# Impact of sea-ice dynamics on the spatial distribution of diatom resting stages in sediments of the Pacific-Arctic Ocean

Yuri Fukai<sup>1,1</sup>, Kohei Matsuno<sup>1,1</sup>, Amane Fujiwara<sup>2,2</sup>, Koji Suzuki<sup>1,1</sup>, Mindy Richlen<sup>3,3</sup>, Evangeline Fachon<sup>3,3</sup>, and Don Anderson<sup>3,3</sup>

<sup>1</sup>Hokkaido University <sup>2</sup>Institute of Arctic Climate and Environment Research, Japan Agency for Marine Science and Technology, Japan <sup>3</sup>Woods Hole Oceanographic Institution

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#### Abstract

The Pacific-Arctic Ocean is characterized by seasonal sea-ice, the spatial extent and duration of which varies considerably. In this region, diatoms are the dominant phytoplankton group during spring and summer. To facilitate survival during periods that are less favorable for growth, many diatom species produce resting stages that settle to the seafloor and can serve as a potential inoculum for subsequent blooms. Since diatom assemblage composition is closely related to sea-ice dynamics, detailed studies of biophysical interactions are fundamental to understanding the lower trophic levels of ecosystems in the Pacific-Arctic Ocean. One way to explore this relationship is by comparing the distribution and abundance of diatom resting stages with patterns of sea-ice coverage. In this study, we quantified viable diatom resting stages in sediments in 2018 and explored their relationship to sea-ice extent during the previous winter. Diatom assemblages were clearly dependent on the variable timing of the sea-ice retreat and accompanying light conditions. In areas where sea-ice retreated earlier, open-water species such as *Chaetoceros* spp. and *Thalassiosira* spp. were abundant. In contrast, proportional abundances of *Attheya* spp. and pennate diatom species that are commonly observed in sea-ice were higher in areas where diatoms experienced higher light levels and longer day length in/under the sea-ice due to the late seasonal ice retreat. This study demonstrates that sea-ice dynamics are an important determinant of diatom species composition in the Pacific-Arctic.

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4 5	Yuri Fukai <sup>1,2</sup> , Kohei Matsuno <sup>2,3</sup> , Amane Fujiwara <sup>4</sup> , Koji Suzuki <sup>1,5</sup> , Mindy L. Richlen <sup>6</sup> , Evangeline Fachon <sup>6</sup> , Donald M. Anderson <sup>6</sup>
6	
7 8	<sup>1</sup> Graduate School of Environmental Science, Hokkaido University, North 10 West 5, Kita-ku, Sapporo, Hokkaido, 060-0810, Japan
9 10	<sup>2</sup> Faculty/Graduate School of Fisheries Sciences, Hokkaido University, 3–1–1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan
11 12	<sup>3</sup> Arctic Research Center, Hokkaido University, North 21 West 11 Kita-ku, Sapporo, Hokkaido, 001-0021, Japan
13 14	<sup>4</sup> Japan Agency for Marine-Earth Science and Technology, 2–15 Natsushima-cho, Yokosuka, Kanagawa, 237-0061, Japan
15 16	<sup>5</sup> Faculty of Environmental Earth Science, Hokkaido University, North 10 West 5, Kita-ku, Sapporo, Hokkaido, 060-0810, Japan
17 18	<sup>6</sup> Biology Department, Woods Hole Oceanographic Institution, 266 Woods Hole Rd., Woods Hole, MA, 02543, USA
19	
20	Corresponding author: Yuri Fukai (fukai@ees.hokudai.ac.jp)
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22	Key Points:
23 24	• Diatom resting stage assemblages were quantified and their relationship to the sea-ice dynamics in the Pacific Arctic region was explored.
25 26	• Diatom composition follows spatial patterns that depend upon the variable timing of sea- ice retreat and accompanying light conditions.
27 28 29	• Abundance of resting stage diatom cells in sediments varied by several orders of magnitude across the study region.

# 30 Abstract (229 words / up to 250 words)

31 The Pacific Arctic region is characterized by seasonal sea-ice, the spatial extent and duration of which varies considerably. In this region, diatoms are the dominant phytoplankton 32 group during spring and summer. To facilitate survival during periods that are less favorable for 33 growth, many diatom species produce resting stages that settle to the seafloor and can serve as a 34 potential inoculum for subsequent blooms. Since diatom assemblage composition is closely 35 related to sea-ice dynamics, detailed studies of biophysical interactions are fundamental to 36 37 understanding the lower trophic levels of ecosystems in the Pacific Arctic. One way to explore this relationship is by comparing the distribution and abundance of diatom resting stages with 38 patterns of sea-ice coverage. In this study, we quantified viable diatom resting stages in 39 sediments collected during summer and autumn 2018 and explored their relationship to sea-ice 40 extent during the previous winter and spring. Diatom assemblages were clearly dependent on the 41 variable timing of the sea-ice retreat and accompanying light conditions. In areas where sea-ice 42 retreated earlier, open-water species such as *Chaetoceros* spp. and *Thalassiosira* spp. were 43 abundant. In contrast, proportional abundances of Attheya spp. and pennate diatom species that 44 are commonly observed in sea-ice were higher in areas where diatoms experienced higher light 45 levels and longer day length in/under the sea-ice. This study demonstrates that sea-ice dynamics 46 are an important determinant of diatom species composition and distribution in the Pacific Arctic 47 region. 48

### 49

# 50 Plain Language Summary (197 words / up to 200 words)

51 The Pacific Arctic region is characterized by seasonal sea-ice, and there is considerable

52 interannual variation in the timing and quality of ice presence. In this region, diatoms are the

dominant phytoplankton group during spring and summer. Under conditions unfavorable for

54 growth, such as low light or limiting nutrients, many diatom species produce resting stages that

are similar to "seeds" of plants. These resting stages settle to the seafloor and can reflect the

diatom assemblages in the overlying water column. Since diatom species distribution is closely

57 related to sea-ice dynamics, detailed studies of this relationship are fundamental to understanding

the basis of marine ecosystems in the Pacific Arctic region. In this study, we explored the

relationship by comparing the distribution of diatom resting stage assemblages with patterns of

sea-ice coverage. Diatom assemblages detected in sediments were dependent on the variable

61 timing of the sea-ice retreat and accompanying light conditions. In areas where sea-ice retreated

earlier, open-water species were abundant, while proportional abundances of ice-associated
 diatoms were higher in areas where diatoms experience favorable light conditions in/under the

sea-ice. This study demonstrates that sea-ice dynamics are an important determinant of diatom

65 composition in the Pacific Arctic region.

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#### 67 **1 Introduction**

The Pacific Arctic region extends from the northern Bering Sea to the Chukchi and 68 69 Beaufort Seas. Within this region, the northern Bering and Chukchi Seas display among the highest daily rates of productivity in the world (Springer et al., 1996). Phytoplankton are 70 71 responsible for high primary productivity in the euphotic layer and delivery of particlulate organic carbon (POC) to the benthos. The sinking POC flux measured in 2018 in the northern 72 73 Bering and Chukchi Seas was the among highest ever documented across global oceans (O'Daly et al., 2020). This POC supports patchy distributions of high benthic biomass known as "benthic 74 75 hotspots" (Grebmeier et al., 1988, 2006). In contrast, primary productivity in the southwestern Beaufort Sea is low (Frost & Lowry, 1984). 76

In the Arctic Ocean, ice algae production occurs in and under the sea ice, and is followed by phytoplankton blooms during the summer retreat of sea-ice (Horner, 1984; Horner & Schrader, 1982). Mean daily water column integrated primary productivity in the southwestern Beaufort Sea is about half of that of the Chukchi Sea, even during peak periods in June and July (Hill et al., 2018). Overall, annual primary production is much higher in the Chukchi shelf than on the Beaufort shelf (Grebmeier et al., 2006).

The Pacific Arctic region is characterized by the presence of seasonal sea-ice, which 83 varies considerably in extent and duration from year to year. The extent of sea-ice has been 84 shown to influence regional phytoplankton assemblages (Neeley et al., 2018), but this 85 relationship is not fully understood. Sea-ice decline has been reported in the region (Frey et al., 86 2018; Grebmeier et al., 2015; Markus et al., 2009), and Arrigo et al. (2008) used satellite 87 observations to show that this decline was associated with increasing annual primary production. 88 89 However, changes in phytoplankton assemblages and particularly in ice-associated assemblages, 90 cannot be evaluated by satellite observations only, necessitating field-based studies to examine the structure of these communities in more detail. 91

Phytoplankton assemblages during spring and summer blooms in the Pacific Arctic
region are dominated by diatoms (von Quillfeldt, 2000; Sergeeva et al., 2010), which drive
sinking POC flux (Lalande et al., 2020). Some diatom genera, *Chaetoceros* spp. and *Thalassiosira* spp., are known to form dense blooms in this region (von Quillfeldt, 2000;
Sergeeva et al., 2010). In particular, *C. socialis s.l.* can constitute more than 90% of
phytoplankton assemblages during blooms in the northern Bering and Chukchi Seas (Sergeeva et al.)

al., 2010). The centric diatoms *Attheya* spp. are reported to be present in the sea-ice of the Arctic

99 (Campbell et al., 2018; Melnikov et al., 2002; von Quillfeldt et al., 2003; Szymanski &

100 Gradinger, 2016; Werner et al., 2007) and can comprise over 60% of diatom abundance in the

sea-ice during spring (Campbell et al., 2018). Pennate diatoms are also known to constitute a

102 large proportion of the sea-ice algal community (von Quillfeldt et al., 2003; Szymanski &

103 Gradinger, 2016).

Many diatom species form resting stages under unfavorable growth conditions such as 104 nutrient limitation (Durbin, 1978; Garrison, 1984; McQuoid & Hobson, 1996; Smetacek, 1985), 105 Fe limitation (Sugie & Kuma, 2008) and low light conditions (McQuoid & Hobson, 1996). High 106 cell concentrations in water column assemblages can also induce formation of resting stages 107 (Pelusi et al., 2020). Resting stages that sink to and accumulate in bottom sediments can 108 109 germinate and resume growth in response to favorable light levels (Hollibaugh et al., 1981). The ability to form resting stages is thus an important life cycle strategy for survival under low 110 temperature and light conditions during winter in seasonal sea-ice areas (Tsukazaki et al., 2013, 111 2018). 112

113 The distribution of diatom resting stage assemblages in sediments is thought to reflect the extent and magnitude of past blooms (Itakura et al., 1997; Pitcher, 1990) and can be used to 114 115 investigate determinants of community structure and bloom dynamics. For example, in the northern Bering Sea, analysis of the diatom resting stages in sediments showed that diatom 116 117 assemblages in early spring were dependent upon the timing of the sea-ice retreat (TSR): iceassociated diatoms were abundant in 2017 when the sea-ice remained until early April, but open-118 water diatoms dominated in 2018 when the TSR was approximately two weeks earlier than the 119 previous year (Fukai et al., 2019). 120

In this study, we enumerated viable diatom resting stages in sediments collected in a broad area across the Pacific Arctic region, from the northern Bering Sea to the Chukchi Sea and the southwestern Beaufort Sea. We describe the features of diatom resting stage assemblages over these regions, and discuss two hypotheses: 1) the concentrations of diatom resting stage assemblages are correlated with primary production in the water column, and 2) the extent and duration of sea-ice during the previous winter and spring determines community structure of diatom resting stage assemblages. In addition, we discuss how observed variations in diatom assemblages may impact organisms at higher trophic levels that rely on diatoms as an importantfood source.

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#### 131 2 Materials and Methods

132 2.1 Sea-ice, primary production and daylight hours

To evaluate the sea-ice extent in each region, the Advanced Microwave Scanning Radiometer 2 (AMSR2) standard sea-ice concentration (SIC) product was obtained from the Japan Aerospace Exploration Agency (JAXA) web portal (https :// gport al.jaxa.jp/gpr/) at a 10km resolution. The TSR was defined as the last day when the SIC fell below 20% prior to the observed annual sea-ice minimum across the study region during summer. Here, we used the SIC data after calculating a 5-day moving average.

To obtain a continuous primary production time-series, we used Level-3 standard mapped 139 image (9-km resolution) of Aqua-MODIS data downloaded as spectral remote sensing 140 reflectance  $(R_{rs})$  and daily photosynthetically available radiation (PAR) from the Goddard Space 141 Flight Centre/Distributed Active Archive Centre, NASA. The absorption coefficient for 443 nm 142  $(a_{\rm ph}(443))$  and euphotic zone depth (Z<sub>eu</sub>) were computed from  $R_{\rm rs}(\lambda)$  using Quasi-Analytical 143 Algorithm (QAA) version 5 (Lee et al., 2007, 2009) and daylength (DL) for the study area 144 calculated according to Brock (1981). We then computed the daily euphotic-depth-integrated 145 primary production (PP<sub>eu</sub>) using  $a_{ph}(443)$ , Z<sub>eu</sub>, PAR, and DL as inputs to an absorption-based 146 147 productivity model (ABPM, (Hirawake et al., 2012)). Missing values in  $a_{ph}(443)$  and  $Z_{eu}$  due to cloud cover were interpolated using their annual medians and hence PPeu was derived for the 148 cloud-covered pixels. From these values we calculated cumulative PPeu (IPeu) from TSR to the 149 date of the *in situ* sediment sampling was conducted for each shipboard observation site. 150

151 2.2 Sampling

Sediment sampling was conducted in the shallow Pacific Arctic region at stations ranging
from 24–194 m bottom depths (the northern Bering Sea, Chukchi Sea and the southwestern
Beaufort Sea; Fig. 1, Table 1) from 2–12 July 2018 aboard T/S *Oshoro-Maru* of Hokkaido
University, and from 9–23 August 2018 and 30 October to 15 November 2018 aboard the U.S.
Coast Guard icebreaker *Healy* (*HLY 1801* and *HLY 1803*, respectively) (Fig. 2 (a)). Sediment
samples were collected using a multiple corer (*Oshoro-Maru* cruise), a Van Veen Grab sampler,

or a HAPS core sampler (*Healy* cruises) at each station. A portion of the 0–1 cm of each 158

159 sediment core was extruded and stored in darkness at 5°C for Oshoro-Maru samples, and for

Healy samples, a portion of the 0–3 cm layer was collected from the grab or the core and stored 160

in air-tight amber jars at 1–4°C. The sediment samples were stored for more than one month in 161

order to eliminate vegetative cells. Since the main driver of diatom resting stage formation is 162

considered to be nitrogen depletion (McQuoid & Hobson, 1996), most resting stages are thought to form in the water column rather than near the benthos, as nutrient concentrations are higher 164

- near the seafloor. 165
- 166

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### 2.3 Quantification of diatom resting stages

The abundance of viable resting stages of diatoms in the sediment samples was analyzed 167 using the most probable number (MPN) method (Imai et al., 1984, 1990). Homogenized wet 168 sediment samples were suspended in Whatman GF/F filtered sterile seawater at a concentration 169 of 0.1 g mL<sup>-1</sup> (= $10^{0}$  dilution), and the subsequent serial tenfold dilutions ( $10^{-1}$  to  $10^{-6}$ ) were made 170 with modified SWM-3 medium (Table 2) (Chen et al., 1969; Itoh & Imai, 1987). Then 1 mL 171 aliquots of diluted suspensions were inoculated into five replicate wells of disposable tissue 172 culture plates (48 wells). Incubation was carried out at a temperature of 5°C and under white 173 fluorescent light of 50 or 116 µmol photons m<sup>-2</sup> s<sup>-1</sup> with a 14 h light:10 h dark photocycle for 10 174 days. The appearance of vegetative cells of planktonic diatoms in each well was examined using 175 an inverted optical microscope. The most probable number (MPN for a series of 5 tenfold 176 dilutions) of diatoms of each species in the sediment sample (MPN cells  $g^{-1}$  wet sediment) was 177 then calculated according to the statistical table by Throndsen (1978). Since we observed wells 178 with  $10^{-2}$ – $10^{-6}$  dilutions, the detectable cell numbers by the MPN method were from  $1.8 \times 10^2$  to 179  $2.4 \times 10^7$  MPN cells g<sup>-1</sup> for each species. Note that we used the dataset of Fukai et al. (2019) for 180 181 the Oshoro-Maru expedition.

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2.4 Statistical analyses

The diatom resting stage communities were distinguished by cluster analysis. To 183 reduce the bias for abundant species, the cell concentration data (X: MPN cells g<sup>-1</sup> wet sediment) 184 for each species were transformed to  $\sqrt[4]{X}$  prior to cluster analysis (Quinn & Keough, 2002). 185 Dissimilarities between samples were examined using the Bray-Curtis index based on the 186 differences in the species composition. To group the samples, the dissimilarity indices were 187

188 coupled using hierarchical agglomerative clustering with a complete linkage method (an

189 unweighted pair group method using the arithmetic mean). A Mann-Whitney U-test was

190 conducted to evaluate environmental factors (the TSR, IP<sub>eu</sub>, and the growth period of ice-

associated assemblages (GP)) between the distinguished groups. The GP was defined as the

integrated daylength during the periods with SIC > 20% after the daylight exceeded 10 hours, as

193 Gilstad and Sakshaug (1990) indicated that ice-associated assemblages could increase their

194 growth rate when daylight hours exceeded 10 h.

We defined the open-water assemblages as the community with centric diatoms,
excluding *Attheya* spp., and the ice-associated assemblages as the community with pennate
diatoms and *Attheya* spp., as *Attheya* spp. and pennate diatoms are often reported to be present in
the sea-ice (e.g. Campbell et al., 2018; Melnikov et al., 2002; von Quillfeldt et al., 2003;
Szymanski & Gradinger, 2016; Werner et al., 2007). Based on this definition, we analyzed the
relationships of ice-associated assemblages with the TSR and the GP using Spearman's rank
correlation coefficient.

All statistical analyses were conducted using R software (version 3.6.1, R Development Core Team, 2019).

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#### 205 **3 Results**

3.1 Sea-ice and primary production 206 207 The TSR was different among regions (Table 1). The sea-ice retreated from south to north in the northern Bering and the Chukchi Seas, and from west to east in the southwestern 208 Beaufort Sea (Fig. 1). 209 The IP<sub>eu</sub> had a regional feature in which high values were observed in the 210 southern Chukchi Sea and low values in the southwestern Beaufort Sea (Table 1, Fig. 2 (b)). 211 3.2 Diatom concentrations and species composition 212 The viable diatom resting stages determined by the MPN method ranged over four orders 213 of magnitude, from  $1.2 \times 10^3$  to  $6.1 \times 10^7$  MPN cells g<sup>-1</sup> wet sediment (Fig. 3). Highest 214 concentrations were found to the south of St. Lawrence Island  $(3.4 \times 10^6 - 6.1 \times 10^7 \text{ MPN cells g}^-)$ 215 <sup>1</sup> wet sediment). In the Chirikov Basin, which extends northwards from St. Lawrence Island to 216

the Bering Strait (DBO2-1, DBO2-4, OS14, OS19, OS20, OS22), diatom concentrations were

relatively high  $(2.8 \times 10^5 - 3.0 \times 10^6 \text{ MPN cells g}^{-1} \text{ wet sediments})$ . Diatom concentrations near 218 Utgiagvik (DBO5-10) were also relatively high  $(1.2 \times 10^6 \text{ MPN cells g}^{-1} \text{ wet sediments})$ . In 219 contrast, cell concentrations were lower in samples from the coastal region of the southwestern 220 Beaufort Sea (DBO6-5, PRW-7, PRB-4, PRB-7, KTO-5, MCK-1, MCK-2, MCK-3, MCK-4) 221  $(1.2 \times 10^3 - 7.8 \times 10^3 \text{ MPN cells g}^{-1} \text{ wet sediments})$ . Nineteen genera and twenty species were 222 observed over the study region - 12 genera and 14 species of centric diatoms and 7 genera and 6 223 species of pennate diatoms. Centric diatoms were dominant at almost all stations, although 224 dominant species varied geographically; proportional abundance of *Chaetoceros* spp. and 225 Thalassiosira spp. were found in samples collected from the northern Bering Sea and Chukchi 226 Sea, whereas Attheya spp. were highest in the southwestern Beaufort Sea (Fig. 4). Pennate 227 diatoms comprised over 50% of the diatom assemblages at some stations (DBO4-4, MCK-1, 228 MCK-2, MCK-3), with highest proportional abundance found in samples from the southwestern 229 230 Beaufort coastal region (Fig. 4). Total cell concentration in sediments were positively correlated with the cell concentrations of *Chaetoceros* spp. and *Thalassiosira* spp. (Spearman,  $\rho = 0.97$ , p < 0.97, p231 0.05) (Fig. 5). 232

In order to test for seasonal effects, diatom assemblages were compared over time in stations in the northern Bering Sea and Southern Chukchi Sea, which included locations from each sampling period (OS14, 19, 20, 22, 30 by *Oshoro-Maru*, DBO2-1, 2-4, 3-6, 3-8 in *HLY 1801*, and DBO 3-1, 3-5, 3-7 in *HLY 1803*). There were no significant differences in species or genera among these samples (one-way ANOVA, p > 0.05), with the exception of *Attheya* spp. and *C. debilis* (one-way ANOVA, p < 0.05).

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3.3 Diatom assemblages by cluster analysis

Cluster analysis based on concentrations of diatom resting stages classified the diatom assemblages into two groups (A, B) and four outgroups at 52% and 64% dissimilarity levels. Group A was distributed from the northern Bering Sea to the Chukchi Sea near Utqiagvik (Fig. 6 (a)). Cell concentrations in group A were very high  $(7.9 \times 10^4 - 1.1 \times 10^7 \text{ MPN cells g}^{-1} \text{ wet}$ sediments,  $avg = 1.2 \times 10^6 \text{ MPN cells g}^{-1}$  wet sediment), and samples in this group with dominated by *Chaetoceros* spp. and *Thalassiosira* spp. (35% and 51%, respectively) (Fig. 6 (b)). Group B included stations from the southwestern Beaufort Sea, where cell concentrations ranged from  $3.2 \times 10^3$  to  $2.1 \times 10^5$  MPN cells g<sup>-1</sup> wet sediment (avg =  $5.8 \times 10^4$  MPN cells g<sup>-1</sup> wet

- sediment) and *Attheya* spp. were dominant (47%) (Fig. 6 (b)). All stations from the easternmost
- transect in the study region (MCK) were classified as outgroups (Fig. 6 (a)).
- 251 3.4 Relationships with environmental factors
- Environmental factors differed between samples comprising diatom groups A and B. The TSR was significantly later at the group B locations compared to group A (*U*-test, p < 0.05) (Fig. 7 (a)), and the GP was significantly longer at group B locations than group A (*U*-test, p < 0.05) (Fig. 7 (b)). The switching between the two diatom groups occurred around 200 Julian day of the TSR and approximately 2500 hours of the GP (Fig. 7 (a), (b), Fig. 8). By contrast, the IP<sub>eu</sub> and the sampling depth were not significantly different between groups (*U*-test, p > 0.05) (Fig. 7 (c), (d)).

In addition, the TSR and the GP were significantly positively correlated with the proportion of pennate diatoms and *Attheya* spp., which are defined as the ice-associated assemblages ( $\rho = 0.63$  and 0.29, respectively, p < 0.05) (Fig. 8).

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## 263 4 Discussion

Examination of the distribution and abundance of diatom resting stages in Pacific Arctic sediments demonstrated a strong correlation with the timing of sea ice retreat and the growth period of ice-associated assemblages. Details regarding spatial community dynamics and relationships between diatom assemblages and TSR, GP, and environmental parameters are discussed below.

4.1 Distribution of diatom resting stages and the relationships with primary production in
 the Pacific Arctic Region

Cell concentrations of diatom resting stages exhibited geographic variability that roughly corresponded with levels of primary production previously reported in the region. However, primary production values estimated by satellite remote sensing in this study did not have any

statistically significant relationships with diatom resting stage assemblages.

This study found high concentrations of diatom resting stages in the northern Bering Sea and the Chukchi Sea (avg =  $3.1 \times 10^6$  MPN cells g<sup>-1</sup> wet sediments), but low concentrations (avg =  $6.2 \times 10^4$  MPN cells g<sup>-1</sup> wet sediments) in the southwestern Beaufort Sea. This is consistent

with prior studies of primary productivity that documented high annual water-column integrated 278 primary production in the northern Bering and Chukchi Seas and low productivity in the western 279 Beaufort Sea (Grebmeier et al., 2006; Hill et al., 2018). However, we did not find a significant 280 relationship between diatom resting stage assemblages and primary production values estimated 281 by satellite. O'Daly et al. (2020) presented similar findings; that higher rates of primary 282 productivity were correlated with higher rates of POC flux, including viable diatoms, but that 283 there is variability in the export efficiency. Thus, while the hypothesis that diatom resting stage 284 concentrations reflect primary productivity in the water column (Imai et al., 1990; Itakura et al., 285 1997; Pitcher, 1990) holds up over broad features of the Pacific Arctic region, additional data are 286 needed to justify this using resting stage assemblages as a strict proxy for productivity. 287

Another cause of high concentrations of resting stages observed in the northern Bering and Chukchi Seas is related to the high sinking flux in this region (O'Daly et al., 2020). Lalande et al. (2020) used a time series of sediment trap observations at single station in the Chukchi Sea to show that diatoms make up a high proportion of POC flux. The characteristically high sinking flux in the northern Bering and Chukchi Seas could drive high concentrations of sediment diatom assemblages reported here, though diatom losses by zooplankton grazing also need to be considered (Campbell et al., 2009; Sherr et al., 2009).

295 We considered the impact that variable sampling times may have had upon the assemblages observed in this study. The sediments were obtained over several different time 296 297 periods (2-12 July 2018, 9-23 August 2018, and 30 October to 15 November 2018), and it is possible that the community structure changed from summer to fall. However, there were no 298 significant differences in species or genera except for Attheya spp. and C. debilis between 299 samples at replicated stations in the northern Bering Sea and Southern Chukchi Sea, where 300 301 sampling was conducted over multiple time periods. Dissimilarity among almost all the samples was less than 40%, and they were also grouped in the cluster analysis. Water temperature is 302 known to influence resting stage survival time, with colder water increasing survival time length 303 (McQuoid & Hobson, 1996). Hargraves and French (1983) reported that Chaetoceros diadema, 304 Detonula confervacea, Leptocylindrus danicus and Thalassiosira nordenskioeldii, which 305 306 sometimes appear in the Pacific Arctic sediments, survived for 291, 220, 400, and 220 days, respectively, at temperatures between  $5-6^{\circ}$ C. These periods are sufficiently longer than the 307 difference in sampling periods (the longest difference is 136 days). Given that temperatures at 308

the seafloor of the Pacific Arctic are lower than  $5-6^{\circ}$ C, we do not believe that the survival time of resting stages impacted our results. For these reasons, differences over sampling periods appeared to be almost negligible in this study.

4.2 The relationship of diatom resting stage assemblages with the TSR and the GP 312 Prior investigators have shown that the magnitude and composition of diatom 313 assemblages in the Arctic spring bloom are influenced by the presence of the sea-ice and the 314 315 timing of the sea-ice retreat (Fujiwara et al., 2016; Fukai et al., 2019; Neeley et al., 2018). In this 316 study, the distribution of diatom resting stage assemblages were clearly related to spatial 317 differences in the TSR. In locations where the ice retreat was early, such as the northern Bering 318 and the Chukchi Seas, *Chaetoceros* spp. including *C. socialis s.l.* and *Thalassiosira* spp. were dominant in sediments (C. socialis s.l.: 0.36–93.1%, Chaetoceros spp.: 0.76–93.6%, 319 Thalassiosira spp.: 2.0–96.4%). Because they are known to form dense spring blooms in these 320 321 regions (von Quillfeldt, 2000; Sergeeva et al., 2010), these data suggest that diatom resting 322 stages were formed and settled to the seafloor after spring blooms of Chaetoceros spp. and Thalassiosira spp. in the northern Bering Sea and the Chukchi Sea. In addition, the positive 323 correlation between *Chaetoceros* spp. and *Thalassiosira* spp. cell concentrations with total cell 324 concentrations indicates that where the TSR was early and the open-water period was long, large 325 diatom blooms of *Chaetoceros* spp. and *Thalassiosira* spp. produced high quantities of resting 326 stage cells (Fukai et al., 2019). 327

The TSR had also an effect on the diatom community composition, especially the 328 proportion of ice-associated diatoms in diatom assemblages. In the southwestern Beaufort Sea, 329 where the TSR was late, diatom assemblages were dominated by ice-associated species (Groups 330 B and outgroups in the transect MCK), again demonstrating that sea-ice is a driver of benthic 331 community structure among the exported diatoms. In addition, the prevalence of ice-associated 332 species was positively correlated with the TSR, suggesting that the proportion of ice algae in 333 diatom assemblages is higher when sea-ice persists. This is likely due in part to their ability to 334 sustain growth under low light levels (< 1  $\mu$ mol photon s<sup>-1</sup> m<sup>-2</sup>) (Cota & Smith, 1991; Mock & 335 Gradinger, 1999); notably, Tsukazaki et al. (2018) demonstrated that the centric genus Attheya 336 spp. could survive in dark for more than six months, and thus can withstand low light conditions 337 in the Arctic. It is possible that this study underestimated the concentrations of pennate diatoms 338

in sediments compared with Attheya spp. and other centric diatoms, as few marine pennate 339 diatoms are known to form resting stages, while many centric diatoms do (McQuoid & Hobson, 340 1996), and the fate of the pennate diatoms in sediment is largely unknown. Despite this potential 341 bias, these data indicate that the proportion of ice-associated species was higher where the TSR 342 occurred later. Interestingly, a spatial change from the assemblage dominated by open-water 343 species to that with high proportion of ice-associated diatoms occurred at stations where the TSR 344 was around the 200th Julian day (mid-July). This indicates a potential threshold between 345 dominant diatom groups based on the TSR parameter. 346

For ice-associated assemblages in the surface sediments, the length of the growth period 347 during which algae receive sufficient light before the TSR is important (Fukai et al., 2019). The 348 proportional abundance of ice-associated diatoms was significantly higher when GP was longer, 349 350 suggesting that photoperiod during sea-ice presence is another important driver of diatom community structure (Cota & Home, 1989; Gosselin et al., 1990; Smith et al., 1988). In addition, 351 a GP boundary of 2500 hours may be an important parameter for the distribution of ice-352 associated assemblages due to corresponding changes that were observed. Future efforts to 353 354 evaluate and predict diatom assemblages should consider both the TSR and the GP.

4.3 Connecting diatom distribution to higher trophic levels

The diatom assemblages had clear relationships with the TSR and the GP. In the northern Bering Sea, the early timing of the sea-ice retreat and subsequent changes in diatom assemblages in the water column and the sediment was reported in 2018 (Fukai et al., 2019, 2020). This indicates that the recent drastic reduction of sea-ice in the Pacific Arctic region may induce a shift in diatom assemblages from relative dominance of ice-associated species to open-water species.

The distribution and composition of diatom species in this study were associated with the 362 zooplankton feeding environment in the Pacific Arctic region. As diatoms comprise the largest 363 portion of the mesozooplankton diet, especially in spring (Campbell et al., 2016), changes in 364 diatom species composition will perturb prey environments of higher trophic-level organisms. 365 The spatial trend of diatom resting stage concentrations exhibited a similar gradient to 366 zooplankton  $\delta^{13}$ C values showed by Pomerleau et al. (2014), which reported values that were 367 more enriched in the western Bering Strait and less enriched on the Beaufort shelf. Nakatsuka et 368 al. (1992) reported an increase in  $\delta^{13}$ C of POC during a diatom bloom in a mesocosm experiment 369

370 in Saanich Inlet, Canada. Additionally, they showed that the main factor influencing the variation of  $\delta^{13}$ C of POC during a phytoplankton bloom in a mesocosm experiment was the specific 371 production rate of POC, which can be proportional to the specific growth rate of phytoplankton, 372 rather than carbon dioxide system or community composition (Nakatsuka et al., 1992). 373 Typically, fast-growing diatoms (e.g. Chaetoceros spp. and Thalassiosira spp.) and zooplankton 374 that feed on these diatoms are enriched with <sup>13</sup>C (Fry & Wainright, 1991). The inflow of nutrient 375 rich Anadyr waters from the western Bering Strait is known to fuel huge blooms of Chaetoceros 376 spp. and *Thalassiosira* spp. (Danielson et al., 2017; Sergeeva et al., 2010), explaining the high 377 concentrations of these species in sediments of the northern Bering and the Chukchi Seas 378 reported here. In addition, regions of high diatom resting stage concentrations roughly 379 corresponded to benthic hotspots, which include waters to the south of St. Lawrence Island, the 380 381 Chirikov Basin, the southeastern Chukchi Sea and the northeastern Chukchi Sea (Grebmeier et al., 2015). In these regions with mean depths from 43 to 65 m, benthic primary production can be 382 lower than pelagic production due to light limitation, and accumulation of microalgae in 383 sediments are the main food source for benthic communities (Grebmeier et al., 2015). In 384 385 particular, diatoms are valuable taxa because they are rich in polyunsaturated fatty acids (PUFAs) (Brown et al., 1997). Furthermore, Wang et al. (2016) analyzed the blubber fatty acid 386 387 composition and stable carbon isotope ratios of ice seals, who feed on pelagic and benthic fishes, in the northern Bering and the southern Chukchi Seas to show that ice algae production 388 389 contributed up to 80% of ice seal diets through trophic transfer. Therefore, changes in diatom assemblages caused by sea-ice dynamics will directly influence zooplankton and benthos 390 production, with indirect effects upon higher trophic levels. 391

392

#### 393 **5 Conclusions**

This study demonstrated that the distribution and community composition of diatom resting stages in the Pacific Arctic region were significantly influenced by the presence of sea-ice and the light environment. Diatom resting stages appear to follow broad spatial patterns of primary productivity across the region, suggesting the potential use of diatom resting stages as one of the proxies for productivity, despite the fact that there was not a significant relationship between diatom assemblages and primary productivity estimated by satellite observations. The TSR and the GP were important drivers of diatom assemblages, and significantly influenced the

composition of diatoms in sediments. In particular, diatom assemblages changed spatially from 401 composition dominated by open-water species to a high proportion of ice-associated diatoms in 402 the region where the TSR occurred after mid-July (around the 200th Julian day) and the GP was 403 over 2500 hours. This result may indicate that a shift to earlier TSR under future climate 404 conditions could induce not only delayed bloom timing (Hirawake & Hunt, 2020; Kikuchi et al., 405 2020) but also a change in the composition of diatom assemblages forming the spring bloom. 406 The distribution of diatom resting stages is a valuable approach for investigating the diatom 407 community, particularly on the Arctic shelves where it is logistically challenging to characterize 408 the rapid seasonal succession in community composition that occurs across this remote and 409 dynamic geographic region. Moreover, this approach provides species-level resolution lacking in 410 satellite observations, providing a more robust assessment of the ecosystem implications of 411 412 community changes. On the ecosystem level, it is interesting that the distribution of diatom resting stages corresponded spatially with benthic hot spots and the feeding environment of 413 414 zooplankton. Based on this research, it is clear that future changes in sea-ice extent and duration will impact diatom communities, and that resulting fluctuations in primary productivity and 415 416 community structure will affect other components of Arctic marine ecosystems. 417

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# 645 **Figure and Table legends**

**Figure 1**. Sediment sampling locations in the northern Bering Sea, Chukchi Sea, and Beaufort

647 Sea in 2018. Color contours indicate the timing of the sea-ice retreat (rainbow contour) and the

- bottom depth (blue contour). Abbreviations indicate the transect names during Healy cruises
- 649 1801 and 1803. SLI: St. Lawrence Island
- Figure 2. Horizontal values of the observation date (a) and the daily cumulative euphotic-depthintegrated primary production from the TSR to the observation date ( $IP_{eu}$ ) (b).
- **Figure 3.** Horizontal distribution of diatom resting stages in the north Bering, Chukchi and
- 653 Beaufort Seas in 2018. Squares indicate benthic hot spots indicated by Grebmeier et al. (2015).
- Figure 4. Cell concentrations and species composition of diatom resting stages in the northernBering, Chukchi and Beaufort Seas in 2018.
- Figure 5. The relationship between the abundances of *Chaetoceros* spp. and *Thalassiosira* spp. and total cell concentrations in MPN.
- **Figure 6.** (a) Spatial distribution of diatom resting stage communities by group. (b) Species composition and cell concentrations in each group.
- **Figure 7**. Comparison of environmental factors between diatom resting stage groups. (a) the
- timing of the sea-ice retreat (TSR). (b) the growth period of ice-associated assemblages (GP). (c)
- the daily cumulative euphotic-depth-integrated primary production from the TSR to the
- 663 observation date (IP<sub>eu</sub>). (d) the bottom depth of sampling station.
- **Figure 8**. Relationships between the proportion of the ice-associated species (*Attheya* spp. and pennate diatoms) in MPN and the TSR (a), and the GP (b). Each color indicate the diatom groups (pink: group A, green: group B, and gray: out groups).
- **Table1.** Locations of sediment sampling stations in the Bering, Chukchi, and Beaufort Seas from
- July to November in 2018. In sample type column, "core" and "Van Veen" indicate that the
- samples were collected by multiple corer and Van Veen grab sampler, respectively. The timing
- of sea ice retreat (TSR) indicates the last date when the sea ice concentration falls below 20%,
- prior to observed annual sea ice minimum across the study region during summer.  $IP_{eu}$  indicates
- daily integrated values of primary production from TSR to the date of the *in situ* sediment
- sampling was conducted. The growth period of the ice-associated assemblages (GP) indicates the integrated daylangth during the periods with SIC > 20% often the daylight hours around 10 hours
- integrated daylength during the periods with SIC > 20% after the daylight hours exceed 10 hours.
- **Table 2**. Components of the modified SWM-3 medium. Solvent is natural filtered sea water.
- 676 Medium pH is 7.7–7.8.

Table 1. Locations of sediment sampling stations in the Bering, Chukchi, and Beaufort Seas from July to November in 2018. In sample type column, "core" and "Van Veen" indicate that the samples were collected by multiple corer and Van Veen grab sampler, respectively. The timing of sea ice retreat (TSR) indicates the last day when the SIC fell below 20% prior to the observed annual sea-ice minimum across the study region during summer. IP<sub>eu</sub> indicates daily integrated values of primary production from TSR to the date of the *in situ* sediment sampling was conducted. The growth period of the ice-associated assemblages (GP) indicates the integrated daylength during the periods with SIC > 20% after the daylight hours exceed 10 hours.

Cruise	Station	Date (Julian day)	Latitude (°N)	Longitude (°W)	Bottom depth (m)	Sample Type	TSR (Julian day)	$IP_{eu}$ (mg C m <sup>-2</sup> )	GP (hours)
Oshoro-maru	OS4	2018/7/2 (183)	63.15	173.83	75	Core	2018/3/22 (81)	80253.9	103.2
	OS6	2018/7/3 (184)	62.88	172.16	55	Core	2018/3/23 (82)	56305.7	158.4
	OS8	2018/7/3 (184)	62.49	170.00	37	Core	2018/3/25 (84)	77752.8	234.2
	OS14	2018/7/5 (186)	64.51	170.87	46	Core	2018/4/17 (107)	66311.6	414.7
	OS19	2018/7/6 (187)	64.51	166.51	28	Core	2018/5/1 (121)	39181.0	755.1
	OS20	2018/7/6 (187)	65.08	168.00	46	Core	2018/4/20 (110)	32002.1	581.4
	OS22	2018/7/7 (188)	65.07	169.70	51	Core	2018/4/17 (107)	106377.2	469.0
	OS30	2018/7/11 (192)	66.73	168.96	42	Core	2018/5/17 (137)	59460.1	1033.1
HLY 1801	DBO2-1	2018/8/9 (221)	64.67	169.93	48	Van Veen	2018/4/16 (106)	104868.8	427.2
	DBO2-4	2018/8/9 (221)	64.96	169.90	49	Van Veen	2018/4/17 (107)	143193.9	469.0
	DBO3-6	2018/8/10 (222)	67.90	168.25	59	Core	2018/5/20 (140)	95858.0	935.9
	DBO3-7	2018/8/11 (223)	67.79	168.60	51	Core	2018/5/20 (140)	104109.1	935.1
	IC-3	2018/8/13 (225)	71.60	165.30	43	Van Veen	2018/6/26 (177)	32304.9	1829.9
	IC-8	2018/8/14 (226)	70.97	163.56	46	Van Veen	2018/6/30 (181)	48394.7	1391.3
	DBO4-2	2018/8/15 (227)	71.22	161.29	50	Core	2018/7/14 (195)	17824.0	1891.3
	DBO4-4	2018/8/15 (227)	71.48	161.50	49	Core	2018/7/15 (196)	15406.3	2377.8
	DBO4-5	2018/8/15 (227)	71.61	161.62	47	Core	2018/7/14 (195)	19747.3	2477.9
	DBO5-9	2018/8/17 (229)	71.58	157.82	66	Van Veen	2018/7/22 (203)	2915.4	2667.8
	DBO5-10	2018/8/17 (229)	71.63	157.90	64	Core	2018/7/22 (203)	2813.1	2669.9
	LB-11	2018/8/22 (234)	70.06	167.66	50	Van Veen	2018/5/13 (133)	95614.2	973.8
	LB-9	2018/8/23 (235)	69.88	166.82	47	Van Veen	2018/5/12 (132)	105276.1	877.1
	LB-7	2018/8/23 (235)	69.68	166.09	42	Van Veen	2018/5/11 (131)	96511.2	800.6

DBO6-1	2018/10/30 (303)	71.16	152.26	32	Van Veen	2018/7/29	(210)	42213.8	2824.9
DBO6-3	2018/10/30(303)	71.25	152.17	48	Van Veen	2018/7/29	(210)	55326.5	2829.3
DBO6-5	2018/10/30(303)	71.34	152.10	71	Van Veen	2018/8/5	(217)	63070.1	2899.2
DBO6-7	2018/10/31 (304)	71.42	152.04	194	Van Veen	2018/8/5	(217)	52153.7	2902.0
PRB-1	2018/11/2 (306)	70.69	148.44	26	Van Veen	2018/8/26	(238)	—	3347.2
PRB-2	2018/11/2 (306)	70.77	148.33	35	Van Veen	2018/9/3	(246)	17622.4	3465.0
PRB-4	2018/11/2 (306)	70.90	148.14	45	Van Veen	2018/9/4	(247)	16083.4	3405.6
PRB-7	2018/11/2 (306)	71.02	147.98	58	Van Veen	2018/9/6	(249)	19897.2	3490.4
MCK-1	2018/11/4 (308)	69.82	139.61	38	Van Veen	2018/8/3	(215)	40557.1	2240.4
MCK-2	2018/11/4 (308)	69.90	139.49	44	Van Veen	2018/8/3	(215)	47209.6	2111.3
MCK-3	2018/11/4 (308)	69.94	139.39	55	Van Veen	2018/8/3	(215)	47343.2	2113.9
MCK-4	2018/11/4 (308)	69.97	139.30	60	Van Veen	2018/8/3	(215)	46782.5	2113.9
KTO-2	2018/11/5 (309)	70.28	143.93	38	Van Veen	2018/8/18	(230)	30870.8	3191.8
KTO-3	2018/11/5 (309)	70.37	143.79	48	Van Veen	2018/8/21	(233)	14101.3	3247.5
KTO-5	2018/11/5 (309)	70.56	143.61	110	Van Veen	2018/8/19	(231)	13958.0	3221.7
PRW-1	2018/11/7 (311)	70.68	148.91	24	Van Veen	2018/8/28	(240)	115525.9	3369.1
PRW-4	2018/11/7 (311)	70.82	148.84	33	Van Veen	2018/8/28	(240)	76570.9	3373.2
PRW-7	2018/11/7 (311)	70.95	148.78	38	Van Veen	2018/9/3	(246)	26140.8	3474.0
DBO5-1	2018/11/14 (318)	71.25	157.13	47	Van Veen	2018/7/22	(203)	79117.8	2661.3
DBO5-3	2018/11/14 (318)	71.33	157.31	91	Van Veen	2018/7/21	(202)	59407.8	2637.3
DBO5-5	2018/11/14 (318)	71.41	157.49	128	Van Veen	2018/7/21	(202)	44093.7	2639.4
DBO5-7	2018/11/14 (318)	71.50	157.66	85	Van Veen	2018/7/22	(203)	35765.2	2667.8
DBO5-9	2018/11/14 (318)	71.58	157.83	66	Van Veen	2018/7/22	(203)	35857.3	2667.8
DBO3-1	2018/11/15 (319)	68.31	166.92	35	Van Veen	2018/5/5	(125)	196800.9	812.4
DBO3-5	2018/11/15 (319)	68.01	167.88	54	Van Veen	2018/5/6	(126)	212878.6	828.9
DBO3-8	2018/11/15 (319)	67.67	168.95	50	Van Veen	2018/5/21	(141)	179194.6	1124.6

HLY 1803

Component	Concentrations in final medium / Amounts per litter	Component	Concentrations / Amounts
NaNO <sub>3</sub>	2.0 mM	P-1 metal in10 mL	
$NaH_2PO_4 \cdot 2H_2O$	0.1 mM	$H_3BO_3$	1.0 mM
$Na_2SiO_3 \cdot 9H_2O$	0.2 mM	$MnCl_2 \cdot 4H_2O$	$3.5 \times 10^{-2}$ mM
Na <sub>2</sub> EDTA	30.0 mM	ZnCl <sub>2</sub>	$4.0 \times 10^{-3}$ mM
Fe-EDTA	2.0 µM	$CoCl_2 \cdot 6H_2O$	1.0×10 <sup>-4</sup> mM
Na <sub>2</sub> SeO <sub>3</sub>	2.0 µM	$CuCl_2 \cdot 2H_2O$	$1.0 \times 10^{-6}$ mM
$Na_2MoO_4 \cdot 2H_2O$	100 µM	S-3 Vitamin in 2mL	
TRIS	500 mg	B <sub>1</sub> -HCl	0.5 mg
P1-metals	10.0 mL	Ca-Pantothenate	0.1 mg
S-3 Vitamins	2.0 mL	Nicotinic acid	0.1 mg
		P-Aminobenzoic acid	10.0 µg
		Biotin	1.0 µg
		Inositol	5.0 mg
		Folic acid	2.0 µg
		Thymine	3.0 mg
		Vitamin B <sub>12</sub>	1.0 µg

Table 2. Components of the modified SWM-3 medium (left column) and detail components of P1-metals and S-3 Vitamin (right column). Solvent of the medium is natural filtered sea water. Medium pH is 7.8.

Figure 1.



Figure 2.



Figure 3.



Figure 4.



Figure 5.



Figure 6.



Figure 7.



Figure 8.

