

HOKKAIDO UNIVERSITY

Title	Spatial changes in the summer diatom community of the northern Bering Sea in 2017 and 2018
Author(s)	Fukai, Yuri; Abe, Yoshiyuki; Matsuno, Kohei; Yamaguchi, Atsushi
Citation	Deep Sea Research Part II Topical Studies in Oceanography, 181-182, 104903 https://doi.org/10.1016/j.dsr2.2020.104903
Issue Date	2020-12
Doc URL	http://hdl.handle.net/2115/87787
Rights	© 2020. This manuscript version is made available under the CC-BY-NC-ND 4.0 license
Rights(URL)	http://creativecommons.org/licenses/by-nc-nd/4.0/
Туре	article (author version)
File Information	Fukai et al. Manuscript.pdf



2	Bering Sea in 2017 and 2018
3	
4	Yuri Fukai <sup>a,*,†</sup> , Yoshiyuki Abe <sup>b,c</sup> , Kohei Matsuno <sup>a,d</sup> , Atsushi Yamaguchi <sup>a,d</sup>
5	
6	<sup>a</sup> Faculty/Graduate School of Fisheries Sciences, Hokkaido University, $3-1-1$ Minato-cho, Hakodate,
7	Hokkaido 041-8611, Japan
8	<sup>b</sup> Atmosphere and Ocean Research Institute, The University of Tokyo, 5-1-5, Kashiwanoha, Kashiwa-shi,
9	Chiba, 277-8564, Japan
10	<sup>c</sup> Research Development Section, Office for Enhancing Institutional Capacity, Hokkaido University, Kita 21,
11	Nishi 10, Kita-ku, Sapporo, Hokkaido, 001-0021, Japan
12	<sup>d</sup> Arctic Research Center, Hokkaido University, Kita-21 Nishi-11 Kita-ku, Sapporo, Hokkaido, 001-0021,
13	Japan
14	<sup>†</sup> Present address: Division of Earth System Science, Graduate School of Environmental Science, Hokkaido
15	University, Kita-10 Nishi-5 Kita-ku, Sapporo, Hokkaido, 060-0810, Japan
16	
17	* Corresponding author, Tel: 81-11-706-2246, Fax: 81-11-706-2247
18	E-mail address: fukai@ees.hokudai.ac.jp (Y. Fukai)
19	
20	
21	ABSTRACT
22	
23	In recent years, the northern Bering Sea has experienced changes in the timing of sea-ice
24	retreat and in hydrographic conditions during the summer. The influence of these
25	environmental changes on the diatom community has not been examined. In this study,

Spatial changes in the summer diatom community of the northern

26 we investigated the spatial changes in the diatom community of the northern Bering Sea 27 during the summers of 2017 and 2018, and evaluated the effects of environmental 28 variability on these communities. We found that the diatom cell density and diversity 29 varied with water masses. A cluster analysis based on cell density revealed that the diatom 30 communities were separated into four groups, and that the distributions of three of these 31 groups were different spatially between 2017 and 2018. In the Bering Strait and the 32 Chirikov Basin regions, the diatom communities differed between 2017 and 2018. In 33 2017, these diatom communities were dominated by cold-water species such as 34 Chaetoceros gelidus and Chaetoceros spp. (subgenus Hyalochaetae), while in 2018, the 35 community was dominated by cosmopolitan species such as Thalassionema nitzschioides and *Chaetoceros* spp. (subgenus *Phaeoceros*). NMDS and multiple regression analysis 36 37 indicated that the timing of the sea-ice retreat was the most important contributor to the 38 differences in the diatom community. In contrast, there was no year-to-year difference 39 south of St. Lawrence Island, possibly because nutrients were depleted and phytoplankton 40 types other than diatoms were dominant.

41

*Keywords:* Northern Bering Sea, Phytoplankton community, Diatoms, Year-to-yearchanges

## 45 **1. Introduction**

46 The northern Bering Sea is one of the most productive ocean regions in the world 47 (Springer and McRoy, 1993). Supported by the high primary production, the area is 48 important for higher trophic level species such as sea birds and marine mammals 49 (Springer et al., 1996). This region is now facing drastic changes in sea-ice cover and 50 hydrographic conditions during summer (Grebmeier et al., 2015; Frey et al., 2018). For 51 example, reduced sea-ice cover in 2018 resulted in a diminished deep cold pool (< 2 °C) 52 south of St. Lawrence Island, and groundfish from the southeastern Bering Sea shifted 53 northward., while the abundance of arctic species decreased in the region (Cornwall, 54 2019; Duffy-Anderson et al., 2019). Given that sea-ice reduction is known to have 55 affected some components of the northern Bering Sea, investigation of other components is required to understand the effects of future changes (Huntington et al., 2020). 56

57 The northern Bering Sea is a shallow shelf region. This region has a complicated 58 hydrographic environment due to the inflow of multiple currents with different 59 hydrographic features. The mixing of these waters results in complex hydrographic 60 environments that affect the distribution of phytoplankton communities (Giesbrecht et al., 61 2019). In the northern Bering Sea, phytoplankton supports a high level of primary 62 production in the upper mixed layer; most of this production settles to the seafloor due to 63 low zooplankton grazing pressure (Grebmeier et al., 1988).

Diatoms play an important role as primary producers in high latitude marine 65 ecosystems. A large diatom bloom occurs in the northern Bering Sea from the late spring 66 to early summer, when the sea ice is melting and the light limit is diminishing; the 67 chlorophyll *a* concentration can exceed 8  $\mu$ g L<sup>-1</sup> during these blooms (Springer and 68 McRoy, 1993). During the spring Arctic bloom, *Chaetoceros gelidus* sometimes dominates (von Quillfeldt, 2000; Sergeeva et al., 2010). The composition of diatom
communities varies among the different hydrographic environments (Taniguchi et al.,
1976; Sergeeva et al., 2010). Diatoms constitute an important taxon in this marine
ecosystem and require evaluation to understand how they respond to environmental
change.

74 From 1978 to 2012, the timing of the sea-ice retreat (TSR) south of St. Lawrence 75 Island, in the Chirikov Basin and in the Chukchi Sea has become earlier (Grebmeier et 76 al., 2015; Frey et al., 2018). In the northern Bering Sea, the magnitude and timing of the 77 phytoplankton bloom varies with the timing of the spring sea - retreat (Fujiwara et al., 2016). In 2018, the TSR was approximately two weeks earlier than it was during the 78 79 previous year; the magnitude of the ice algal bloom was small and zooplankton abundance 80 decreased (Cornwall, 2019; Fukai et al., 2019). However, despite the importance of 81 diatoms for primary production, there is no information on how the diatom community 82 responds to changes in sea-ice dynamics in the northern Bering Sea.

The purpose of our paper is to examine the phytoplankton communities, particularly with a focus on the diatom communities of the northern Bering Sea from 62°N to the Bering Strait. To this end, we describe the species composition of diatoms, and test three hypotheses: 1) that the cell density and species composition of the diatom community differ by water mass, 2) that the diatom community differed between 2017 and 2018, and 3) that the hydrography, including sea-ice condition before sampling, will affect the diatom community.

90

91

92 **2. Materials and methods** 

Sampling was conducted along the northern Bering Sea shelf from July 9–21,
2017 and July 2–12, 2018 during the 40th and 56th cruises, respectively, of the *T/S Oshoro-Maru* of Hokkaido University (Fig. 1). The study areas were the waters south of
St. Lawrence Island, the Chirikov Basin (from the north of St. Lawrence Island to the
south of Bering Strait), and the Bering Strait.

101

102 2.2. Sea Ice

103

104 Data on sea ice concentration (SIC) were obtained from the Advanced 105 Microwave Scanning Radiometer 2 (AMSR2) to evaluate the extent of the sea ice. These 106 AMSR2 data were supplied by the Japan Aerospace Exploration Agency via the Arctic 107 Data archive System (ADS) (https://ads.nipr.ac.jp/), through the cooperation of the 108 National Institute of Polar Research and JAXA. We used the SIC data after calculating a 109 5-day moving average. Sea-ice covered regions were defined as having a SIC > 20%. In 110 addition, the TSR was defined as the last date when the SIC was at 20% prior to the 111 observed annual sea ice minimum across the study region.

112

113 *2.3. Physical Oceanography* 

114

115 Conductivity-temperature-depth (CTD) casts were conducted at 40 stations in 116 2017 and 28 stations in 2018 to obtain vertical profiles of the temperature, salinity, and 117 chlorophyll *a* fluorescence (see Appendix Fig. 1). We used a CTD (SBE911, Sea-Bird 118 Electronics, Inc.) calibrated prior to the cruise. The mixed-layer depth was defined as the depth where density was 0.10 kg m<sup>3</sup> greater than the value at 5 m depth (Danielson et al.,
2011).

121

122 2.4. Nutrients

123

124 At 26 of the CTD stations (14 stations in 2017 and 12 stations in 2018), water 125 samples for nutrient analysis were collected from 4-6 layers every 10 m from the surface 126 to 5 m above the seafloor using a bucket and Niskin bottles (Fig. 1). The obtained 127 unfiltered nutrient samples (n = 128) in Spitz tubes were frozen on board at -80 °C. In the 128 shore-based laboratory, the major nutrients (NO<sub>2</sub>-N + NO<sub>3</sub>-N, NH<sub>4</sub>-N, PO<sub>4</sub>-P, and Si 129 (OH)<sub>4</sub>) were measured by colorimetric methods using a QuAAtro 2-HR system certified 130 with standard reference materials for nutrient analysis (KANSO, standard Lot BT, BZ, 131 Osaka, Japan) in accordance with "The GO-SHIP Repeat Hydrography Manual" (Hydes 132 et al., 2010).

133

134 2.5. Phytoplankton

135

136 Water samples for phytoplankton counts were collected from the same stations 137 and layers as the nutrient samples. A total of 141 phytoplankton samples was collected 138 and preserved as follows: in 2017, 500 mL water samples were concentrated 50-fold using 139 a nucleopore filter (3.0 µm) before being preserved with glutaraldehyde at a final 140 concentration of 1%. Note that the diatoms and dinoflagellates addressed in this study 141 experience little damage from filtering (Dahl and Naustvoll, 2010). In 2018, 1 L of each 142 water sample was preserved on board with glutaraldehyde at a final concentration of 1%. 143 The samples were then settled and concentrated 24- to 33- fold using siphon tubes in the 144 land laboratory.

145 Aliquots (1 mL) of the concentrated samples were transferred to a glass slide to 146 count and identify the diatoms and dinoflagellates with an inverted microscope at 200-147  $600 \times$  magnification. The diatoms and dinoflagellates were counted and identified from 148 approximately 300 cells. When the cell number count was less than 300 cells, the 149 minimum numbers were 18 cells in 2017 and 21 cells in 2018. In addition, the detection limits were 20 cells L<sup>-1</sup> in 2017 and 30 cells L<sup>-1</sup> in 2018, suggesting that there was not 150 151 much difference (ability to detect low numbers of cells in a sample) between the years. 152 As explained in Hasle and Syvertsen (1997) and Hoppenrath et al. (2009), the diatoms 153 were identified to the species or genus level and the dinoflagellates were identified to the 154 genus level. Distinguishing Cylindrotheca closterium from Nitzschia longissima was 155 difficult (Hasle and Syvertsen, 1997), so these species were treated as Cy. closterium. In 156 addition, C. convolutus, C. concavicornis and C. borealis were nearly indistinguishable 157 because they were damaged by current transportation, as mentioned by Taniguchi et al. 158 (1976), collectively counted and identified С. so they were as 159 convolutus/concavicornis/borealis.

160

Using the counting data, the diversity of diatoms was evaluated by Shannon-161 Wiener index (H').

162

$$H' = -\sum \frac{n}{Ni} \times \ln \frac{n}{Ni}$$

where *n* is the cell density (cells  $mL^{-1}$ ) of *i*th species and *Ni* is the total diatom cell density 163 (cells mL<sup>-1</sup>) at each station (Shannon and Weaver, 1949). 164

165

166 2.6. Statistical analyses

167

Differences in phytoplankton cell density among the water masses in the upper 168

169 mixed-layer was tested by Mann-Whitney U-test. For comparison of the diatom 170 community among the water masses, we performed cluster analyses, nonmetric 171 multidimensional scaling (NMDS) ordinations, and multiple regression analyses for each 172 year or with each water mass, but the results could not be interpreted (cf. Appendix Figs. 173 2, 3). Also, to compare the diatom diversity (H') among the water masses, a one-way 174 analysis of variance (ANOVA) was used. If the ANOVA identified statistically significant 175 differences (p < 0.05), a post hoc Tukey-Kramer test was used to clarify the interactions 176 among the water masses.

Differences between the years of the  $NO_2-N + NO_3-N$  concentration, which was likely to be a limiting factor among nutrients, were compared by a Mann-Whitney U-test for each region. Similarly, differences of the phytoplankton cell density between 2017 and 2018 in the Bering Strait, and of diatom diversity (*H'*) between 2017 and 2018 were tested using a Mann-Whitney U-test.

182 To compare the diatom community between 2017 and 2018, we first performed 183 a cluster analysis based on the cell density within each water mass (Appendix Fig. 2). 184 Several patterns of the cluster analysis were tested in each year, by water mass, and by 185 depth (cf. Appendix Figs. 2, 3). The results of these tests were uninterpretable, so we used 186 analyses based on all diatom samples from a given year. Thus, this analysis focused on 187 describing year-to-year changes in the diatom community (species composition) between 188 2017 and 2018. To reduce the bias for abundant species, the cell density data (X: cells mL<sup>-1</sup>) for each species were transformed to  $\sqrt[4]{X}$  prior to cluster analysis (Quinn and 189 190 Keough, 2002). The similarities between samples were examined using the Bray-Curtis 191 index based on the differences in the species composition. To group the samples, the 192 similarity indices were coupled using hierarchical agglomerative clustering with a 193 complete linkage method (an unweighted pair group method using the arithmetic mean)

194 (Field et al., 1982).

195 To delineate the sample groups on a two-dimensional map, NMDS ordination 196 was conducted. Thereafter, multiple regression analyses (Y = aX1 + bX2 + c, where Y is197 the environmental variable and X1 and X2 are axes 1 and 2 of NMDS, respectively) were 198 performed to clarify which environmental variables (temperature, salinity, chlorophyll a 199 fluorescence, concentrations of NO<sub>2</sub>-N + NO<sub>3</sub>-N, NH<sub>4</sub>-N, dissolved inorganic nitrogen 200 (DIN), PO<sub>4</sub>-P, and Si (OH)<sub>4</sub>, the ratio of the DIN concentration to that of PO<sub>4</sub>-P (N:P ratio), 201 the timing of the sea-ice retreat (TSR), observation date, and sampling depth) had 202 significant relationships with the phytoplankton groups.

Furthermore, to test intergroup differences in the diatom cell density and hydrographic environments (temperature, salinity, chlorophyll *a* fluorescence, concentrations of  $NO_2$ -N + NO\_3-N, NH<sub>4</sub>-N, DIN, PO<sub>4</sub>-P, and Si (OH)<sub>4</sub>, the N:P ratio, and the TSR), a one-way ANOVA and a post hoc Tukey-Kramer test were used. All the analyses were conducted with PRIMER 7 (PRIMER-E Ltd.) or Stat View v5 (SAS Institute Inc.).

209

210

```
211 3. Results
```

212

```
213 3.1. Sea Ice
```

214

In 2017, the study region south of St. Lawrence Is. was first completely icecovered on January 19, and in 2018, sea-ice cover was not complete until February 5. The sea ice first covered the Bering Strait and the Chirikov Basin, except for the most eastern station, on January 11, 2017 and December 28, 2018. In some stations in 2018 (St. 11 and St. 14), the SIC was repeatedly over and below 20%. In the most eastern stations in the
Chirikov Basin (St. 5 in 2017 and St. 19 in 2018), the SIC exceeded 20% on December
8, 2016 and 2017.

South of St Lawrence Island, in 2017, sea ice was completely gone by May 3, whereas in 2018, ice left over a month earlier, on March 24. In 2017, the first day in the study area when the Chirikov Basin had an ice concentration < 20% was on April 5, whereas, in 2018, open water was first detected on March 25, 11 days earlier.

226

227 *3.2. Hydrography and nutrient chemistry* 

228

We identified four water masses that differed in physical characteristics; Bering Chukchi Summer Water (BCSW) (moderate/cold with high salinity), Bering Chukchi Winter Water (BCWW) (cold with high salinity), Alaskan coastal water (ACW) (warm with low salinity), and Melting Water (MW) (cold with low salinity) (Danielson et al., 2017) (Figs. 2, 3). The water masses (> 12 °C in ACW and > 7 °C in BCSW) that were unidentified by Danielson et al. (2017) were defined as ACW or BCSW based on their salinity (Fig. 3).

In 2017, the BCWW (< 0 °C) was present at the bottom south of St. Lawrence Island (Fig. 4). The BCSW was present throughout the water column in the Bering Strait and the northern Chirikov Basin. By contrast, in the eastern coastal area and south of 65 °N in the Chirikov Basin, the ACW was present in the surface layer and the BCSW was observed in the lower layer (Fig. 4).

In 2018, the BCWW (< 0 °C) was not present at the bottom in the region South of St. Lawrence Island (Fig. 4). The BCSW was present throughout the water column in the Bering Strait and the Chirikov Basin, except for the eastern coastal area where the ACW was observed in the surface layer (Fig. 4).

The distribution of water masses differed between the years. In 2017, ACW was present in the surface layer of the southwestern Chirikov Basin and there was BCSW at the bottom south of St. Lawrence Island; these were not present in 2018.

In both years south of St. Lawrence Island, fluorescence above the pycnocline (avg = 0.07 and 0.16 in 2017 and 2018, respectively) was lower than that below the pycnocline (avg = 0.39 and 0.60 in 2017 and 2018, respectively) (Fig. 5). In Bering Strait, fluorescence was similar in both years (2017, avg = 0.90: 2018, avg = 0.78) (Fig. 5). In the Chirikov Basin, fluorescence above the pycnocline was higher in 2017 (avg = 0.69) than in 2018 (avg = 0.26), while, below the pycnocline fluorescence was similar in both years (Fig. 5).

255 To the south of St. Lawrence Island, the NO<sub>2</sub>-N + NO<sub>3</sub>-N was depleted in the 256 upper mixed layer in both years, but it was high below the pycnocline (Fig. 5) with no 257 significant differences between the years (*U*-test, p > 0.05). In the Bering Strait, NO<sub>2</sub>-N 258 + NO<sub>3</sub>-N did not differ significantly between years (*U*-test, p > 0.05) (Fig. 5). In this 259 region, the lowest concentration of nitrate plus nitrite was at the eastern station (st. 5) in 260 2017, whereas in 2018, the highest concentrations were found in the northern Bering Strait (st. 29). In the Chirikov Basin, these nutrients were not significantly different 261 262 between the years (*U*-test, p > 0.05); in both years, the lowest concentrations were 263 detected at the eastern stations (st. 11 in 2017 and st. 19 in 2018).

Concentrations of other nutrients were generally similar between years at the same station. In both years in each region, NH<sub>4</sub>-N concentrations were similar (Fig. 5). Likewise, the PO<sub>4</sub>-P concentrations did not vary between years within regions; the highest value detected was in the Bering Strait in 2017 (st.1, 6.62  $\mu$ M) (Fig. 5). We found high concentrations of Si (OH)<sub>4</sub> over major portions of the study region in both years, except for some stations in 2018 in the eastern Chirikov Basin (st. 11 in 2018) and the south of St. Lawrence Island (sts. 4, 6, 8 in 2018), where this nutrient was not detectable (Fig. 5). In both years, the N:P ratio was below 16 throughout most of the study area.

272

273 *3.3. Phytoplankton community* 

274

275 *3.3.1. Cell density* 

276 In the upper mixed layer, the cell density of diatoms and dinoflagellates was 277 significantly different in each water mass, and it was higher in BCSW than in ACW 278 (Mann-Whitney U-test, p < 0.05), whereas, cell densities below the pycnocline did not 279 differ among water masses (one-way ANOVA, p > 0.05). In both 2017 and 2018, the highest cell densities were observed in the Bering Strait (2017:  $1.6 \times 10^6$  cells L<sup>-1</sup> and in 280 2018:  $3.4 \times 10^5$  cells L<sup>-1</sup>) with diatoms and dinoflagellates in this region more abundant 281 282 in 2017 (stations 1–3) than in 2018 (stations 27–30) (Mann-Whitney U-test, p < 0.05) (Fig. 283 6).

284

## 285 *3.3.2. Phytoplankton species and their diversity*

A total of 29 genera and 30 species of diatoms (centric diatoms: 19 genera and 287 25 species and pennate diatoms: 10 genera and 5 species) and 6 genera and 5 species of 288 dinoflagellate were observed over the two years (Table 1).

The diversity of the diatoms (*H'*) ranged from 0–3.56 in 2017 and 0.36–2.98 in 2018. The *H'* varied among water masses, with values significantly higher in BCWW and BCSW than in ACW (*one-way ANOVA*, p < 0.05). There were no significant differences in the diversity of diatoms between the years (*Mann-Whitney U-test*, p > 0.05).

295 Phytoplankton communities were classified into four groups (A–D) by a cluster analysis at 27% and 37% similarity levels (Fig. 7a). Group A was low-density  $(1.3 \times 10^3 -$ 296  $1.3 \times 10^5$  cells L<sup>-1</sup>, avg =  $4.6 \times 10^4$  cells L<sup>-1</sup>) and was composed primarily of C. gelidus 297 (Fig. 7b). Group B had the highest cell density  $(1.6 \times 10^3 - 1.6 \times 10^6 \text{ cells L}^{-1}, \text{ avg} = 2.5 \times 10^6 \text{ cells L}^{-1}$ 298 10<sup>5</sup> cells L<sup>-1</sup>), and Hyalochaetae such as C. gelidus, C. furcellatus, and C. debilis were 299 300 dominant (64%) (Fig. 7b). The cell density of C. gelidus, C. diadema, and Chaetoceros spp. in group B was significantly higher than it was in groups C and D. The cell density 301 of group C was nearly as low as it was in group A  $(3.3 \times 10^3 - 1.2 \times 10^5 \text{ cells } \text{L}^{-1}, \text{ avg} =$ 302  $3.4 \times 10^4$  cells L<sup>-1</sup>); however, the community composition was very different. *Phaeoceros* 303 304 such as C. convolutus/concavicornis/borealis had a relatively high density in group C 305 (13%), and the pennate diatoms such as Thalassionema nitzschioides and Cylindrotheca 306 *closterium* had a significantly higher density in group C than it did in the other groups (Table 2). Group D had the lowest cell density  $(3.6 \times 10^2 - 4.4 \times 10^5 \text{ cells L}^{-1}, \text{ mean } 2.5 \times 10^{-1} \text{ mean }$ 307 10<sup>4</sup> cells L<sup>-1</sup>) and *Leptocylindrus* spp. dominated (85%). 308

309 The phytoplankton communities were different in each region (Fig. 7c). In both 310 years south of St. Lawrence Island, group D was present in the upper layer (0 m or 0-20 311 m) and groups A, B, and C occurred in the deeper layers. From 65°N (the Chirikov Basin) 312 to the Bering Strait, the distribution varied across years; group B was observed throughout 313 the area in 2017, but group C was observed in 2018. In these regions (the Chirikov Basin 314 and the Bering Strait), the spatial distribution of water masses and phytoplankton community groups as determined by the cluster analysis did not match (Fig.4, Fig.7c), 315 316 thus, the groups were different between years even though BCSW was occupied in both 317 years.

On the NMDS ordination, phytoplankton plots had significant relationships with various environmental variables (p < 0.05), including chlorophyll *a* fluorescence ( $r^2 =$ 0.30), TSR ( $r^2 = 0.28$ ), observation date ( $r^2 = 0.16$ ), sampling depth ( $r^2 = 0.13$ ), salinity ( $r^2 = 0.11$ ), Si (OH)<sub>4</sub> ( $r^2 = 0.08$ ) and NO<sub>2</sub>+NO<sub>3</sub> ( $r^2 = 0.05$ ) (Fig. 7d), but the other parameters did not. Especially note that temperature did not have a significant relationship with phytoplankton plots (p > 0.05), and that the contribution of TSR to diatom groups was the highest among environmental factors except for chlorophyll *a* fluorescence.

327 In addition, the one-way ANOVA and Tukey-Kramer test indicated that the PO<sub>4</sub> 328 and DIN concentrations and the N:P ratio did not differ significantly among phytoplankton groups (one-way ANOVA, p > 0.05). However, the other hydrographic 329 330 variables differed between groups B and D. Group D had a higher temperature and lower 331 salinity, nutrients (NO<sub>2</sub>+NO<sub>3</sub>, PO<sub>4</sub>-P, NH<sub>4</sub>-N, Si (OH)<sub>4</sub>), and chlorophyll *a* fluorescence than the other groups. Groups B and C differed only in their salinity, chlorophyll a 332 333 fluorescence and TSR (Table 3). Especially note that temperature was not significantly 334 different between Group B and C.

335

336

```
337 4. Discussion
```

- 338
- 339 *4.1. The influence of water masses*

340

341 Diatom community structure (i.e. species composition and their cell density) was 342 not consistently correlated with water mass during summer except for the stations south 343 of St. Lawrence Island. However, there were significant differences among the water 344 masses in the cell density in the upper mixed layer and in diatom diversity. These 345 differences may have been related to differences in the nutrient content of the water 346 masses. Differences in characteristics of water masses are known to influence 347 phytoplankton cell density (Coachman et al., 1975; Danielson et al., 2017; Giesbrecht et 348 al., 2019). The N:P ratio was below 16 throughout the study area, which indicated that 349 the DIN was the limiting nutrient concentration, and differences in DIN concentrations in 350 the various water masses was one of the most important factors for the growth of 351 phytoplankton upper the mixed layer over the study area. Thus, phytoplankton cell 352 density was higher in the upper mixed layer in the BCSW, including the nutrient-rich AW, 353 than in the nutrient-poor ACW (Coachman et al., 1975; Danielson et al., 2017).

The diversity of diatoms indicated by *H*' was higher in BCWW and BCSW than in ACW in the same way as the DIN concentration was. We suggest that the differences in the diversity of diatoms between water masses was related to difference in nutrient concentrations between water masses, especially the DIN concentrations. As mentioned above, DIN was the limiting factor in the nutrient concentration and thus, in the water masses with high DIN such as BCWW and BCSW, competition for DIN may have been minimal, thus resulting in many diatom species surviving in these waters.

361

### 362 4.2. The phytoplankton community of the south of St. Lawrence Island

363

In contrast to the Chirikov Basin and the Bering Strait regions, south of St Lawrence Island year-to-year changes in the phytoplankton community were not observed. In the upper mixed layer south of St. Lawrence Island, nutrient-poor ACW was present in both years, and the DIN concentrations and, at some stations the Si (OH)<sub>4</sub> concentrations, were too low to support diatom growth (Justic et al., 1995). The lack of 369 DIN may have resulted in the dominance of phytoplankton group D, which was 370 predominately non-diatom species that can thrive in low nutrient conditions (Parsons et 371 al., 1978). The timing and magnitude of the spring phytoplankton bloom in the region 372 south of St. Lawrence Island differed in 2017 and 2018, and we hypothesize that this was 373 due to differences in the TSR (Fukai et al., 2019; Hirawake, per. comm.). Thus, after the 374 nutrients were depleted from the upper mixed layer, phytoplankton, other than diatoms, 375 dominated. A similar succession may occur in the eastern Bering Sea where 376 coccolithophore blooms during the summer were reported after the diatom bloom 377 (Stockwell et al., 2001; Iida et al., 2002). Coccolithophore blooms were also observed by 378 satellite observation from the eastern Bering Sea to south of St. Lawrence Island after 379 2000s (Harada et al., 2012). In our study, it is not clear whether the phytoplankton 380 community changed at the species level, because dinoflagellates and phytoplankton other 381 than diatoms were not identified to the species level.

382

383 4.3. The changes in the summer diatom community in the Chirikov Basin and the Bering
384 Strait, 2017-2018

385

From 65°N (the Chirikov Basin) to the Bering Strait, between 2017 and 2018, phytoplankton cell density declined and community structure changed. In this region in 2017, the highest cell density  $(1.6 \times 10^6 \text{ cells L}^{-1})$  was nearly the same as that reported by Sergeeva et al. (2010) for July 2003 and by Giesbrecht et al. (2019) (the highest density was approximately 10<sup>6</sup> cells L<sup>-1</sup>). In 2018, the highest cell density ( $3.4 \times 10^5$  cells L<sup>-1</sup>) was only 34% of the values observed in 2017.

With respect to the phytoplankton community, in 2017, group B was widely distributed and had a high cell density that was dominated (64%) by *Hyalochaetae* such 394 as C. gelidus and C. furcellatus. C. gelidus and C. furcellatus are cold-water species and 395 are common in the Arctic (Hasle and Syvertsen, 1997; Hoppenrath, 2009). These species 396 are typically found in the Chukchi Sea adjacent to the study area (von Quillfeldt et al., 397 2003). In 2018, Group C, which was mostly composed of Thalassionema nitzschioides, 398 was widely distributed. The abundance of Chaetoceros spp. was low (20%), and 399 Phaeoceros such as C. convolutus/concavicornis/borealis made up most of the 400 Chaetoceros spp. T. nitzschioides and C. convolutus are known as cosmopolitan species; 401 the former does not occur in the high Arctic and the latter is common in temperate waters 402 (Hasle and Syvertsen, 1997; Hoppenrath, 2009). T. nitzschioides has also been reported 403 in temperate water after the melting of the sea ice (Neeley et al., 2018), and it is a 404 characteristic species of the Pacific-Arctic region in the autumn (Matsuno et al., 2014). 405 These results suggest that between 2017 and 2018, the summer diatom community in the 406 Bering Strait and the Chirikov Basin changed from cold water to cosmopolitan species.

407 Interestingly, the NMDS, the multiple regressions, and the one-way ANOVA did 408 not suggest any significant differences in temperature between 2017 and 2018 in the 409 region north of 65°N. By contrast, the TSR was the most important contributing factor 410 among the environmental factors for explaining the differences in the diatom 411 communities between the two years. There was also a significant difference in the TSR 412 between group B in 2017 and C in 2018. Because the TSR differed between 2017 and 413 2018 in the northern Bering Sea (Cornwall, 2019; Fukai et al., 2019; Grebmeier et al., 414 2019), the effect of the TSR on the summer diatom community cannot be ignored.

The TSR affects the magnitude and timing of the spring bloom in the seasonal sea ice area (Hunt et al., 2002; Fujiwara et al., 2016). The magnitude of the phytoplankton bloom in the open water is usually large when the TSR is early (Hunt et al., 2002; Fujiwara et al., 2016). In 2018, when the TSR was early, large increases in sea surface chlorophyll 419 a in the Chirikov Basin were observed with satellite remote sensing from early to late 420 May after the sea ice had completely retreated (Hirawake, per. comm.). Hence, in 2018, 421 when the TSR was early, the available nutrients may have been consumed by the large 422 open-water bloom during early spring after the sea ice retreat, resulting in the wide 423 distribution of phytoplankton community group C during summer, with a low cell density. 424 In summer 2018, the cosmopolitan species composition of group C, some of which, such 425 as T. nitzschioides, are species characteristic of the autumn (Matsuno et al., 2014), and 426 might been the result of the early TSR in 2018 and an early depletion of nutrients.

427

428

#### 429 **5.** Conclusions

430

431 This study described and compared northern Bering Sea diatom communities in 432 the summers of 2017 and 2018. The diatom cell density and diatom diversity differed by 433 water mass. Year-to-year differences in the diatom community between 2017 and 2018 434 were found, depending on the region examined. South of St. Lawrence Island, we found 435 no changes in the diatom community between 2017 and 2018. Nitrate and nitrite were 436 depleted in the upper mixed layer in both years, and phytoplankton types other than 437 diatoms dominated this region. Since we focused our study on diatoms, it is possible that 438 there were interannual changes in other elements of the phytoplankton community that 439 we did not detect.

In the Chirikov Basin and Bering Strait, diatom communities in 2017 and 2018 differed, even though the same water masses were present in both years. The TSR was much earlier in 2018 than in 2017, though summer water temperatures were similar in the two years. Since nutrient concentrations were lower in 2018, we hypothesize that the open water bloom in 2018 may have depleted the nutrients, with the result that in 2018 several sub-arctic or cosmopolitan species were abundant compared to 2017, when arctic species predominated. It will be important to evaluate the influence of the changing diatom community on the marine ecosystem of the northern Bering and Chukchi Seas. To this end, focus on the entire phytoplankton community, including dinoflagellates, coccolithophores and others, will be required.

450

451

#### 452 Acknowledgments

453

454 We thank the captain, officers, crew, and researchers on board the T/S Oshoro-455 Maru, of Hokkaido University, for their contributions during field sampling. We thank 456 Toru Hirawake, chief scientist of the cruises. We also thank two anonymous reviewers for 457 their helpful comments. This study was conducted by the Arctic Challenge for 458 Sustainability (ArCS) project and Arctic Challenge for Sustainability II (ArCS II) project. 459 The ADS dataset is archived and was provided by the Arctic Data archive System (ADS), 460 which was developed by the National Institute of Polar Research. Part of this study was 461 supported through Grants-in-Aid for Scientific Research 17H01483 (A), 19H03037 (B), 462 20H03054 (B), 18K14506 (Early-Career Scientists) and 20K20573 (Challenging 463 Research (Pioneering)) from the Japan Society for the Promotion of Science.

464

467	Coachman, L.K., Aagaard, K., Tripp, R.B., 1975. Bering Strait: The regional physical
468	oceanography. University of Washington Press, Seattle, WA.

- 469 Cornwall, W., 2019. Vanishing Bering Sea ice poses climate puzzle for second winter in
  470 a row, ice cover shrinks to lowest levels seen in at least 4 decades. Science
  471 364, 616–617.
- Dahl, E., Naustvoll, L.J., 2010. Filtering semitransparent filters for quantitative
  phytoplankton analysis. In: Karlson, B., Cusack, C., Bresnan, E. (Eds.).
  Microscopic and molecular methods for quantitative phytoplankton analysis.
  UNESCO, Paris, 37–39.
- Danielson, S., Eisner, L., Weingartner, T., Aagaard, K., 2011. Thermal and haline
  variability over the central Bering Sea shelf: Seasonal and interannual
  perspectives. Cont. Shelf Res., 31, 539–554.
- Danielson, S.L., Eisner, L., Ladd, C., Mordy, C., Sousa, L., Weingartner, T.J., 2017. A
  comparison between late summer 2012 and 2013 water mass, macronutrients,
  and phytoplankton standing crops in the northern Bering and Chukchi. DeepSea Res. II, 135, 7–26.
- Duffy-Anderson, J.T., Stabeno, P., Andrews III, A.G, Cieciel, K., Deary, A., Farley, E.,
  Fugate, C., Harpold, C., Heintz, R., Kimmel, D., Kuletz, K., Lamb, J., Paquin,
  M., Porter, S., Rogers, L., Spear, A., Yasumiishi, E., 2019. Responses of the
  Northern Bering Sea and southeastern Bering Sea pelagic ecosystems
  following record-breaking low winter sea ice. Geophys. Res. Let. 46, 9833–
  9842.
- 489 Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analyzing

multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8, 37–52.

- Frey, K.E., Comiso, J.C., Cooper, L.W., Grebmeier, J.M., Stock, L.V., 2018. Arctic ocean
  primary productivity: the response of marine algae to climate warming and
  sea ice decline. In: Arctic Report Card. Arctic Region 2018,
  (http://www.arctic.noaa.gov/ reportcard).
- Fujiwara, A., Hirawake, T., Suzuki, K., Eisner, L., Imai, I., Nishino, S., Kikuchi, T., Saitoh,
  S.-I., 2016. Influence of timing of sea ice retreat on phytoplankton size
  during marginal ice zone bloom period on the Chukchi and Bering shelves.
  Biogeosciences 13, 115–131.
- Fukai, Y., Matsuno, K., Fujiwara, A., Yamaguchi, A., 2019. The community composition
  of diatom resting stages in sediments of the northern Bering Sea in 2017
  and 2018: the relationship to the interannual changes in the extent of the sea
  ice. Polar Biol. 42, 1915–1922.
- Giesbrecht, K.E., D.E. Varela, J. Wiktor, J.M. Grebmeier, B. Kelly, J.E. Long, 2019. A
  decade of summertime measurements of phytoplankton biomass,
  productivity and assemblage composition in the Pacific Arctic Region from
  2006 to 2016. Deep-Sea Res. II 162, 93–113.
- Grebmeier, J.M., McRoy, C.P., Feder, H.M., 1988. Pelagic-benthic coupling on the shelf
  of the northern Bering and Chukchi Seas. I. Food supply source and benthic
  biomass. Mar. Ecol. Prog. Ser. 48, 57–67.
- 510 Grebmeier, J.M., Bluhm, B.A., Cooper, L.W., Danielson, S.L., Arrigo, K.R., Blanchard,
- 511 A.L., Clarke, J.T., Day, R.H., Frey, K.E., Gradiner, R.R., Kędra, M., Konar,
- 512 B., Kuletz, K.J., Lee, S.H., Lovvorn, J.R., Norcross, B.L., Okkonen, S.R.,
- 513 2015. Ecosystem characteristics and processes facilitating persistent 514 macrobenthic biomass hotspots and associated benthivory in the Pacific

- 515 Arctic. Prog. Oceanogr. 136, 92–114.
- Grebmeier, J.M., Moore, S.E., Cooper, L.W., Frey, K.E., 2019. The Distributed Biological
  Observatory: A change detection array in the Pacific Arctic An introduction.
  Deep-Sea Res. II 162, 1–7.
- 519 Harada, N., Sato, M., Oguri, K., Hagino, K., Okazaki, Y., Katsuki, K., Tsuji, Y., Shin, K.-
- H., Tadai, O., Saitoh, S.-I., Narita, H., Konno, S., Jordan, R.W., Shiraiwa, Y.,
  Grebmeier, J., 2012. Enhancement of coccolithophorid blooms in the Bering
  Sea by recent environmental changes. Global Biogeochem. Cycles 26,
  GB2036.
- Hasle, G.R., Syvertsen, E.E., 1997. Marine diatoms. In: Tomas, C.R. (Ed). Identifying
  marine phytoplankton. Academic Press, San Diego, 5–385
- Hoppenrath, M., Elbrächter, M., Drebes, G., 2009. Marine phytoplankton: selected
  microphytoplankton species from the North Sea around Helgoland and Sylt.,
  Schweizerbart Science Publishers.
- Hunt, G.L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R.D., Napp, J.M., Bond, N.A.,
  2002. Climate change and control of the southeastern Bering Sea pelagic
  ecosystem. Deep-Sea Res. II 49, 5821–5853.
- Huntington, H.P., Danielson, S.L., Wiese, F.K., Baker, M.R., Boveng, P., Citta, J.J., De
  Robertis, A., Dickson, D.M.S., Farley, E.V., George, J.C., Iken, K., Kimmel,
  D.G., Kuletz, K., Ladd, C., Levine, R., Quakenbush, L., Stabeno, P., Stafford,
  K.M., Stockwell, D., Wilson C., 2020. Evidence suggests potential
  transformation of the Pacific Arctic ecosystem is underway. Nat. Clim.
  Change 10, 342–349.
- Hydes, D.J., Aoyama, M., Aminot, A., Bakker, K., Becker, S., Coverly, S., Daniel, A.,
  Dickson, A.G., Grosso, O., Kerouel, R., van Ooijen, J., Sato, K., Tanhua, T.,

540	Woodward, E.M.S., Zhang, J.Z., 2010. Determination of dissolved nutrients
541	(N, P, Si) in seawater with high precision and inter-comparability using gas-
542	segmented continuous flow analysers. In: Hood, E.M., Sabine, C.L., Sloyan,
543	B.M. (Eds.). The GO-SHIP Repeat Hydrography Manual: A Collection of
544	Expert Reports and Guidelines. IOCCP report number 14, ICPO publication
545	series number 134, U.N. Educ. Sci. and Cult. Organ. Intergov. Oceanotr.
546	Comm., Paris, 1–88.
547	Iida, T., Saitoh, S.I., Miyamura, T., Toratani, M., Fukushima, H., Shiga, N., 2002.
548	Temporal and spatial variability of coccolithophore blooms in the eastern
549	Bering Sea, 1998-2001. Prog. Oceanogr. 55, 165-175.
550	Justic, D., Rabalais, N.N., Turner R.E., Dortch, Q., 1995. Changes in nutrient structure of
551	river-dominated coastal waters: Stoichiometric nutrient balance and its
552	consequences. Estuar. Coast. Shelf Sci. 40, 339–356.
553	Matsuno, K., Ichinomiya, M., Yamaguchi, A., Imai, I., Kikuchi, T., 2014. Horizontal
554	distribution of microprotist community structure in the western Arctic Ocean
555	during late summer and early fall of 2010. Polar Biol. 37, 1185–1195.
556	Neeley, A.R., Harris, L.A., Frey, K.E., 2018. Unraveling phytoplankton community
557	dynamics in the northern Chukchi Sea under sea-ice-covered and sea-ice-
558	free conditions. Geophys Res. Let. 45, 7663–7671.
559	Parsons, T.R., Harrison, P.J., Waters, R., 1978. An experimental simulation of changes in
560	diatom and flagellate blooms. J. Exp. Biol. Ecol. 32, 285-294.
561	Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists.
562	Cambridge University Press, New York.
563	Sergeeva, V.M., Sukhanova, I.N., Flint, M.V., Pautova, L.A., Grebmeier, J.M., Cooper,
564	L.W., 2010. Phytoplankton community in the western Arctic in July–August 23

565	2003. Oceanology 50, 184–197.
566	Shannon, C.E., Weaver, W., 1949. The mathematical theory of communication. The
567	University of Illinois Press, Urbana.
568	Springer, A.M., McRoy, C.P., 1993. The paradox of pelagic food webs in the northern
569	Bering Sea III. Patterns of primary production. Cont. Shelf. Res. 13, 575-
570	599.
571	Springer, A.M., McRoy, C.P., Flint, M.V., 1996. The Bering Sea Green Belt: shelf-edge
572	processes and ecosystem production. Fish. Oceanogr. 5(3/4), 205–223.
573	Stockwell, D.A., Whitledge, T.E., Zeeman, S.I., Coyle, K.O., Napp, J.M., Brodeur, R.D.,
574	Pinckuk, A.I., Hunt, G.L. 2001. Anomalous conditions in the south-eastern
575	Bering Sea, 1997: nutrients, phytoplankton and zooplankton. Fish. Oceanogr.
576	10, 99–116.
577	Taniguchi, A., Saito, K., Koyama, A., Fukuchi, M., 1976. Phytoplankton communities in
578	the Bering Sea and adjacent seas I. Communities in early warming season in
579	southern areas. J. Oceanogr. Soc. Jpn. 32, 99–106.
580	von Quillfeldt, C.H., 2000. Common diatom species in Arctic spring blooms: Their
581	distribution and abundance. Bot. Mar. 43, 499–516.
582	von Quillfeldt, C.H., Ambrose Jr., W.G., Clough, L.M., 2003. High number of diatom
583	species in first-year ice from the Chukchi Sea. Polar Biol. 26, 806–818.

## 585 Figure legends

- Fig. 1. Location of stations in the northern Bering Sea from July 9–21, 2017 and
  July 2–12, 2018. The numbers indicate the station ID. The open and solid
  circles indicate stations with hydrographic observations only taken by CTD
  and those with water sampling and hydrographic observations, respectively.
  Fig. 2. Cross-sectional distributions of the temperature, salinity, and fluorescence in
- the northern Bering Sea in 2017 (upper) and 2018 (lower).
- Fig. 3. T-S diagrams of all the stations in 2017 (upper) and 2018 (lower). Note that
  the symbols of the stations vary with the geographical location.
- Fig. 4. Spatial distribution of water masses as defined by Danielson et al. (2017).
  BCSW: Bering-Chukchi Summer Water, ACW: Alaskan Coastal Water, MW:
  Melting Water, and BCWW: Bering-Chukchi Winter Water.
- 597 **Fig. 5.** Cross-sectional distributions of nutrient (NO<sub>2</sub>-N + NO<sub>3</sub>-N, NH<sub>4</sub>-N, PO<sub>4</sub>-P, 598 and Si (OH)<sub>4</sub>) concentrations in the northern Bering Sea in 2017 (upper) and 599 2018 (lower).
- Fig. 6. Horizontal distribution of the average phytoplankton cell density in 2017
  (left) and 2018 (right). The circles indicate the mean cell density in the water
  column.
- Fig. 7. (a) Results of the cluster analysis based on the phytoplankton cell density
  found by Bray-Curtis similarity. (b) Species composition and cell density of
  each group. (c) Spatial distribution of the phytoplankton community in the
  northern Bering Sea during the summers of 2017 (left) and 2018 (right). (d)
  Nonmetric multidimensional scaling plots of the four groups, with *arrows*and *percentages* indicating the directions of the environmental parameters

609and the coefficient of determination  $(r^2)$ , respectively. Obs. date: observation610date, Si: silicate, Sal: salinity, N: nitrate and nitrite, TSR: the timing of sea ice611retreat, Fluor: fluorescence, and Dep: sampling depth.

612

613 **Appendix Fig 1.** Relationship between the chlorophyll *a* concentration and the 614 fluorescence.

Appendix Fig 2. Spatial distribution of the phytoplankton communities in each water mass (the BCSW (a) and the ACW (b)) by cluster analyses. The cluster analyses were conducted in each water mass independently. White boxes indicated water masses that were not the focus of this analysis. Color codes for the communities were shown different groups analyzed by the cluster analysis.

Appendix Fig 3. Spatial distribution of the phytoplankton communities in each year.
 Cluster analyses were conducted in each year independently. Color codes for
 the communities were shown different groups analyzed by the cluster
 analysis.

# Table 1. List of phytoplankton species identified in the water samples that were collected

627 from	the northern	Bering	Sea and	Bering	Strait in	July	2017	and 2018.
----------	--------------	--------	---------	--------	-----------	------	------	-----------

Class Bacillariophyceae		
Order Centrales		
Actinocyclus spp.	C. furcellatus	Ditylum spp.
Actinoptychus spp.	C. gelidus	Eucampia spp.
Attheya spp.	C. laciniosus	Lauderia annulata
Bacterosira bathyomphala	C. lorenzianus	Leptocylindrus danicus
Chaetoceros conturtus	C. mitra	L. minimus
C. convolutus/concavicornis/borealis	C. subtilis	Odontella aurita
C. curvicetus	C. teres	Paralia sulcata
C. danicus	Chaetoceros spp.	Rhizosolenia spp.
C. debilis	Corethron hystrix	Skeletonema spp.
C. decipiens	Coscinodiscus spp.	Stephanopyxis turris
C. diadema	Detonula pumuila	Thalassiosira spp.
C. didymus	Dactyliosolen fragilissimus	Other centric diatoms
Order Pennales		
Asteroplanus karianus	Pauelia taeniata	Navicula spp.
Asterionellopsis glacialis	Pleurosigma spp.	Nitzschia spp.
Cylindrotheca closterium	Pseudo-nitzschia spp.	Other pennate diatoms
Thalassionema nitzschioides	Fragilariopsis spp.	
Class Dinophyceae		
Alexandrium spp.	Protoperidinium spp.	Dinophysis norvegica
Ceratium spp.	Heterocapsa triquetra	Dinophysis rudgei
Prorocentrum triestinum	Dinophysis acuta	Other dinofalagellates

Table 2. Comparison of phytoplankton species in the phytoplankton community groups (A–D). The values are given as the mean cell density (×  $10^3$  cells L<sup>-1</sup>) and standard deviation in each group. The numbers in parentheses indicate the number of stations. The differences among the phytoplankton communities were evaluated by a one-way ANOVA and a Tukey-Kramer test. Any groups not connected by the underlines are significantly different (\*: p < 0.05, \*\*: p < 0.01, and \*\*\*: p < 0.005).

636

Species	Group name					Tukey-Kramer			
species	A (5)	B (74)	C (41)	D (21)	ANOVA	test			
C. convolutus/concavicornis/borealis	$4.49~\pm6.47$	$3.56~\pm7.79$	$4.37~\pm9.50$	$0.26~\pm~1.01$	NS				
C. debilis	—	$16.45\pm42.68$	$0.20~\pm~~1.05$	_	*	Not detected			
C. diadema	$0.65~\pm~~1.29$	$3.35~\pm~4.73$	$0.06~\pm~~0.20$	$0.01 \pm  0.02$	***	D C A B			
C. furcellatus	—	$49.95\pm118.66$	—	-	**	Not detected			
C. gelidus	$31.28\pm44.80$	$65.46 \pm 114.33$	$0.02~\pm~~0.06$	$0.12 \pm  0.33$	***	C D A B			
Chaetoceros spp.	$2.22~\pm~~2.81$	$13.94 \pm 20.48$	$0.84~\pm~~2.91$	$0.50 \pm  1.36$	***	D C A B			
Leptocylindrus danicus	—	$15.43\pm30.69$	$3.08 \pm 10.43$	$21.01\pm89.63$	NS				
Cylindrotheca closterium	$0.05~\pm~0.05$	$1.09~\pm~1.03$	$1.79~\pm~1.60$	$0.15~\pm~0.27$	***	A D B C			
Thalassionema nitzschioides	$0.21 \pm  0.28$	$0.68~\pm~~1.05$	$7.51\pm15.35$	$0.47 \pm 0.95$	***	A D B C			
Pseudo-nitzschia spp.	_	$5.23 \pm 12.90$	$1.45~\pm~4.94$	$0.08~\pm~~0.34$	NS				
Fragilariopsis spp.	$0.02 \pm  0.04$	$2.92 \pm 10.65$	$0.41~\pm~~1.09$	$0.05 \pm  0.21$	NS				

Table 3. Hydrographic environmental factors among the phytoplankton communities (A– D). The values are given as the average and standard deviation of each factor. The numbers in parentheses indicate the number of stations. The differences among the phytoplankton communities were evaluated by a one-way ANOVA and a Tukey-Kramer test. Any groups not connected by the underlines are significantly different (\*: p < 0.05, \*\*: p < 0.01, and \*\*\*: p < 0.005).

Factors		(	Group name		One-way	Tul	key-	Kraı	ner
Factors	A (5)	B (74)	C (41)	D (21)	ANOVA		te	st	
Temperature	$1.97 \pm  3.29$	$3.56~\pm~1.66$	$2.89~\pm~~2.49$	$6.21 \pm 2.78$	**	Α	С	В	D
Fluorescence	$0.54 \pm  0.56$	$0.75~\pm~0.53$	$0.44~\pm~~0.17$	$0.20\pm0.13$	***	D	С	A	В
Salinity	$32.00 \pm 0.32$	$32.49 \pm 0.41$	$32.10 \pm 0.87$	$31.58\pm0.36$	***	D	А	С	В
NO <sub>2</sub> +NO <sub>3</sub>	$5.68~\pm~~6.55$	$9.34~\pm~~6.38$	$7.88~\pm~~6.29$	$0.96\pm1.01$	**	D	A	С	В
PO <sub>4</sub> -P	$1.18~\pm~0.65$	$1.35~\pm~0.83$	$1.42~\pm~0.39$	$0.80\pm0.32$	NS				
NH <sub>4</sub> -N	$1.11~\pm~1.43$	$0.78~\pm~0.48$	$0.84 \pm  0.61$	$0.18\pm0.13$	*	D	В	С	A
Si (OH) <sub>4</sub>	$29.48\pm40.68$	$25.01 \pm 13.25$	$19.10 \pm 12.29$	$8.60\pm7.69$	*	D	С	В	Α
DIN	$6.79~\pm7.95$	$10.41 \pm  6.76$	$10.59\pm13.33$	$1.13 \pm 1.11$	NS				
N/P	$4.30 \pm  3.34$	$7.24~\pm~~3.46$	$6.94~\pm~~9.78$	$1.28\pm1.02$	NS				
TSR	$91.00~\pm~~8.22$	$115.28 \pm 14.44$	$107.78 \pm 11.67$	99.38 ± 15.44	***	Α	D	С	В

645



Fig. 1. Location of stations in the northern Bering Sea from July 9–21, 2017 and July 2–12, 2018. The numbers indicate the station ID. The open and solid circles indicate stations with hydrographic observations only taken by CTD and those with water sampling and hydrographic observations, respectively.



Fig. 2. Cross-sectional distributions of the temperature, salinity, and fluorescence in the northern Bering Sea in 2017 (upper) and 2018 (lower).



Fig. 3. T-S diagrams of all the stations in 2017 (upper) and 2018 (lower). Note that the symbols of the stations vary with the geographical location.



Fig. 4. Spatial distribution of water masses as defined by Danielson et al. (2017). BCSW: Bering-Chukchi Summer Water, ACW: Alaskan Coastal Water, MW: Melting Water, and BCWW: Bering-Chukchi Winter Water.



Fig. 5. Cross-sectional distributions of nutrient (NO<sub>2</sub>-N + NO<sub>3</sub>-N, NH<sub>4</sub>-N, PO<sub>4</sub>-P, and Si (OH)<sub>4</sub>) concentrations in the northern Bering Sea in 2017 (upper) and 2018 (lower).



Fig. 6. Horizontal distribution of the average phytoplankton cell density in 2017 (left) and 2018 (right). The circles indicate the mean cell density in the water column.



Fig. 7. (a) Results of the cluster analysis based on the phytoplankton cell density found by Bray-Curtis similarity. (b) Species composition and cell density of each group. (c) Spatial distribution of the phytoplankton community in the northern Bering Sea during the summers of 2017 (left) and 2018 (right). (d) Nonmetric multidimensional scaling plots of the four groups, with *arrows* and *percentages* indicating the directions of the environmental parameters and the coefficient of determination ( $r^2$ ), respectively. *Obs. date*: observation date, *Si*: silicate, *Sal*: salinity, *N*: nitrate and nitrite, *TSR*: the timing of sea ice retreat, *Fluor*: fluorescence, and *Dep*: sampling depth.



Appendix Fig 1. Relationship between the chlorophyll *a* concentration and the fluorescence.



Appendix Fig 2. Spatial distribution of the phytoplankton communities in each water mass (the BCSW (a) and the ACW (b)) by cluster analyses. The cluster analyses were conducted in each water mass independently. White boxes indicated water masses that were not the focus of this analysis. Color codes for the communities were shown different groups analyzed by the cluster analysis.



Appendix Fig 3. Spatial distribution of the phytoplankton communities in each year. Cluster analyses were conducted in each year independently. Color codes for the communities were shown different groups analyzed by the cluster analysis.