP	Small Contribution to Surface chl-a	Small Contribution to POC	PP (mg C m <sup>-2</sup> d <sup>-1</sup> )	Chl-a (mg m <sup>-3</sup> )	POC (mg m <sup>-3</sup> )
1	3.5	32.7	6.0%	2.9%	25.0%	1992.9	66.3	349.0
2	5.5	32.7	6.9%	0.7%	18.6%	3100.1	128.8	479.5
3	0.1	29.7	40.5%	39.1%	40.9%	79.6	13.9	177.7
4	5.6	31.7	26.7%	39.1%	43.9%	559.2	60.7	236.1

![](_page_11_Figure_1.jpeg)

**Figure 10.** Dendrogram stands for sampling stations were divided into four clusters by agglomerative hierarchical clustering (AHC).

The primary production contributions of small phytoplankton are rather different from their chlorophyll-*a* contributions in this study. Normally, the contributions of small phytoplankton are higher to primary production in comparison to those in chlorophyll-a concentrations in the polar oceans [21,41] and temperate oceans [42]. This is probably due to the considerably higher POC contribution of small phytoplankton (and consequently higher production contributions of small phytoplankton) than the chlorophyll-*a* contribution [21,40,42]. We also observed the higher POC:chlorophyll-*a* ratio in small phytoplankton than large phytoplankton during both cruises (Figure 11) as discussed later. However, the case in the northern Bering Sea in this study is against the general pattern previously reported. The lower contribution of small phytoplankton was observed in the primary production rather than chlorophyll-*a* concentration in the northern Bering Sea. This indicates higher standing stock (represented by chlorophyll-*a* concentrations) of small phytoplankton but their significantly lower contribution to the primary productions in the northern Bering Sea. [20] argued that seasonal

increasing contribution of small phytoplankton is not caused by their increasing biomass and photosynthetic rate but caused by relative declining in biomass and photosynthetic rate of large phytoplankton in the Amundsen Sea, Antarctic Ocean. Based on these results, the biomass of large phytoplankton could have had decreased faster than their photosynthetic rate in the northern Bering Sea during our observation period.

![](_page_12_Figure_2.jpeg)

**Figure 11.** Comparison of (**a**) POC:chlorophyll-*a* ratios, (**b**) PON:chlorophyll-*a* ratios and (**c**) C:N ratios between small and large phytoplankton in the northern Bering and Chukchi seas. Only POC:chlorophyll-*a* data available for the OS040. (**d**) C:N ratio and chlorophyll-a of each size group.

The regional contributions of small phytoplankton to the primary production are summarized at various regions in the Arctic Ocean (Table 4). The average contribution of small phytoplankton in this study is comparable to the previous results in the Chukchi Sea. However, it is considerably lower than those (average  $\pm$  SD = 56.7  $\pm$  20.0%) in the Kara, Laptev and East Siberian Seas [43]. Similarly, reference [41] found a similar contribution (average  $\pm$  SD = 60  $\pm$  7.9%) of small phytoplankton in the high northern Chukchi Sea and Canada Basin. Because of no data in the northern Bering Sea, the small phytoplankton contribution to the primary production in this study could not be compared. Regionally, the primary production contribution of small phytoplankton in the northern Bering Sea (average  $\pm$  SD = 25.0  $\pm$  12.8%) is considerably lower than those in others (Table 4). At this point, we do not know whether this is a latitudinal pattern (i.e., increasing contribution of small phytoplankton in higher latitude) or simply seasonal difference among the different regions in the Pacific Arctic Ocean. Indeed, [12] found a seasonal patterns of different phytoplankton size compositions with increasing contribution of small phytoplankton in the northern Bering Sea. Since the seasonal contribution of small phytoplankton to the primary production would be different, further seasonal observations on the small phytoplankton contribution to the primary production will be warranted for better understanding their ecological roles in the Bering and Chukchi Seas.

Table 4. Small phytoplankton contributions to the total primary production in the Arctic Ocean.

Study Area	Year	Season	Smallcontribution	Methods	Size	References
Northern Chukchi Sea and Canada Basin	2008	August-September	19.8–60.3%	In situ	<5 µm	[41]
Bering Strait and Chukchi Sea	2004	August-September	$31.72 \pm 23.59\%$	In situ	<5 µm	[22]
Kara, Laptev and East Siberian Sea	2013	August-September	52.7-71.2%	In situ	<5 µm	[43]
Barents Sea	2003–2005	Early to late bloom period	31-87%	In situ	<10 µm	[44]
North water polynya	1998	April–July	19%	In situ	<5 µm	[45]
Chukchi Sea and Bering Strait	2016	August	$38.0\pm19.9\%$	In situ	<2 µm	This study
Northern Bering Sea and Bering Strait	2017	July	$25.0\pm12.8\%$	In situ	<2 µm	

Biochemical compositions (POC:chlorophyll-a, PON:chlorophyll-a and C:N ratios) were compared between small and large phytoplankton in Figure 11. Large phytoplankton group has relatively lower POC:chlorophyll-*a* ratios (*t*-test, p < 0.01) which were 78.0–3549.0 (mean  $\pm$  SD = 1358.6  $\pm$  1170.8) for the ARA07B and 41.4–340.2 (mean  $\pm$  SD = 173.8  $\pm$  110.4) for the OS040 (Figure 9a). In comparison, POC:chlorophyll-a ratios of small phytoplankton were 408.5–6547.4 (mean  $\pm$  SD = 2590.2  $\pm$  1523.0) for ARA07B and 274.9–2303.6 (mean  $\pm$  SD = 623.4  $\pm$  639.2) for the OS040. The PON:chlorophyll-*a* ratio of large phytoplankton was 1.9–184.2 (mean  $\pm$  SD = 62.4  $\pm$  48.7) whereas the ratio of small phytoplankton ranged from 50.0 to 328.7 (mean  $\pm$  SD = 211.9  $\pm$  88.3) for the ARA07B (no data for OS040). The C:N ratios were 7.5–251.9 (mean  $\pm$  SD = 34.1  $\pm$  58.9) for large phytoplankton and 7.0–19.9 (mean  $\pm$  SD = 11.9  $\pm$  3.8) for small phytoplankton during the ARA07B cruise. Small phytoplankton showed a comparatively higher POC:chlorophyll-a ratio than large phytoplankton during both cruises (Figure 11). This result is consistent with the previous result in the Chukchi Sea, which suggests that higher carbon contents per unit of chlorophyll-a concentration in small phytoplankton in comparison to large phytoplankton [21]. In the Antarctic Ocean, [41] observed the consistent results in non-polynya and polynya regions in the Amundsen Sea. A similar pattern was observed for the PON:chlorophyll-a ratio in this study. However, the C:N ratios of small phytoplankton were lower than those of large phytoplankton in this study. Similarly, the overall C:N assimilation ratio of small

phytoplankton was previously reported as significantly lower than that of large phytoplankton [21]. These results are consistent with the result in the Gulf of St. Lawrence, Canada [44]. In the Antarctic Ocean, the similar result was obtained in the Amundsen Sea [41]. The C:N ratios were negatively correlated with chlorophyll-*a* concentrations for small and large phytoplankton in this study ( $R^2 > 0.6$ ). However, there was no statistically significant difference in the relationship between small and large phytoplankton (p > 0.05; Figure 11).

## 4. Summary and Conclusions

For determining the dominant phytoplankton communities and the relative contribution of small phytoplankton (<2 μm) to the total primary production, two arctic research cruises were conducted in the Chukchi Sea onboard the icebreaker R/N Araon in 2016 (ARA07B) and mainly in the northern Bering Sea onboard T/S Oshoro-Maru in 2017 (OS040) for this study. The dominant phytoplankton communities were diatoms and phaeocystis during the ARA07B, whereas diatoms and Prasinophyte (Type 2) during the OS040. Based on the AHC analysis, the primary productions of total and small phytoplankton communities were different depending on the sea area. Overall, high primary productions and low contributions of small phytoplankton during both study periods were distributed in the Bering Strait region which was affected by nutrient-enriched BSW. Different biochemical compositions between small and large phytoplankton were observed in this study. The small phytoplankton group had a higher POC:chlorophyll-a (t-test, p < 0.01) and PON:chlorophyll-a ratio than large phytoplankton in this study, which suggests that small phytoplankton have higher carbon and nitrogen contents per unit of chlorophyll-a concentration [21]. In addition, small phytoplankton had lower C:N ratios than large phytoplankton in this study. Together with these results, we could conclude that small phytoplankton incorporate more nitrogen in relation to carbon into their bodies and thus produce nitrogen-rich organic matters [43] which could be relatively faster regenerated than carbon-rich organic matters such as carbohydrates [46]. Therefore, the study for small phytoplankton which could be an important basic food source in the Arctic ecosystem should be further conducted under the current warming ocean scenario.

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