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The community composition of diatom resting stages in sediments of the northern Bering Sea in 2017 and 2018: relationship with the inter-annual changes in the sea-ice extent

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Abstract (within 150 words, now 150 words)

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 sea ice retreat was late and 2018 when sea ice retreat was early. North of St. Lawrence Island, no clear annual changes were detected for germination cell number and species composition. While south of St. Lawrence Island, germination cell number was 10–100 times greater in 2018. The taxonomic composition also showed large annual differences: *Fragilariopsis/Fossula* spp., ice algae species, were abundant in 2017, but *Thalassiosira* spp. dominated in 2018. Satellite observation confirmed that sea ice diminished before the ice-edge bloom in 2018, but sea ice remained until the ice-edge bloom in 2017. Through this study, it became clear that the community composition of viable diatom resting stages was largely affected by the timing of sea ice retreat.

Keywords Bering Sea · diatom resting stages · sea-ice · ice algae

Introduction

Phytoplankton have an important role as a primary producers in the marine ecosystem. In high latitude oceans, diatoms are the most dominant phytoplankton during spring blooms and the magnitude of blooms are extremely larger compared to lower latitude. 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, which then sink to bottom sediments (Hargraves and French 1975; Durbin 1978; Garrison 1984; Smetacek 1985; McQuoid and Hobson 1996). The resting stages that have accumulated in bottom sediments have high viability. Since their germination is triggered by appropriate light intensity, when they are resuspended to the euphotic layer from the seafloor, they can begin to grow under favorable condition (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 varies with the variable timing of 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 1988, 2006). From the Bering Sea to the Chukchi Sea, there are three principal currents, and it is known that the hydrographic environment and phytoplankton community are different in each current (Giesbrecht et al. 2018). Due to the differences in the current flow rate and 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 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 the 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). It is reported that ice algae blooms often occur in the Bering and Chukchi Sea during March–May (Leu et al. 2015). Recently, it has been reported that ice algae are 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 sea ice extent is large, the distribution of ice algae can be considered to have large annual fluctuation, but 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 sea ice retreat timing 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 in order to 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 were 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 (Throndsen 1978).

To evaluate the sea ice extent in each year, the AMSR2 (Advanced Microwave Scanning Radiometer 2) standard sea ice concentration (SIC) product was obtained from the JAXA (Japan Aerospace Exploration Agency) 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 samplings was counted for each pixel. We also calculated the timing of sea ice retreat (TSR). The TSR was defined as the last date when the SIC fell below 20%, prior to observed annual sea

ice minimum across the study region during summer. Daylight hours at each station were calculated referred to Brock (1981).

Results

In the bottom sediments, the cell density of diatom resting stages estimated by the MPN method ranged from 3.0 x 10^4 to 1.9 x 10^6 MPN cells g^{-1} wet sediments in 2017 and 2.8 x 10^5 to 6.1 x 10^7 MPN cells g^{-1} wet sediments in 2018 (Table 1, Fig. 2). In 2017, the cell density of 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). On the other hand, the cell density was lowest (3.0 x 10^4 MPN cells g^{-1} wet sediments) at a nearshore station in the Bering Strait (St. 5). In 2018, the cell density of resting stages was very high (>10^6 MPN cells g^{-1} wet sediments) south of the 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 *Chaetocero*s 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 x 10^4–2.6 x 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 accounts for a large percentage of the abundance (24–35%). On the other hand, *Fragilariopsis/Fossula* spp. were rarely (0–6.7%) noted throughout the study area in 2018 (Fig. 2).

From satellite data, the sea ice concentration was 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 in 2018 (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, $p < 0.05$), which 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 hours 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 exceeds 12 hours 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, it is known that *C. socialis s. l.* and *Thalassiosira* spp. 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 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. 2018). On the other hand, 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 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 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 fine-grained sand with particle size φ>3 or silt and clay (Grebmeier and Cooper 1995). In this less dynamic area, diatom resting stages are considered to relatively reflect the productivity of diatoms in the water column.

South of St. Lawrence Island, the density of diatom resting stages in the sediment in 2018 were 10–100 times higher 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) 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 Bering Sea (Alexander and Niebauer 1981). In 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, development of water column stability delays, 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 condition shown by satellite chl. *a* (Table 1). 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 hours day^{-1} (Gilstad and Sakshaug 1990) and massive ice algae blooms are reported to occur when the timing of daylight hours exceeds 15 hours 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 much longer than 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, while in 2018, it seems that ice algae production was much less because sea ice melted on 22–24 March 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 sea ice extent.

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 condition and may sink to the seafloor (Gradinger 2009; Leu 2015; Wang et al. 2015). In this study, it became clear that ice algae populations decline when sea ice retreat is earlier, allowing open water bloom of *Thalassiosira* spp. to dominate in the south of St. Lawrence Island, where 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 condition to higher trophic level organisms in early spring in the region. The resulting change in algal production is thought to have the potential to alter the material cycle and flux in the marine ecosystem of the seasonal ice area (Grebmeier et al. 2006).

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Compliance with Ethical Standards

Y. Fukai, K. Matsuno, A. Fujiwara and A. Yamaguchi state that there are no conflicts of interest.

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Figure legends

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

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.

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.

Fig. 4. (a) 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) 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 and 2018, respectively.

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. Stations with underlines indicate that their location is south of the St. Lawrence Island where prominent inter-annual changes were detected. The median value of chlorophyll *a* (chl. *a*) is that from the timing of 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 hours day^{-1}.

Year	Station No.	Latitude (N)	Longitude (W)	Date	Bottom depth (m)	(a) Date when the daylight hours exceed 12 h d^{-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

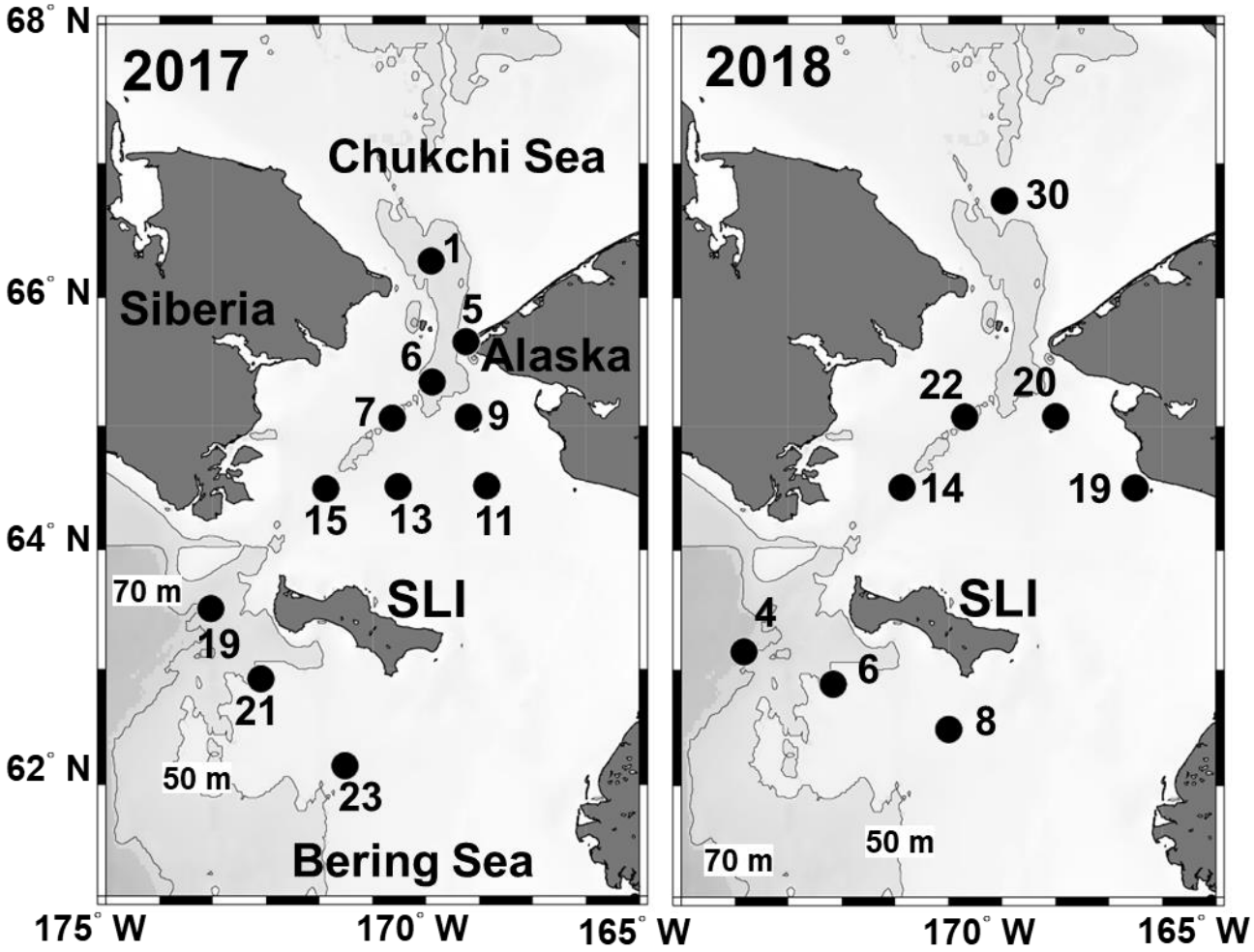


Fig. 1 (Fukai et al.)

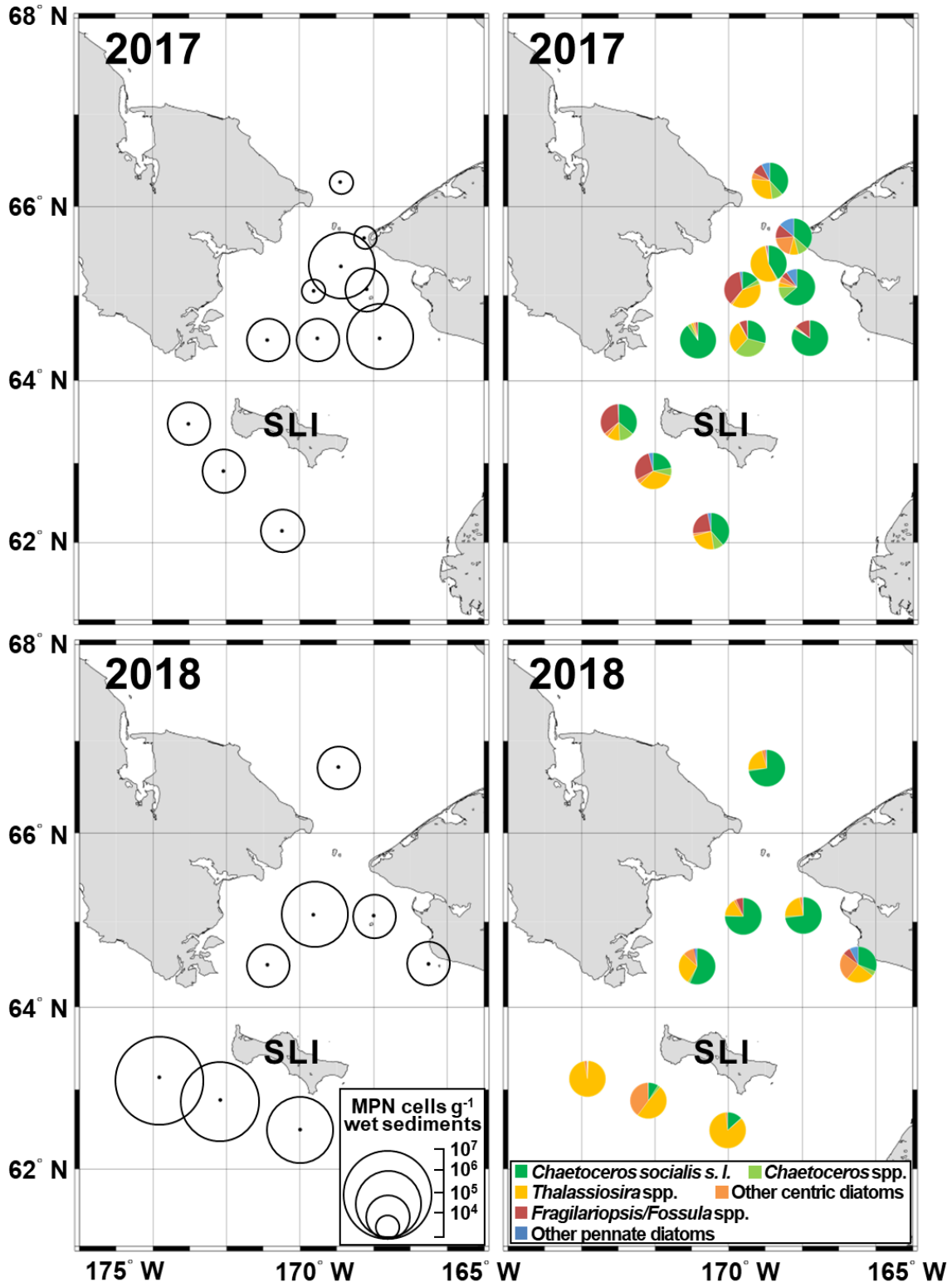


Fig. 2 (Fukai et al.)

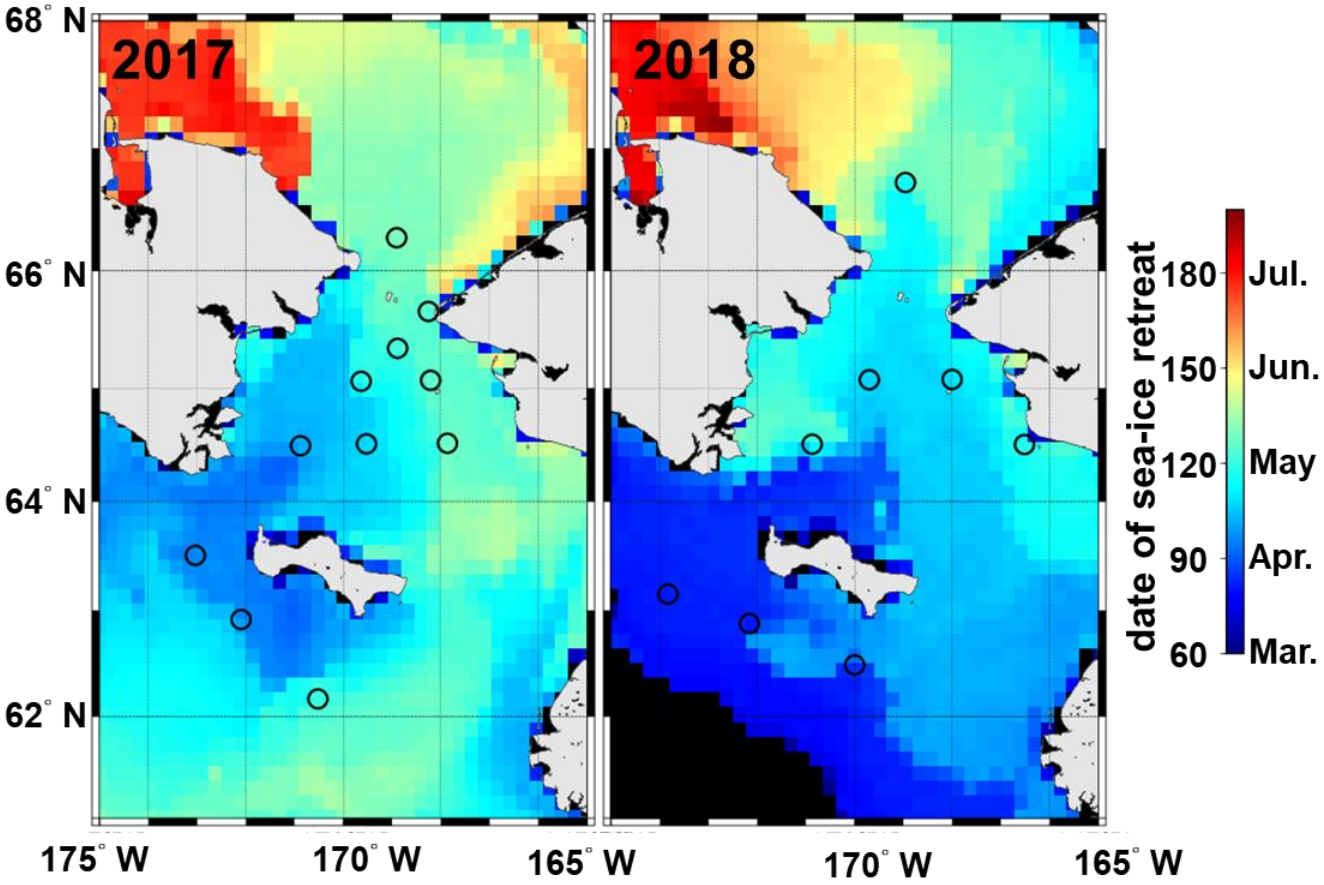


Fig. 3 (Fukai et al.)

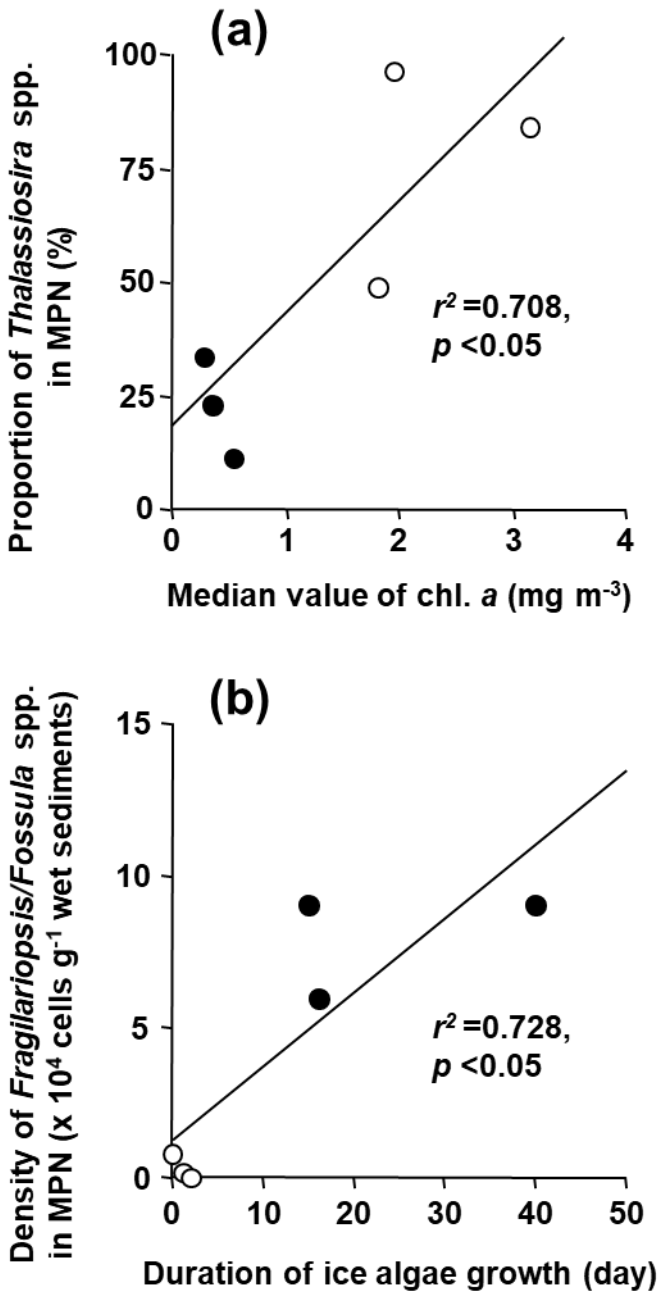


Fig. 4 (Fukai et al.)