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Spatial changes in the summer diatom community of the northern Bering Sea in 2017 and 2018



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ARTICLE INFO

Keywords: Northern Bering Sea Phytoplankton community Diatoms Year-to-year changes

ABSTRACT

In recent years, the northern Bering Sea has experienced changes in the timing of sea-ice retreat and in hydrographic conditions during the summer. The influence of these environmental changes on the diatom community has not been examined. In this study, we investigated the spatial changes in the diatom community of the northern Bering Sea during the summers of 2017 and 2018, and evaluated the effects of environmental variability on these communities. We found that the diatom cell density and diversity varied with water masses. A cluster analysis based on cell density revealed that the diatom communities were separated into four groups, and that the distributions of three of these groups were different spatially between 2017 and 2018. In the Bering Strait and the Chirikov Basin regions, the diatom communities differed between 2017 and 2018. In 2017, these diatom communities were dominated by cold-water species such as *Chaetoceros gelidus* and *Chaetoceros* spp. (subgenus *Hyalochaetae*), while in 2018, the community was dominated by cosmopolitan species such as *Thalassionema nitzschioides* and *Chaetoceros* spp. (subgenus *Phaeoceros*). NMDS and multiple regression analysis indicated that the timing of the sea-ice retreat was the most important contributor to the differences in the diatom community. In contrast, there was no year-to-year difference south of St. Lawrence Island, possibly because nutrients were depleted and phytoplankton types other than diatoms were dominant.

1. Introduction

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

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

Diatoms play an important role as primary producers in high latitude marine ecosystems. A large diatom bloom occurs in the northern Bering Sea from the late spring to early summer, when the sea ice is melting and the light limit is diminishing; the chlorophyll *a* concentration can exceed 8 μ g L⁻¹ during these blooms (Springer and McRoy, 1993). During the

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https://doi.org/10.1016/j.dsr2.2020.104903

Received 24 December 2019; Received in revised form 9 October 2020; Accepted 12 November 2020 Available online 27 November 2020 0967-0645/© 2020 Elsevier Ltd. All rights reserved.

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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.

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

2. Materials and methods

2.1. Study area

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.

2.2. Sea ice

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

2.3. Physical Oceanography

Conductivity-temperature-depth (CTD) casts were conducted at 40 stations in 2017 and 28 stations in 2018 to obtain vertical profiles of the temperature, salinity, and chlorophyll *a* fluorescence (see Appendix Fig. 1). We used a CTD (SBE911, Sea-Bird Electronics, Inc.) calibrated prior to the cruise. The mixed-layer depth was defined as the depth where density was 0.10 kg m³ greater than the value at 5 m depth (Danielson et al., 2011).

2.4. Nutrients

At 26 of the CTD stations (14 stations in 2017 and 12 stations in 2018), water samples for nutrient analysis were collected from 4–6 layers every 10 m from the surface to 5 m above the seafloor using a bucket and Niskin bottles (Fig. 1). The obtained unfiltered nutrient samples (n = 128) in Spitz tubes were frozen on board at -80 °C. In the shore-based laboratory, the major nutrients (NO₂–N + NO₃–N, NH₄–N, PO₄–P, and Si (OH)₄) were measured by colorimetric methods using a QuAAtro 2-HR system certified with standard reference materials for nutrient analysis (KANSO, standard Lot BT, BZ, Osaka, Japan) in accordance with "The GO-SHIP Repeat Hydrography Manual" (Hydes et al., 2010).

2.5. Phytoplankton

Water samples for phytoplankton counts were collected from the



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.

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

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

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

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

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

2.6. Statistical analyses

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

Differences between the years of the NO₂–N + NO₃–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.

To compare the diatom community between 2017 and 2018, we first performed a cluster analysis based on the cell density within each water mass (Appendix Fig. 2). Several patterns of the cluster analysis were tested in each year, by water mass, and by depth (cf. Appendix Figs. 2 and 3). The results of these tests were uninterpretable, so we used analyses based on all diatom samples from a given year. Thus, this analysis focused on describing year-to-year changes in the diatom community (species composition) between 2017 and 2018. To reduce the bias for abundant species, the cell density data (X: cells mL⁻¹) for each species were transformed to $\sqrt[4]{X}$ prior to cluster analysis (Ouinn and Keough. 2002). The similarities between samples were examined using the Bray-Curtis index based on the differences in the species composition. To group the samples, the similarity indices were coupled using hierarchical agglomerative clustering with a complete linkage method (an unweighted pair group method using the arithmetic mean) (Field et al., 1982).

To delineate the sample groups on a two-dimensional map, NMDS

201 20 66 40 60 20 64° N 30 00 40 60 62° N 20 Fluor 40 Depth (m) 165° W 175[°] W 170° W 60 65.6 66.0 169.5 172 171 172 171 168.5 169 167 0 2018 20 66° M 40 60 20 64° N 40 60 62° N 20 40 170° W 175° W 165° W 60 65.8 66.4 170 169 168170 168 173 171 172 Long. (°W) Lat. (°N)

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.

ordination was conducted. Thereafter, multiple regression analyses (Y = aX1+ bX2+c, where Y is the environmental variable and X1 and X2 are axes 1 and 2 of NMDS, respectively) were performed to clarify which environmental variables (temperature, salinity, chlorophyll *a* fluorescence, concentrations of NO₂–N + NO₃–N, NH₄–N, dissolved inorganic nitrogen (DIN), PO₄–P, and Si (OH)₄, the ratio of the DIN concentration to that of PO₄–P (N:P ratio), the timing of the sea-ice retreat (TSR), observation date, and sampling depth) had 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 NO₂–N + NO₃–N, NH₄–N, DIN, PO₄–P, and Si (OH)₄, 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.).

3. Results

3.1. Sea ice

In 2017, the study region south of St. Lawrence Is. was first completely ice-covered 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.

3.2. Hydrography and nutrient chemistry

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 and 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,



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.

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).

To the south of St. Lawrence Island, the NO₂–N + NO₃–N was depleted in the upper mixed layer in both years, but it was high below the pycnocline (Fig. 5) with no significant differences between the years (*U test*, p > 0.05). In the Bering Strait, NO₂–N + NO₃–N did not differ significantly between years (*U test*, p > 0.05) (Fig. 5). In this region, the lowest concentration of nitrate plus nitrite was at the eastern station (st. 5) in 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 between the years (*U test*, p > 0.05); in both years, the lowest concentrations were 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, NH₄–N concentrations were similar (Fig. 5). Likewise, the PO₄–P concentrations did not vary between years within regions; the highest value detected was in the Bering Strait in 2017 (st.1, 6.62 μ M) (Fig. 5). We found high concentrations of Si (OH)₄ 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.

3.3. Phytoplankton community

3.3.1. Cell density

In the upper mixed layer, the cell density of diatoms and dinoflagellates was significantly different in each water mass, and it was higher in BCSW than in ACW (*Mann-Whitney U test*, p < 0.05), whereas, cell densities below the pycnocline did not 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: 1.6×10^6 cells L⁻¹ and in 2018: 3.4×10^5 cells L⁻¹) with diatoms and dinoflagellates in this region more abundant in 2017 (stations 1–3) than in 2018 (stations 27–30) (*Mann-Whitney U test*, p < 0.05) (Fig. 6).

3.3.2. Phytoplankton species and their diversity

A total of 29 genera and 30 species of diatoms (centric diatoms: 19 genera and 25 species and pennate diatoms: 10 genera and 5 species) and 6 genera and 5 species of 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).

3.3.3. Phytoplankton community by cluster analysis

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 $(1.3 \times 10^3 - 1.3 \times 10^5 \text{ cells } \text{L}^{-1}, \text{ avg} = 4.6 \times 10^4 \text{ cells}$ L^{-1}) and was composed primarily of *C. gelidus* (Fig. 7b). Group B had the highest cell density $(1.6 \times 10^3 - 1.6 \times 10^6 \text{ cells L}^{-1}, \text{ avg} = 2.5 \times 10^5 \text{ cells}$ L^{-1}), and Hyalochaetae such as C. gelidus, C. furcellatus, and C. debilis were 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 of group C was nearly as low as it was in group A $(3.3 \times 10^3 - 1.2 \times 10^5 \text{ cells } \text{L}^{-1}, \text{ avg} = 3.4 \times 10^4 \text{ cells } \text{L}^{-1});$ however, the community composition was very different. Phaeoceros such as C. convolutus/concavicornis/borealis had a relatively high density in group C (13%), and the pennate diatoms such as Thalassionema nitzschioides and Cylindrotheca 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 10²–4.4 \times 10⁵ cells L^{-1} , mean 2.5 \times 10⁴ cells L^{-1}) and *Leptocylindrus* spp. dominated (85%).

The phytoplankton communities were different in each region (Fig. 7c). In both years south of St. Lawrence Island, group D was present in the upper layer (0 m or 0-20 m) and groups A, B, and C occurred in the



Fig. 5. Cross-sectional distributions of nutrient ($NO_2-N + NO_3-N$, NH_4-N , PO_4-P , and Si (OH)₄) concentrations in the northern Bering Sea in 2017 (upper) and 2018 (lower).

deeper layers. From 65°N (the Chirikov Basin) to the Bering Strait, the distribution varied across years; group B was observed throughout the area in 2017, but group C was observed in 2018. In these regions (the Chirikov Basin and the Bering Strait), the spatial distribution of water masses and phytoplankton community groups as determined by the cluster analysis did not match (Figs. 4 and 7c), thus, the groups were different between years even though BCSW was occupied in both years.

3.3.4. Relationships between phytoplankton communities and environmental factors

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)₄ ($r^2 = 0.08$) and NO₂+NO₃ ($r^2 = 0.05$) (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.

In addition, the one-way ANOVA and Tukey-Kramer test indicated that the PO₄ 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 variables differed between groups B and D. Group D had a higher temperature and lower salinity, nutrients (NO₂+NO₃,PO₄-P,NH₄-N,Si (OH)₄), and chlorophyll *a* fluorescence than the other groups. Groups B and C differed only in their salinity, chlorophyll *a* fluorescence and TSR (Table 3). Especially note that temperature was not significantly different between Group B and C.

4. Discussion

4.1. The influence of water masses

Diatom community structure (i.e. species composition and their cell density) was not consistently correlated with water mass during summer except for the stations south of St. Lawrence Island. However, there were significant differences among the water masses in the cell density in the upper mixed layer and in diatom diversity. These differences may have



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

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/	C. subtilis	Odontella aurita		
borealis				
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	Other centric		
	fragilissimus	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 norvegice		
Ceratium spp.	Heterocapsa triquetra	Dinophysis rudgei		
Prorocentrum triestinum	Dinophysis acuta	Other		
		dinofalagellates		

Differences in characteristics of water masses are known to influence phytoplankton cell density (Coachman et al., 1975; Danielson et al., 2017; Giesbrecht et al., 2019). The N:P ratio was below 16 throughout the study area, which indicated that the DIN was the limiting nutrient concentration, and differences in DIN concentrations in the various water masses was one of the most important factors for the growth of phytoplankton upper the mixed layer over the study area. Thus, phytoplankton cell density was higher in the upper mixed layer in the BCSW, including the nutrient-rich AW, 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.

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

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)₄ concentrations, were too low to support diatom growth (Justic et al., 1995). The lack of DIN may have resulted in the dominance of phytoplankton group D, which was predominately non-diatom species that can thrive in low nutrient conditions (Parsons et al., 1978). The timing and magnitude of the spring phytoplankton bloom in the region south of St. Lawrence Island differed in 2017 and 2018, and we hypothesize that this was due to differences in the TSR (Fukai et al., 2019; Hirawake, per. comm.). Thus, after the nutrients were depleted from the upper mixed layer, phytoplankton, other than diatoms, dominated. A similar succession may occur in the eastern Bering Sea where coccolithophore blooms during the summer were reported after the diatom bloom (Stockwell et al., 2001; Iida et al., 2002). Coccolithophore blooms were also observed by satellite observation from the eastern Bering Sea to south of St. Lawrence Island after 2000s (Harada et al., 2012). In our study, it is not clear whether the phytoplankton community changed at the species level, because dinoflagellates and phytoplankton other than diatoms were not identified to the species level.

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

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} 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 10^6 cells L⁻¹). In 2018, the highest cell density (3.4 \times 10^5 cells L⁻¹) was only 34% of the values observed in 2017.

With respect to the phytoplankton community, in 2017, group B was



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.

Table 2

Comparison of phytoplankton species in the phytoplankton community groups (A–D). The values are given as the mean cell density (\times 10³ cells L⁻¹) 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).

Species	Group name				one-way	Tukey-Kramer test			
-1	A (5)	B (74)	C (41)	D (21)	ANOVA				
C. convolutus/concavicornis/borealis	4.49 ± 6.47	3.56 ± 7.79	4.37 ± 9.50	0.26 ± 1.01	NS				
C. debilis	-	16.45 ± 42.68	0.20 ± 1.05	-	*	Not detected			
C. diadema	0.65 ± 1.29	3.35 ± 4.73	0.06 ± 0.20	0.01 ± 0.02	***	D	С	A	В
C. furcellatus	_	49.95 ± 118.66	-	-	**	** Not det		ected	
C. gelidus	31.28 ± 44.80	65.46 ± 114.33	0.02 ± 0.06	0.12 ± 0.33	***	С	D	A	В
Chaetoceros spp.	2.22 ± 2.81	13.94 ± 20.48	0.84 ± 2.91	0.50 ± 1.36	***	D	С	A	В
Leptocylindrus danicus	_	15.43 ± 30.69	3.08 ± 10.43	21.01 ± 89.63	NS				
Cylindrotheca closterium	0.05 ± 0.05	1.09 ± 1.03	1.79 ± 1.60	0.15 ± 0.27	***	Α	D	В	С
Thalassionema nitzschioides	0.21 ± 0.28	0.68 ± 1.05	7.51 ± 15.35	0.47 ± 0.95	***	Α	D	В	С
Pseudo-nitzschia spp.	-	5.23 ± 12.90	1.45 ± 4.94	0.08 ± 0.34	NS				
Fragilariopsis spp.	0.02 ± 0.04	2.92 ± 10.65	0.41 ± 1.09	0.05 ± 0.21	NS				

widely distributed and had a high cell density that was dominated (64%) by *Hyalochaetae* such as *C. gelidus* and *C. furcellatus*. *C. gelidus* and *C. furcellatus* are cold-water species and are common in the Arctic (Hasle and Syvertsen, 1997; Hoppenrath, 2009). These species are typically found in the Chukchi Sea adjacent to the study area (von Quillfeldt et al., 2003). In 2018, Group C, which was mostly composed of *Thalassionema*

nitzschioides, was widely distributed. The abundance of *Chaetoceros* spp. was low (20%), and *Phaeoceros* such as *C. convolutus/concavicornis/borealis* made up most of the *Chaetoceros* spp. *T. nitzschioides* and *C. convolutus* are known as cosmopolitan species; the former does not occur in the high Arctic and the latter is common in temperate waters (Hasle and Syvertsen, 1997; Hoppenrath, 2009).

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	Talaas Vaansen teet			
	A (5)	B (74)	C (41)	D (21)	ANOVA	i ukey-kramer test			
Temperature	1.97 ± 3.29	3.56 ± 1.66	2.89 ± 2.49	6.21 ± 2.78	**	Α	С	В	D
Fluorescence	0.54 ± 0.56	0.75 ± 0.53	0.44 ± 0.17	0.20 ± 0.13	***	D	С	Α	В
Salinity	32.00 ± 0.32	32.49 ± 0.41	32.1 ± 0.87	31.58 ± 0.36	***	D	А	С	В
NO ₂ +NO ₃	5.68 ± 6.55	9.34 ± 6.38	7.88 ± 6.29	0.96 ± 1.01	**	D	Α	С	В
PO ₄ -P	1.18 ± 0.65	1.35 ± 0.83	1.42 ± 0.39	0.80 ± 0.32	NS				
NH4-N	1.11 ± 1.43	0.78 ± 0.48	0.84 ± 0.61	0.18 ± 0.13	*	D	В	С	A
Si (OH)4	29.48 ± 40.68	25.01 ± 13.25	19.10 ± 12.29	8.60 ± 7.69	*	D	С	В	Α
DIN	6.79 ± 7.95	10.41 ± 6.76	10.59 ± 13.33	1.13 ± 1.11	NS				
N/P	4.30 ± 3.34	7.24 ± 3.46	6.94 ± 9.78	1.28 ± 1.02	NS				
TSR	91.00 ± 8.22	115.28 ± 14.44	107.78 ± 11.67	99.38 ± 15.44	***	А	D	С	В

T. nitzschioides has also been reported in temperate water after the melting of the sea ice (Neeley et al., 2018), and it is a characteristic species of the Pacific-Arctic region in the autumn (Matsuno et al., 2014). These results suggest that between 2017 and 2018, the summer diatom community in the Bering Strait and the Chirikov Basin changed from cold water to cosmopolitan species.

Interestingly, the NMDS, the multiple regressions, and the one-way ANOVA did not suggest any significant differences in temperature between 2017 and 2018 in the region north of 65°N. By contrast, the TSR was the most important contributing factor among the environmental factors for explaining the differences in the diatom communities between the two years. There was also a significant difference in the TSR between group B in 2017 and C in 2018. Because the TSR differed between 2017 and 2018 in the northern Bering Sea (Cornwall, 2019; Fukai et al., 2019; Grebmeier et al., 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 *a* in the Chirikov Basin were observed with satellite remote sensing from early to late May after the sea ice had completely retreated (Hirawake, per. comm.). Hence, in 2018, when the TSR was early, the available nutrients may have been consumed by the large open-water bloom during early spring after the sea ice retreat, resulting in the wide distribution of phytoplankton community group C during summer, with a low cell density. In summer 2018, the cosmopolitan species composition of group C, some of which, such as *T. nitzschioides*, are species characteristic of the autumn (Matsuno et al., 2014), and might been the result of the early TSR in 2018 and an early depletion of nutrients.

5. Conclusions

This study described and compared northern Bering Sea diatom communities in the summers of 2017 and 2018. The diatom cell density and diatom diversity differed by water mass. Year-to-year differences in the diatom community between 2017 and 2018 were found, depending on the region examined. South of St. Lawrence Island, we found no changes in the diatom community between 2017 and 2018. Nitrate and nitrite were depleted in the upper mixed layer in both years, and phytoplankton types other than diatoms dominated this region. Since we focused our study on diatoms, it is possible that there were interannual changes in other elements of the phytoplankton community that 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.

Author statement

Yuri Fukai: Formal analysis, Investigation, Writing - Original Draft, Visualization, Yoshiyuki Abe: Investigation, Kohei Matsuno: Conceptualization, Writing - Review & Editing, Supervision, Project administration, Atsushi Yamaguchi: Conceptualization, Investigation, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr2.2020.104903.

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