Polar Biology (2019) 42:1915–1922
https://doi.org/10.1007/s00300-019-02552-x

SHORT NOTE

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

Yuri Fukai[1] · Kohei Matsuno[1,2] · Amane Fujiwara[3] · Atsushi Yamaguchi[1,2]

Received: 11 March 2019 / Revised: 18 July 2019 / Accepted: 5 August 2019 / Published online: 16 August 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract
In the Bering Sea shelf, annual changes in the sea ice extent are large. In this study, we compare the viable diatom resting stages in sediments during the summer of 2017 when the sea ice retreat was late and 2018 when the sea ice retreat was early. South of St. Lawrence Island, the germinating cell number was 10–100 times greater in 2018 than it was in 2017. The taxonomic composition also showed large annual differences: *Fragilariopsis/Fossula* spp., which are ice algae species, were abundant in 2017, but *Thalassiosira* spp. dominated in 2018. Satellite observations confirmed that sea ice diminished before the ice-edge bloom in 2018, but sea ice remained until the ice-edge bloom in 2017. This study shows that the community composition of viable diatom resting stages is largely affected by the timing of the sea ice retreat.

Keywords Bering Sea · Diatom resting stages · Sea ice · Ice algae

Introduction

Phytoplankton have an important role as primary producers in the marine ecosystem. In high latitude oceans, diatoms are the most dominant phytoplankton during spring blooms, and the magnitude of blooms is extremely larger compared to lower latitudes. Many diatom species produce resting stages under unfavorable growth conditions (Hargraves and French 1983; McQuoid and Hobson 1996). Diatoms form resting stages under nutrient limitation and low light conditions and then sink to the bottom sediments (Hargraves and French 1975; Durbin 1978; Garrison 1984; Smetacek 1985; McQuoid and Hobson 1996). The resting stages that have accumulated in the bottom sediments have high viability. Since their germination is triggered by appropriate light intensity, when they are resuspended in the euphotic layer from the seafloor, they can begin to grow under favorable conditions (Itakura 2000). As a result of having such a life strategy with a resting stage, diatoms can survive in variable environments. It is suggested that the distribution of diatom resting stages in the sediment may reflect the past blooms that have occurred in the water column (Pitcher 1990; Itakura et al. 1997).

The northern Bering Sea shelf is a shallow seasonal sea ice area with a water depth of approximately 50 m. Primary productivity is high in the spring, and the magnitude and timing of the phytoplankton bloom vary with the variable timing of the spring sea ice retreat (Fujiwara et al. 2016). The majority of phytoplankton settles to the seafloor due to the low grazing pressure of zooplankton in the water column, supporting the benthic community in the Bering Sea and the Chukchi Sea (Grebmeier et al. 1988, 2006). From the Bering Sea to the Chukchi Sea, there are three principal currents, and the hydrographic environment and phytoplankton community are known to be different in each current (Giesbrecht et al. 2019). Due to the differences in the current flow rate and the spatial area covered, cells in sediments can be variable (Tsukazaki et al. 2018). Thus, the species composition of diatom resting stages in sediments reflects not only the productivity

✉ Yuri Fukai
y.fukai@fish.hokudai.ac.jp

[1] Laboratory of Marine Biology, Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan

[2] Arctic Research Center, Hokkaido University, Kita-21 Nishi-11 Kita-ku, Sapporo, Hokkaido 001-0021, Japan

[3] Japan Agency for Marine-Earth Science and Technology, 2-15 Natsushima-cho, Yokosuka, Kanagawa 237-0061, Japan

and dominant species in the water column, but also the physical conditions such as current velocity.

Ice algae have been reported from the sediments in the Chukchi Sea (Tsukazaki et al. 2018). Ice algae adhere specifically to sea ice and have a major role in primary production in the seasonal ice area (Gradinger 2009). Ice algae can grow even under dim light conditions such as < 1 μmol photon s^{-1} m^{-2} (Cota and Smith 1991; Mock and Gradinger 1999). In polar regions, timing of ice algae growth is controlled by the light environment (Smith et al. 1988; Cota and Home 1989; Gosselin et al. 1990). Ice algae blooms are often reported to occur in the Bering and Chukchi Sea during March–May (Leu et al. 2015). Recently, ice algae have been reported to be an important food source for various zooplankton and benthic species (Brown and Belt 2012; Wang et al. 2015). In the Bering Sea, since the annual variation of the extent of the sea ice is large, the distribution of ice algae can be considered to have a large annual fluctuation, but the distribution details are unknown.

In this study, we investigated diatom resting stages in sediments of the northern Bering Sea during the summer in 2017 and 2018, when the sea ice retreat timing varied greatly. Through this analysis, we aimed to evaluate the influence of changes in the timing of the sea ice retreat on the viable diatom assemblage: *Fragilariopsis/Fossula* spp., ice algae species, were abundant in 2017, but *Thalassiosira* spp. dominated in 2018.

Materials and methods

Sampling was conducted in the northern Bering Sea shelf on 9–21 July 2017 and 2–12 July 2018 during the 40th and 56th cruises of the T/S *Oshoro-Maru* of Hokkaido University (Fig. 1). Sediment samples were collected by a multiple corer or Smith-Mclntyre bottom sampler at each station. The top 1 cm or 3 cm of sediment core was extruded and stored in darkness at 5 °C for more than 1 month into eliminate vegetative cells.

Sediment samples were analyzed following the procedure of the most probable number (MPN) method, and the abundance of viable resting stages of diatoms in the sediments was estimated (Imai et al. 1984, 1990). Homogenized wet sediment samples were suspended in filtered sea water at a concentration of 0.1 g mL^{-1} ($=10^0$ dilution), and serial tenfold dilutions (10^{-1} to 10^{-6}) were made with modified SWM-3 medium. Then, 1-mL aliquots of diluted suspensions was inoculated into five replicate wells of disposable tissue culture plates (48 wells). Incubation was carried out at a temperature of 5 °C and under illumination of 50 μmol photons m^{-2} s^{-1} with a 14-h light:10-h dark photocycle for 10–14 days. The appearance of vegetative cells of planktonic diatoms in each well was examined using an inverted epifluorescence microscope. The most probable number (MPN for a series of 5 tenfold dilutions) of diatoms in the sediment sample (MPN cells g^{-1} wet sediment) was then calculated according to the statistical table by Throndsen (1978).

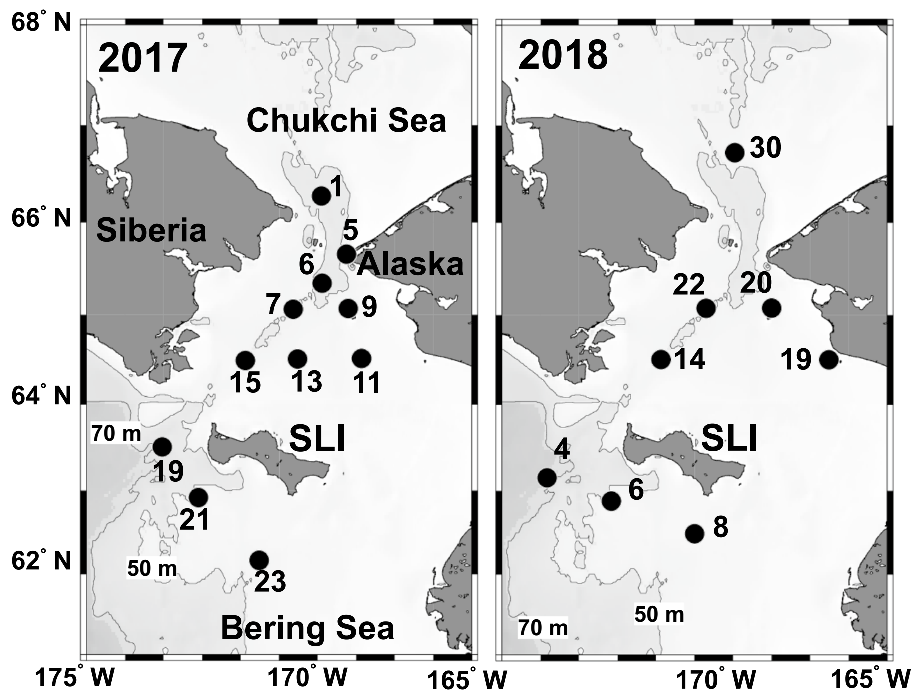

Fig. 1 Location of the sediment sampling in the northern Bering Sea during the summers of 2017 and 2018. The numbers indicate the station ID. *SLI* St. Lawrence Island

To evaluate the sea ice extent in each year, 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://gportal.jaxa.jp/gpr/) at a 10-km resolution. The ice-covered pixel was defined as SIC > 20%, and then the number of ice-covered days during the cold season prior to the field sampling was counted for each pixel. We also calculated the timing of the sea ice retreat (TSR). The TSR was defined as the last date when the SIC fell below 20% prior to the observed annual sea ice minimum across the study region during summer. We also acquired Aqua-MODIS daily L3-binned sea-surface chlorophyll-*a* concentration (chl. *a*) from NASA/GSFC/DAAC website (https://oceancolor.gsfc.nasa.gov/) at a 9-km resolution. Daylight hours at each station were calculated with reference to Brock (1981).

Results

In the bottom sediments, the cell density of the diatom resting stages estimated by the MPN method ranged from 3.0×10^4 to 1.9×10^6 MPN cells g^{-1} wet sediments in 2017 and 2.8×10^5 to 6.1×10^7 MPN cells g^{-1} wet sediments in 2018 (Table 1, Fig. 2). In 2017, the cell density of the resting stages was very high (> 10^6 MPN cells g^{-1} wet sediments) south of the Bering Strait (St. 6) and in the easternmost station of the study area (St. 11). Interestingly, the cell density was lowest (3.0×10^4 MPN cells g^{-1} wet sediments) at a nearshore station in the Bering Strait (St. 5). In 2018, the cell density of the resting stages was very high (> 10^6 MPN cells g^{-1} wet sediments) south of St. Lawrence Island (Sts. 4, 6, 8) and in the central station of the study area (St. 22). Twenty taxa and twenty-two species (centric diatom: 12 taxa and 17 species, pennate diatom: 8 taxa and 5 species) were observed over the two years. In 2017, centric diatoms, especially *Chaetoceros* spp., *C. socialis s. l.*, and *Thalassiosira* spp. dominated (67–98%) the study area (Fig. 2). Even in 2018, centric diatoms dominated (85.5–99.8%), but the dominant species varied within the region. Thus, *Thalassiosira* spp. dominated (48.9–96.4%) south of St. Lawrence Island, while *C. socialis s. l.* dominated (30.9–75.1%) in other areas. The pennate diatom *Fragilariopsis/Fossula* spp., a known ice alga, were numerous (5.9×10^4–2.6×10^5 MPN cells g^{-1} wet sediments) at St.11 and south of St. Lawrence Island in 2017. Particularly south of St. Lawrence Island, they accounted for a large percentage of the abundance (24–35%). On the other hand, *Fragilariopsis/Fossula* spp. were rarely (0–6.7%) observed throughout the study area in 2018 (Fig. 2).

From satellite data, the sea ice concentration varied greatly between 2017 and 2018. In 2017, sea ice existed south of St. Lawrence Island even in mid-April whereas in April 2018, the sea ice had completely retreated to the north of St. Lawrence Island (Fig. 3). The TSR at each station was evaluated for 6 April to 10 May in 2017 and 22 March to 8 May. When comparing the sea-surface chl. *a* (the median value from the TSR to the observation day) at each station, there was no significant difference for all stations between 2017 and 2018 (*U*-test, $p > 0.36$). However, south of St. Lawrence Island, the chl. *a* concentration was significantly different between years (*U*-test, $p < 0.05$); it was 3.6–11 times higher in 2018 (1.81–3.15 mg m^{-3}; Sts. 4, 6, 8) than in 2017 (0.27–0.53 mg m^{-3}; Sts. 19, 21, 23) (Table 1). The daylight hours exceeded 12 h day^{-1} on 22 March for both 2017 and 2018 (Table 1). The duration of ice algae growth, which was indexed by the days between the date when the daylight hours exceed 12 h day^{-1} and the TSR, ranged from 0 to 49 days throughout the study area. South of St. Lawrence Island, the duration of ice algae growth was 15–40 days in 2017, while only 0–2 days in 2018 (Table 1). Thus, the duration of ice algae growth in 2017 was substantially longer than in 2018.

Discussion

In the Arctic Ocean, *C. socialis s. l.* and *Thalassiosira* spp. are known to dominate in phytoplankton blooms (von Quillfeldt 2000; Sukhanova et al. 2009; Sergeeva et al. 2010). Distribution of resting stages in sediment is greatly affected by the distribution of phytoplankton in the water column (Pitcher 1990). This distribution is considered to be the reason that the resting stages of *C. socialis s. l.* and *Thalassiosira* spp. were dominant in the sediments of this study. The density of resting stages observed in this study is comparable to eutrophic coastal areas (Itakura et al. 1997). This study area, the northern Bering Sea shelf, is known to have high primary productivity (Springer and McRoy 1993). Thus, the results of this study are considered to reflect high primary productivity in the water column. In the northern Bering Sea, the resting stages are formed after the phytoplankton bloom and are thought to have settled and accumulated on the seafloor.

In the Pacific-side of the Arctic Ocean, the nutrient-rich Anadyr Water flows west, while the nutrient-limited Alaskan Coastal Water flows east. East–west differences also exist in the species composition, biomass, and productivity of the phytoplankton community in these waters (Giesbrecht et al. 2019). However, the resting stage cell population in the sediment showed similar community structure throughout the study area (similarity: > 51.3%). The long-term accumulation of diatom resting stages in the bottom sediment may reflect the seasonal changes in the phytoplankton community (Pitcher 1990). While phytoplankton respond rapidly to environmental changes such as current and nutrient

Table 1 Information on the sediment sampling, and environmental data from satellite observations and the most probable number (MPN) of diatoms in the sediment samples

Year	Station no.	Latitude (N)	Longitude (W)	Date	Bottom depth (m)	(a) Date when the daylight hours exceed 12 h day^{-1}	Median value of chl. *a*	(b) Timing of sea ice retreat (TSR)	Duration of ice algae growth (day) (= b − a)	Total MPN (cells g^{-1} wet sediments)
2017	1	66°16′	168°54′	9-Jul	57	22-Mar	6.11	10-May	49	62,770
	5	65°39′	168°15′	11-Jul	41	22-Mar	2.44	4-May	43	30,180
	6	65°21′	168°53′	12-Jul	56	22-Mar	5.65	30-Apr	39	1,303,520
	7	65°04′	169°38′	12-Jul	51	22-Mar	2.18	29-Apr	38	73,200
	9	65°04′	168°12′	13-Jul	43	22-Mar	1.86	5-May	44	251,250
	11	64°31′	167°52′	17-Jul	35	22-Mar	0.57	7-May	46	1,911,790
	13	64°31′	169°31′	17-Jul	43	22-Mar	3.46	17-Apr	26	223,240
	15	64°30′	170°53′	18-Jul	46	22-Mar	1.47	11-Apr	20	288,250
	19	63°31′	173°02′	19-Jul	67	22-Mar	0.53	6-Apr	15	255,940
	21	62°55′	172°06′	20-Jul	56	22-Mar	0.34	7-Apr	16	246,290
	23	62°10′	170°31′	21-Jul	47	22-Mar	0.27	1-May	40	313,860
2018	4	63°09′	173°50′	2-Jul	75	22-Mar	1.95	22-Mar	0	10,732,620
	6	62°53′	172°10′	3-Jul	55	22-Mar	1.81	23-Mar	1	60,897,100
	8	62°29′	169°60′	3-Jul	37	22-Mar	3.15	24-Mar	2	3,440,190
	14	64°31′	170°52′	5-Jul	46	22-Mar	2.17	16-Apr	25	282,990
	19	64°30′	166°31′	6-Jul	28	22-Mar	5.77	30-Apr	39	515,070
	20	65°05′	167°60′	6-Jul	46	22-Mar	1.38	18-Apr	27	722,420
	22	65°05′	169°42′	7-Jul	51	22-Mar	2.67	17-Apr	26	2,092,930
	30	66°44′	168°58′	11-Jul	42	22-Mar	2.62	8-May	47	436,070

Stations with underlines indicate that their location is south of the St. Lawrence Island where prominent interannual changes were detected. The median value of chlorophyll-*a* (chl. *a*) is from the timing of the sea ice retreat (TSR) to the observation day. The duration of ice algae growth was calculated by TSR-date when the daylight hours exceeded 12 h day^{-1}

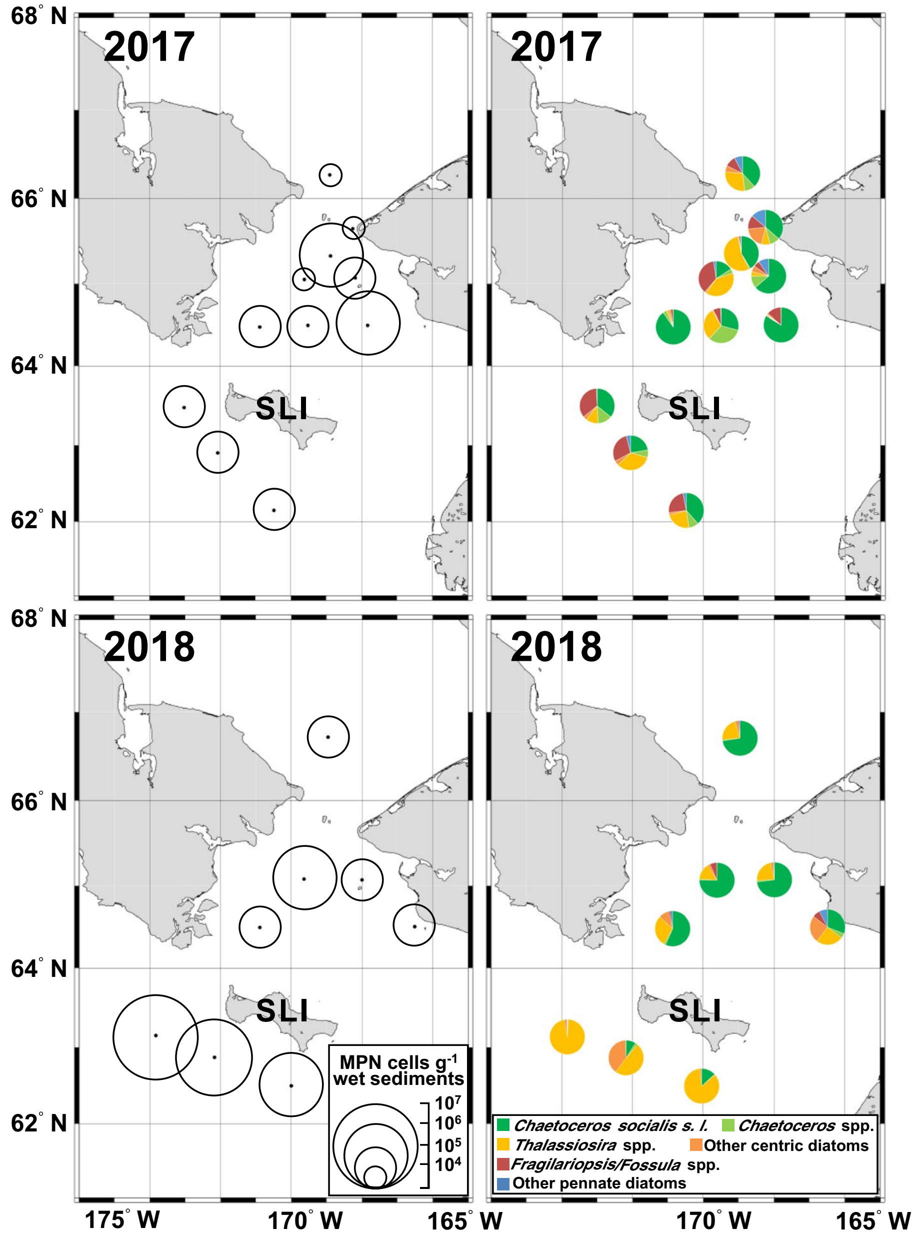

Fig. 2 Horizontal distribution of the abundance (left panels) and species composition (right panels) of viable diatom resting stages from the bottom sediments in the northern Bering Sea during the summers of 2017 and 2018. *SLI* St. Lawrence Island

conditions, resting stages accumulating on the bottom are suitable for evaluating the phytoplankton community on a relatively long-time scale.

In the study area, flow velocity varies greatly depending on location, and the resulting particle size deposited on the ocean floor also varies greatly with location (Grebmeier et al. 2006). Because the flow velocity in the Bering Strait is very fast (the annual mean: 0.8 Sv) (Woodgate et al. 2010), sediments are mainly sand, pebbles, and rock. Sediment in the Chirikov Basin north of St. Lawrence Island is sandy under the influence of the fast flow velocity (Grebmeier et al. 2006). The resting stages in the sediments are also considered to be influenced by ocean currents during the sedimentation process (Tsukazaki et al. 2018). Therefore, it may not be appropriate to compare the resting stage cell community in sediments between regions with vastly different physical environments. Meanwhile, sediments south of St. Lawrence Island have been reported to be largely fine-grained sand with a particle size $\varphi > 3$ or silt and clay (Grebmeier and Cooper 1995). In this less dynamic area, diatom resting stages are considered to be relatively representative of the productivity of diatoms in the water column.

An unusually less sea ice extent in 2018 is thought to be driven by wind pattern during winter, that is, southerly wind has continuously blown over the Bering Sea in 2018 and refused southward extent of sea ice (Cornwall, 2019). South of St. Lawrence Island, the density of diatom resting stages in the sediment in 2018 was 10–100 times higher

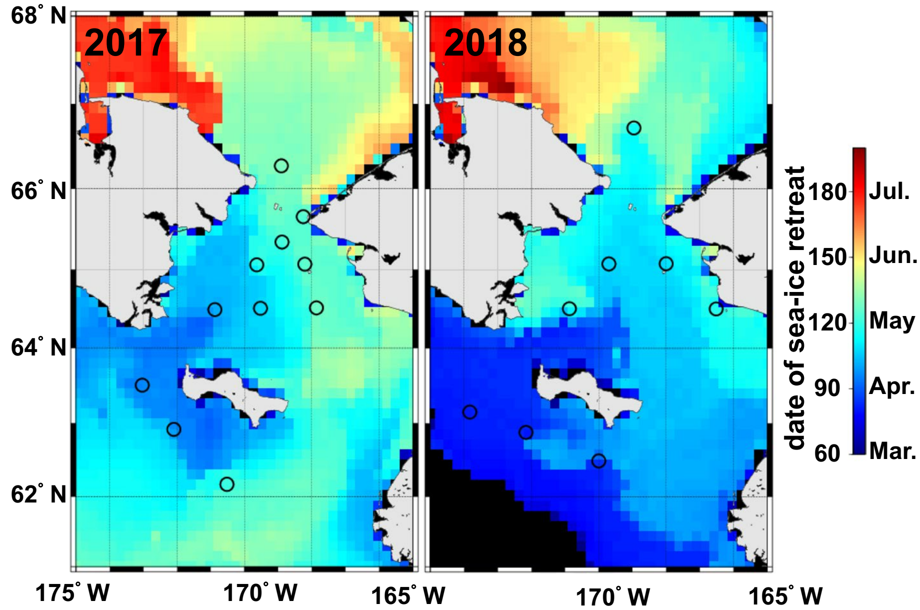

Fig. 3 Horizontal distribution of the sea ice retreat date derived from AMSR2 SIC data in the northern Bering Sea during 2017 (left panel) and 2018 (right panel). Open circles indicate the sampling station in each year

than in 2017. In particular, *Thalassiosira* spp. in 2018 was 27–522 times higher than in 2017. Chl. *a* (median from the TSR to observation date), which is based on satellite data, was 3.6–11 times higher in 2018 than in 2017. This high chlorophyll is presumed to be a result of much earlier sea ice retreat in 2018. The developments of both salinity and thermal stratification are known to induce water column stability, which generally triggers the ice-edge bloom in the Bering Sea (Alexander and Niebauer 1981). In an early sea ice retreat year, such as 2018, the thermal stratification is likely to be delayed as a result of the weak solar radiation and low air temperature in early spring. Hence, the development of water column stability is delayed, and surface-nutrient conditions are expected to remain for a longer period after the sea ice melts because nutrients are not consumed by ice algae and the under-ice bloom (Fujiwara et al. 2016). Therefore, in 2018, planktonic diatoms could fully utilize available nutrients, and *Thalassiosira* spp. formed dense blooms under the open-water conditions, as shown by satellite chl. *a* (Table 1) levels. Indeed, the proportion of *Thalassiosira* spp. in sediment was correlated with the median value of chl. *a* south of St. Lawrence Island (Fig. 4a).

South of St. Lawrence Island, ice algae *Fragilariopsis/Fossula* spp. resting stages were found at relatively high densities in 2017, whereas they were extremely rare in 2018 (Fig. 2). The growth rate of ice algae is known to increase even when the daylight hours exceed 10 h day^{-1} (Gilstad and Sakshaug 1990), and massive ice algae blooms are reported to occur when the timing of daylight hours exceeds 15 h day^{-1} (Cota et al. 1991). In the Bering Strait, chl. *a* in the sea ice has been reported to reach an annual maximum in April–May (Leu et al. 2015). South of St. Lawrence Island, the duration of ice algae growth in 2017 was

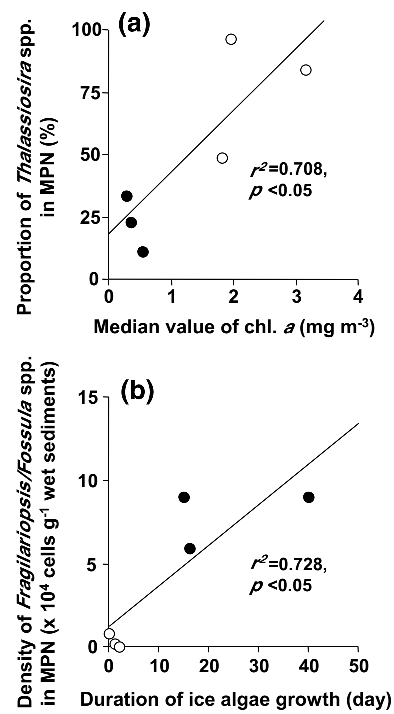

Fig. 4 **a** The relationship between the proportion of *Thalassiosira* spp. in MPN (cf. Fig. 2) and the median value of sea-surface chlorophyll-*a* (Table 1), and **b** the relationship between the density of *Fragilariopsis/Fossula* spp. in MPN and the duration of ice algae growth (Table 1) in the south of St. Lawrence Island. Solid and open symbols denote data from 2017 to 2018, respectively

much longer than it was in 2018 (15–40 days vs 0–2 days) (Table 1). The density of *Fragilariopsis/Fossula* spp. in sediments was correlated with the duration of ice algae growth (Fig. 4b). Thus, in 2017, sea ice existed until April–May under favorable conditions; however, in 2018, it seems that there was much less ice algae production because the sea ice melted on 22–24 March, which was before light conditions were favorable for the growth of ice algae (Table 1). Therefore, the annual variation of ice algae in the sediments seems to reflect the annual differences in the extent of the sea ice.

Ice algae have an important role as food for higher trophic level organisms such as zooplankton and benthos in early spring because they can grow under the limited light conditions and may sink to the seafloor (Gradinger 2009; Leu et al. 2015; Wang et al. 2015). In this study, it became clear that ice algae populations decline when the sea ice retreat is earlier, allowing open-water bloom of *Thalassiosira* spp. to dominate in the south of St. Lawrence Island, which is one of the famous biological hot spots in the Bering Sea and the Chukchi Sea (Grebmeier et al. 2006, 2015). The results of this study suggest that changes in sea ice retreat timing could alter the food supply conditions to the higher trophic level organisms in early spring in the region. It is still unclear that the less ice condition in 2018 is because of climate shift or random phenomena (Cornwall 2019), though rapid responses to climate change of primary producers captured in this study can alter the material cycle and flux in the marine ecosystem of the seasonal ice area (Grebmeier et al. 2006).

Acknowledgements We thank the captain, officers, crew and researchers on board the T/S *Oshoro-Maru*, Hokkaido University, for their great efforts during the field sampling. We thank Toru Hirawake, chief scientist of the cruises. This work was conducted by the Arctic Challenge for Sustainability (ArCS) project. Philip Alatalo of Woods Hole Oceanographic Institution provided comments which improved the text. We also acknowledge the JAXA Earth Observation Research Center and NASA Godard Space Flight Center for providing AMSR2 SIC data and Aqua-MODIS chlorophyll-*a* concentration data, respectively. Part of this study was supported through a Grant-in-Aid for Scientific Research 17H01483 (A), 16H02947 (B), 19H03037 (B), 15KK0268 (Joint International Research) and 18K14506 (Early-Career Scientists) from the Japan Society for the Promotion of Science (JSPS).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

References

Alexander V, Niebauer HJ (1981) Oceanography of the eastern Bering Sea ice-edge zone in spring. Limnol Oceanogr 26:1111–1125

Brock TD (1981) Calculating solar radiation for ecological studies. Ecol Model 14:1–19

Brown TA, Belt ST (2012) Identification of the sea ice diatom biomarker IP25 in Arctic benthic macrofauna: direct evidence for a sea ice diatom diet in Arctic heterotrophs. Polar Biol 35:131–137

Cornwall W (2019) Vanishing Bering Sea ice poses climate puzzle for second winter in a row, ice cover shrinks to lowest levels seen in at least 4 decades. Science 364:616–617

Cota GF, Home EPW (1989) Physical control of arctic ice algal production. Mar Ecol Prog Ser 52:111–121

Cota GF, Smith REH (1991) Ecology of bottom ice algae: II. Dynamics, distributions and productivity. J Mar Syst 2:279–295

Cota GF, Legendre L, Gosselin M, Ingram RG (1991) Ecology of bottom ice algae: I. Environmental controls and variability. J Mar Syst 2:257–277

Durbin EG (1978) Aspects of the biology of resting spores of *Thalassiosira nordenskioeldii* and *Detonula confervacea*. Mar Biol 45:31–37

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

Garrison DL (1984) Planktonic diatoms. In: Steidinger KA, Walker LM (eds) Marine plankton life cycle strategies. CRC Press, Boca Raton, pp 1–17

Giesbrecht KE, Varela DE, Wiktor J, Grebmeier JM, Kelly B, Long JE (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 162:93–113. https://doi.org/10.1016/j.dsr2.2018.06.010

Gilstad M, Sakshaug E (1990) Growth rates of ten diatom species from the Barents Sea at different irradiances and day lengths. Mar Ecol Prog Ser 64:169–173

Gosselin M, Legendre L, Therriault JC, Demers S (1990) Light and nutrient limitation of sea-ice microalgae (Hudson Bay, Canadian Arctic). J Phycol 26:220–232

Gradinger R (2009) Sea-ice algae: major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. Deep-Sea Res II 56:1201–1212

Grebmeier JM, Cooper LW (1995) Influence of the St. Lawrence Island Polynya upon the Bering Sea benthos. J Geophys Res 100:4439–4460

Grebmeier JM, McRoy CP, Feder HM (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

Grebmeier JM, Cooper LW, Feder HM, Sirenko BI (2006) Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. Prog Oceanogr 71:331–361

Grebmeier JM, Bluhm BA, Cooper LW, Danielson SL, Arrigo KR, Blanchard AL, Clarke JT, Day RH, Frey KE, Gradiner RR, Kędra M, Konar B, Kuletz KJ, Lee SH, Lovvorn JR, Norcross BL, Okkonen SR (2015) Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. Prog Oceanogr 136:92–114

Hargraves PE, French FW (1975) Observations on the survival of diatom resting spores. Beih Nova Hedw 53:229–238

Hargraves PE, French FW (1983) Diatom resting spore: significance and strategies. In: Fryxell GA (ed) Survival strategies of the Algae. Cambridge University Press, Cambridge, pp 49–68

Imai I, Ito K, Anraku M (1984) Extinction dilution method for enumeration of dormant cells of red tide organisms in marine sediments. Bull Plankton Soc Jpn 31:123–124

Imai I, Itakura S, Itoh K (1990) Distribution of diatom resting cells in sediments of Harima-Nada and northern Hiroshima Bay, the Seto Island Sea, Japan. Bull Coast Oceanogr 28:75–84 (Japanese)

Itakura S (2000) Physiological ecology of the resting stage cells of coastal planktonic diatoms. Bull Fish Environ Inland Sea 2:67–130 **(in Japanese)**

Itakura S, Imai I, Itoh K (1997) "Seed bank" of coastal planktonic diatoms in bottom sediments of Hiroshima Bay, Seto Inland Sea, Japan. Mar Biol 128:497–508

Leu E, Mundy CJ, Assmy P, Campbell K, Gabrielsen TM, Gosselin M, Juul-Pedersen T, Gradinger R (2015) Arctic spring

awakening—steering principles behind the phenology of vernal ice algal blooms. Prog Oceanogr 139:151–170
McQuoid MR, Hobson LA (1996) Diatom resting stages. J Phycol 32:889–902
Mock T, Gradinger R (1999) Determination of Arctic ice algal production with a new in situ incubation technique. Mar Ecol Prog Ser 177:15–26
Pitcher GC (1990) Phytoplankton seed populations of the Cape Peninsula upwelling plume, with particular reference to resting spores of *Chaetoceros* (Bacillariophyceae) and their role in seeding upwelling waters. Estuar Coast Shelf Sci 31:283–301
Sergeeva VM, Sukhanova IN, Flint MV, Pautova LA, Grebmeier JM, Cooper LW (2010) Phytoplankton community in the Western Arctic in July–August 2003. Oceanology 50:184–197
Smetacek VS (1985) Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Mar Biol 84:239–251
Smith WO, Keene NK, Comiso JC (1988) Interannual variability in estimated primary productivity of the antarctic marginal ice zone. In: Sahrhage D (ed) Antarctic ocean and resources variability. Springer, Berlin, pp 131–139
Springer AM, McRoy CP (1993) The paradox of pelagic food webs in the northern Bering Sea-III. Patterns of primary production. Cont Shelf Res 13:575–599
Sukhanova IN, Flint MV, Pautova LA, Stockwell DA, Grebmeier JM, Sergeeva VM (2009) Phytoplankton of the western Arctic in the spring and summer of 2002: structure and seasonal changes. Deep-Sea Res II 56:1223–1236
Throndsen J (1978) The dilution-culture method. In: Sournia A (ed) Phytoplankton Manual. UNESCO, Paris, pp 218–224
Tsukazaki C, Ishii K, Matsuno K, Yamaguchi A, Imai I (2018) Distribution of viable resting stage cells of diatoms in sediments and water columns of the Chukchi Sea, Arctic Ocean. Phycologia 57:440–452
von Quillfeldt C (2000) Common diatom species in Arctic spring blooms: their distribution and abundance. Bot Mar 43:499–516
Wang SW, Budge SM, Iken K, Gradinger RR, Springer AM, Wooller MJ (2015) Importance of sympagic production to Bering Sea zooplankton as revealed from fatty acid-carbon stable isotope analyses. Mar Ecol Prog Ser 518:31–50
Woodgate RA, Weingartner T, Lindsay R (2010) The 2007 Bering Strait oceanic heat flux and anomalous Arctic sea-ice retreat. Geophys Res Lett 37:L01602

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.